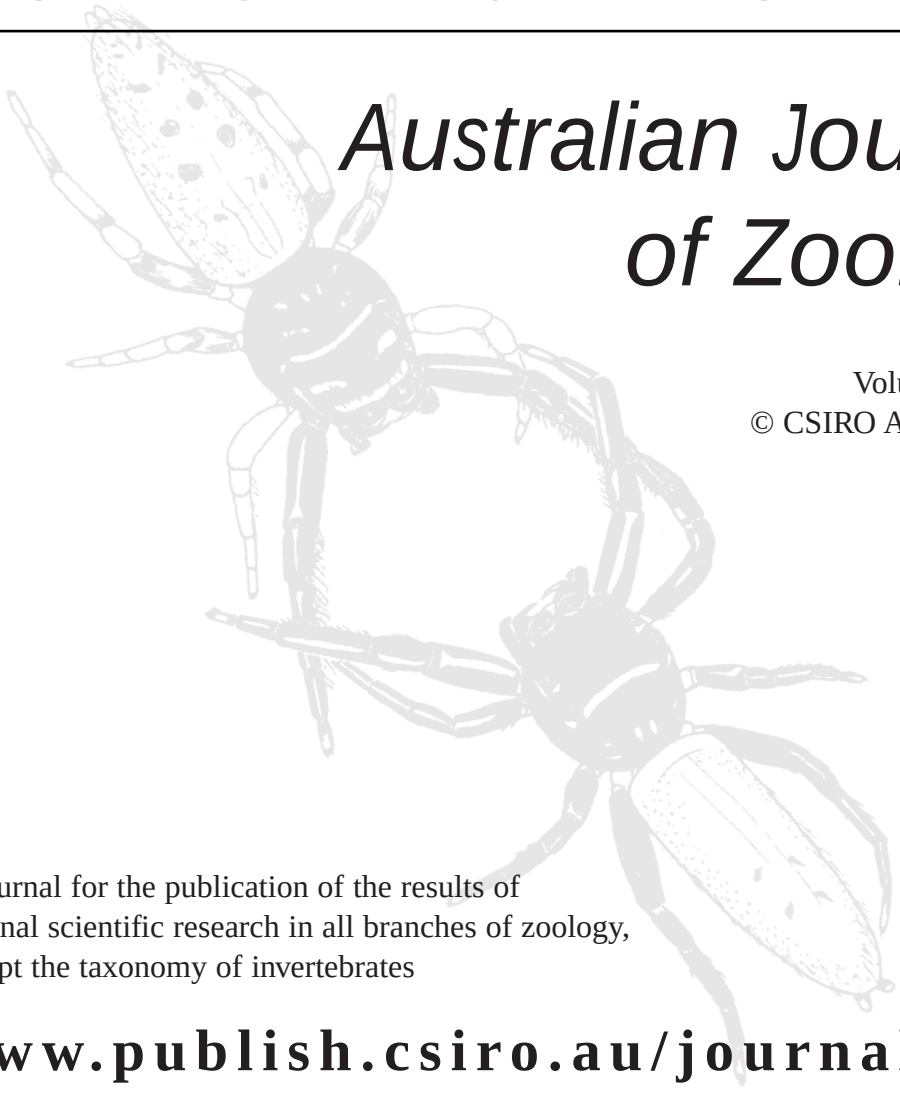
CSIRO PUBLISHING



Australian Journal of Zoology

Volume 45, 1997

A journal for the publication of the results of original scientific research in all branches of zoology, except the taxonomy of invertebrates

www.publish.csiro.au/journals/ajz

All enquiries and manuscripts should be directed to
Australian Journal of Zoology
CSIRO PUBLISHING
PO Box 1139 (150 Oxford St)
Collingwood Telephone: 61 3 9662 7622
Vic. 3066 Facsimile: 61 3 9662 7611
Australia Email: david.morton@publish.csiro.au

Published by **CSIRO** PUBLISHING
for CSIRO Australia and
the Australian Academy of Science

 Australian Journal of Zoology, 1997, **45**, 561–571

Digestive Physiology of the Ground Cuscus (*Phalanger gymnotis*), a New Guinean Phalangerid Marsupial

I. D. Hume, M. J. Runcie and J. M. Caton

School of Biological Sciences and Institute of Wildlife Research A08,
University of Sydney, NSW 2006, Australia.

Abstract

Digestive-tract morphology and function were studied in the ground cuscus (*Phalanger gymnotis*), reported to be the most frugivorous of eight species of New Guinean phalangerid marsupials. When offered a mixed diet of fruit and foliage, captive animals selected a diet of more than 90% fruit. Fibre digestibility was low and variable, but apparent digestibilities of both dry matter (90%) and energy (87%) were high, and intake of digestible energy was similar to that of the Australian phalangerid *Trichosurus vulpecula* (common brushtail possum) in captivity. The small intestine of *P. gymnotis* was the longest and heaviest region of the gastrointestinal tract, but the stomach contained more digesta. The total nitrogen content of digesta was low in the stomach and small intestine, but increased four-fold in the hindgut, because of microbial activity. No difference in nitrogen concentration or in the proportions of small or medium particles was found along the hindgut, but the caecum contained a smaller proportion of large particles than the distal colon. The transit time of a large particle marker was much longer than that of a solute marker, but mean retention times (MRTs) of the two markers did not differ. Both transit times and MRTs were long relative to those reported in *T. vulpecula*. Although fermentation rates in the caecum and proximal colon were similar to those in *T. vulpecula* on a foliage diet, fluid volumes were less than one-third those of *T. vulpecula*, and, consequently, daily production of short-chain fatty acids (SCFAs) was less than half that in *T. vulpecula*, and contributed only 5% of digestible energy intake (*v.* 15% in *T. vulpecula*). These results are consistent with reports that the natural diet of *P. gymnotis* is based largely on fruit rather than on foliage.

Introduction

The New Guinean marsupial fauna contains eight species within the family Phalangeridae (the brushtail possums and cuscuses). Little is known about their physiology. Hume *et al.* (1993) examined digestive-tract morphology and some aspects of gut function in preserved museum specimens of four New Guinean phalangerids, including the ground cuscus (*Phalanger gymnotis*). This species is unusual in that it usually rests during the day in a burrow under tree roots or in caves, but is quite capable of climbing and tends to feed in trees at night. Its diet is the most frugivorous of the New Guinean phalangerids (Flannery 1994).

Most other New Guinean phalangerids are much more folivorous, and several have a dentition convergent on that of pseudocheirids (ringtail possums), with reduced premolars and large, coarsely selenodont molars. In contrast, *P. gymnotis* has small, bunodont molars with a fine reticulate crown pattern and very large premolars (Hume *et al*. 1993). These features are consistent with a higher degree of frugivory in *P. gymnotis* than in other New Guinean phalangers. Fruits reported as being eaten include those of *Elaeocarpus* (family Elaeocarpaceae), *Ficus* (Moraceae), *Pipturus* (Urticaceae), *Poikilospermum* (Umbelliferaceae) and *Pandanus* (Pandanaceae), and also the herbs *Oenathe* (Umbelliferaceae) and *Rungia* (Acanthaceae) (Bulmer and Menzies 1972; Menzies and Pernetta 1986). Hume *et al*. (1993)

10.1071/ZO97037 0004-959X/97/060561$05.00

identified the fruits (as well as leaves and bark) of *Ficus*, *Nothofagus* (Fagaceae) and *Syzygium* (Myrtaceae) in the stomach contents of museum specimens. A common feature of many of these genera is that they produce seeds with oily endosperms (Willis 1955).

The only *in vivo* studies on the digestive physiology of a phalangerid have been on the Australian common brushtail possum (*Trichosurus vulpecula*), a generalist folivore/frugivore (Kerle 1984). These studies (Wellard and Hume 1981; Foley and Hume 1987*a*, 1987*b*; Foley *et al.* 1989; Sakaguchi and Hume 1990) all suggested that although *T. vulpecula* had an active microbial fermentation in its caecum and proximal colon, it had none of the derived features of the more strictly folivorous Pseudocheiridae such as selective retention of solutes and small particles in the caecum, or caecotrophy (ingestion of high-nutrient faeces derived from caecal contents).

In contrast to these findings, results from Hume *et al*. (1993) suggested that the four New Guinean phalangerids they studied selectively retained small food particles in their caecum. It is possible that this apparent difference arises from the use of formalin-preserved specimens by Hume *et al*. (1993).

This paper describes two studies on captive ground cuscuses that provided the opportunity to address this question and, at the same time, to extend our knowledge of digestive-tract function in a little-known phalangerid species.

Materials and Methods

Feeding Study

Five adult male and one adult female *Phalanger gymnotis* held at the Australian Reptile Park, Gosford, New South Wales, were available for the measurement of intake and digestibility of food and rate of passage of digesta. The female had a six-month-old dependent young. All animals were held in galvanised-iron mesh metabolism cages that were 152 cm × 91 cm and 84 cm tall. Each cage contained a wooden nest box and several dead tree branches for climbing. The cages were in a non-display room at the Park with natural light and temperature cycles. The animals were held in the cages for one week prior to and during the 10-day feeding study. They were normally on open display in a nocturnal house and were accustomed to close human presence. During the feeding study the animals were offered a mixture of fresh fruit (rock melon, honeydew melon, apple, banana) and fresh leaves of *Eucalyptus microcorys* (tallowwood) *ad libitum* daily. On a dry-matter basis the fruit contained 0.4–2.0% nitrogen, 15.8–17.3 kJ gross energy g^{-1}, and 5.7–13.2% neutral-detergent fibre (NDF). The foliage contained 2.1% nitrogen, 20.5 kJ gross energy g^{-1}, and 28.8% NDF. All food items were familiar to and readily accepted by the animals, including tallowwood despite it being a non-New Guinean species. Water was available *ad libitum* throughout.

During the 10-day experimental period uneaten food was collected just before feeding time, bulked for each cuscus and stored frozen. Faeces were collected from newsprint that covered the flat galvanised tray beneath each cage. Fresh newsprint was used each day. Urine could not be collected, but was absorbed by the newsprint. Feeding took place between 1530 and 1630 hours each day.

On the first day of the experimental period each animal was given a pulse dose of the inert digesta markers Co-EDTA (Co-ethylenediaminetetraacetic acid) (0.4 g) (to mark the solute phase of digesta) (Udén *et al.* 1980) and Cr-mordanted plant cell walls (0.8 g) (to mark the large particle phase of digesta). The plant cell walls were prepared by extracting ground oaten hay with neutral detergent (Van Soest *et al.* 1991) and washing through a nest of Endicott (London, UK) sieves. Only those particles that passed through the 1000-μm seive and were retained on the 500-μm seive were mordanted with Cr (Udén *et al*. 1980) and used as the large particle marker. The markers were mixed into 10 g mashed ripe avocado fruit and offered to the animal in a plastic bowl. All animals consumed the dose within 5 min of presentation. The usual food was then presented: the chopped fruit in a similar plastic bowl, the leaves on small branches standing in water in plastic containers to retain freshness. Fresh fruit was always avidly consumed first, followed by more-steady consumption of a mixture of fruit and leaves throughout the rest of the 24-h period.

Following dosing, collection trays were checked and any faeces present were collected at 3-h intervals for 48 h, then at 6-h intervals for 48 h, then at 12-h intervals for 48 h, then every 24 h for the remaining 96 h. Collected faeces were separately weighed, then stored frozen in small plastic bags. The mid-point of the collection interval was assumed to be the defaecation time.

Bulked food samples, bulked food residues, and the separate faecal samples were dried to constant weight in a forced-draught oven at 50°C. The total nitrogen content of food, food residues, and faeces bulked after subsampling for marker analysis, was determined by a semi-micro Kjeldahl method with a

selenium catalyst and a Tecator (Model 2030) auto-distillation apparatus. The gross energy content of food, food residues and bulked faeces was determined in a Gallenkamp adiabatic bomb calorimeter, with benzoic acid as the standard. The NDF content of similar samples was determined by the method of Van Soest *et al*. (1991) with the addition of heat-stable α-amylase (Sigma A3306) to remove starch. The separate faecal samples were wet-ashed with concentrated nitric acid and hydrogen peroxide in a microwave oven. Digests were analysed for Co and Cr by flame atomic-absorption spectroscopy.

Transit time for each marker was taken as the time of the first defecation to contain that marker (Warner 1981). Mean retention time (MRT, in hours), the best single overall measure of passage time through the digestive tract (Warner 1981), was calculated using the following equation:

$$\text{MRT} = \sum_{i=1}^{n} M_i T_i \Big/ \sum_{i=1}^{n} M_i$$

where M_i is the amount of marker excreted in the *i*th defecation at time T_i after dosing, and n is the total number of defecations in which marker could be detected (Blaxter *et al.* 1956).

Differences in transit times and MRTs between markers were tested for statistical significance by paired *t*-tests (Snedecor and Cochran 1989).

Fermentation Study

For this study, four of the adult animals from the feeding study were available. The animals were maintained on the same fruit–leaf diet *ad libitum* as before, for 10 days prior to euthanasia. They were killed by intraperitoneal injection of sodium pentabarbitone (Lethabarb) between 1600 and 1800 hours, at the time when normally they would have been presented with fresh food. The complete digestive tract was quickly removed from the carcass, dissected free of mesentery, and the lengths and weights (both with and without contents) of the stomach, small intestine, caecum, proximal colon and distal colon were recorded. The junction between proximal and distal colon was taken to be the point where faecal pellets were discernable (Hume *et al*. 1993). Representative samples of the contents of each of these gut regions were taken and frozen for subsequent analysis of dry matter, total nitrogen and short-chain fatty acid (SCFA) concentrations, and particle-size distributions.

The rate of production of SCFAs in the combined contents of the caecum and proximal colon was determined by *in vitro* incubation. This was done by transferring the digesta into pre-warmed screw-top glass jars (300 mL) that had been flushed with CO_2 and incubating without addition of buffer or substrate at 37°C under CO_2 and in the dark for 2.5 h. A zero-time subsample was taken immediately and strained through four layers of surgical gauze into a 20-mL plastic vial containing 0.5 mL saturated mercuric chloride to stop the fermentation. Further subsamples were taken and preserved in the same way after 30, 60, 90, 120 and 150 min incubation. All preserved subsamples were stored frozen until analysis for SCFAs. Concentrations of total SCFAs and the molar proportions of the individual acids (acetic, propionic, n-butyric, isobutyric and isovaleric) were determined by gas chromatography at 120°C on a column packed with 10% SP 1200 and 1% H_3PO_4 on Chromosorb WAW (Supelco). Nitrogen was used as the carrier gas, the SCFAs were detected by flame ionisation, and n-valeric acid was used as the internal standard (Ottenstein and Bartley 1971). Hourly rates of production of individual and total SCFAs were determined by the zero-time method of Carrol and Hungate (1954). Total daily production of SCFAs was calculated on the assumption that caecal- and proximal-colon fluid volumes and measured rates were representative of volumes and rates throughout the 24-h cycle (Foley *et al*. 1989). SCFAs were converted to their energy equivalents by means of the energy values given by Blaxter (1962).

The distribution of particle sizes in the contents of the stomach, caecum and distal colon of each animal was determined by washing samples (0.3 g dry matter) through a nest of Endicott sieves of 75-, 125-, 250-, 500- and 1000-µm mesh. The dry matter that passed through the 125-µm screen was classed as small particles, medium particles were those that passed through the 500-µm screen but were retained on the 125-µm screen, and large particles were those that were retained on the 500- and 1000-µm screens.

Differences among gut regions in chemical composition and particle-size distribution were tested for statistical significance by one-way ANOVA (Snedecor and Cochran 1989).

Gastrointestinal-tract Morphology

The juvenile young of the female animal was used for description of the morphology of the gastrointestinal tract. At slaughter it was 18 months old and its body mass was 850 g, approximately half that of its mother.

Results

Feeding Study

All animals lost body mass during the 10-day collection period (Table 1). This may have been the result of limitation of food intake due to disturbance when faecal-collection trays were checked at regular intervals throughout the 24-h cycle. Nevertheless, dry-matter intakes were consistent among animals, especially on a metabolic body-mass basis (Table 1). Apparent digestibilities of dry matter and energy were high (Table 1), reflecting the readily digestible nature of the fruit offered. Intake of the leaf offered was small, less than 10% of dry matter consumed. Less than one-third of consumed fibre was digested (Table 1).

The transit time of the particulate marker (Cr-mordanted cell walls) through the gut was much greater ($P < 0.01$) than that of the solute marker (Co-EDTA) (Table 1). However, MRTs were not significantly different between the two markers. One animal (No. 4) had a MRT for the particulate marker greater by 61 h (62%) than the average for the other five animals (99 h). A large part of this difference can be accounted for by the long transit time for this marker (83 h *v.* 47 h for the other animals) (Table 1).

Gastrointestinal-tract Morphology

The stomach of *P. gymnotis* (Fig. 1) is unilocular. The lesser curvature is much shorter that the greater curvature; thus cardiac and pyloric sphinters are in close juxtaposition. The body and fundus are thin-walled compared with the muscular pylorus. A strong band of longitudinal muscle is evident around the greater curvature; it commences at the base of the oesophagus, extends around the fundus, and ends at the junction of the body and pylorus. The thicker wall of the pylorus (both antrum and canal) is due to the increased thickness of the tunica muscularis. There is an abrupt constriction of the lumen at the pyloric sphincter, which is a well-developed ridge extending into and encircling the lumen at the pyloro–duodenal junction, where there is an abrupt reduction in the thickness of the wall. On the internal surface of the stomach, parallel longitudinal folds (rugae) run from the cardia along the lesser curvature to end abruptly at the beginning of the pylorus; these rugae are separated from each other by clefts 4 mm deep. The mucosa of the pylorus has fewer and less-developed rugae that are also concentrated along the lesser curvature.

The small intestine is a long, narrow, thin-walled tube. The duodenum is the widest part. The small intestine is lined with pronounced villi throughout its length, giving the surface of the mucosa a carpet-like appearance; villi are longest in the duodenum. The ileum opens into the caecum. The caecum is haustrated by two taeniae, one underneath the mesotyphlon, the other running parallel to it on the opposite wall. The caecum is of similar length to the proximal colon, but more capacious. It is of uniform calibre throughout, but tapers sharply at its apex. No taeniae are present on the short apical segment. There is a constriction at the caeco–colic junction, with a sharp reduction in the calibre of the lumen. The colon is smooth-walled, without taeniae and with a complete longitudinal-muscle coat throughout its length. The contents of the proximal colon are homogenous. As stated in Materials and Methods, the junction between proximal and distal colon is marked by the formation of faecal pellets.

Fermentation Study

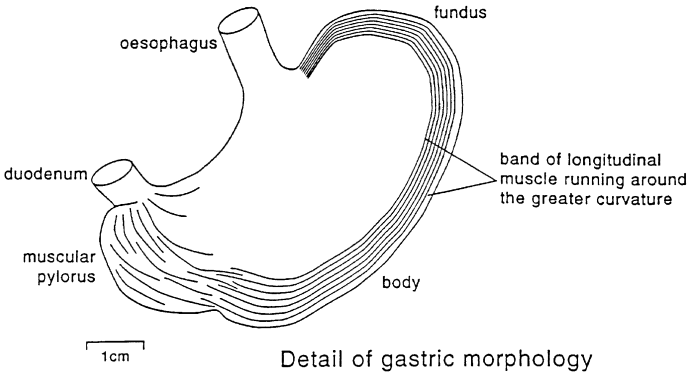
The small intestine was the longest ($P < 0.001$) and heaviest ($P < 0.001$) region of the gastrointestinal tract, but the stomach contained more digesta ($P < 0.05$) (Table 2). The dry-matter content of the digesta was consistent from the stomach through to the proximal colon (14–16%), but it increased markedly from the proximal colon to the distal colon ($P < 0.001$) and reached a maximum ($P < 0.05$) of 35% in the most caudal section (Table 2).

Total nitrogen content of digesta was low in the stomach and small intestine (Table 2), reflecting the low protein content of the mainly fruit diet. It was approximately four times higher in the hindgut ($P < 0.001$), and slightly higher in the distal colon than in the caecum and proximal colon ($P < 0.05$).

Table 1. Body mass, food intake and digestibility, and rate of digesta passage in *Phalanger gymnotis* (the ground cuscus)

Variable	Cuscus No.						Mean ± s.d.
	1	2	3	4	5[A]	6	
Body mass (kg)							
Initial	2.80	2.35	2.90	2.55	1.95	2.65	2.53 ± 0.34
Final	2.50	2.10	2.60	2.20	1.54	2.30	2.21 ± 0.38
Change (kg per 10 days)	–0.30	–0.25	–0.30	–0.35	–0.41	–0.35	–0.33 ± 0.06
Dry matter							
Intake (g day^{-1})	53.8	56.0	52.9	52.8	56.0	50.4	53.7 ± 2.0
Intake (g $kg^{-0.75}$ day^{-1})	25.9	30.7	24.8	27.6	36.8	25.5	28.6 ± 4.6
Apparent digestibility (%)	90.8	90.0	91.1	90.3	90.4	89.8	90.4 ± 0.5
Intake digestible DM (g $kg^{-0.75}$ day^{-1})	23.5	27.6	22.6	24.9	33.6	22.9	25.9 ± 4.2
Energy							
Gross-energy Intake (kJ $kg^{-0.75}$ day^{-1})	422.4	506.9	402.2	451.0	607.0	425.5	469.2 ± 76.6
Apparent digestibility (%)	88.0	87.0	88.4	87.0	87.2	85.9	87.2 ± 0.8
Digestible-energy intake (kJ $kg^{-0.75}$ day^{-1})	371.7	441.0	355.5	392.4	529.3	365.5	409.2 ± 66.2
Nitrogen							
Intake (g day^{-1})	0.43	0.47	0.42	0.42	0.45	0.37	0.43 ± 0.03
Intake (g $kg^{-0.75}$ day^{-1})	0.21	0.26	0.20	0.22	0.30	0.19	0.23 ± 0.04
Apparent digestibility (%)	45.6	60.6	55.3	46.7	42.6	51.1	50.3 ± 6.7
Fibre							
Intake NDF[B] (g $kg^{-0.75}$ day^{-1})	1.71	2.24	1.43	1.83	2.53	1.47	1.87 ± 0.44
Digestibility (%)	42.7	25.2	27.9	31.7	44.4	12.4	30.7 ± 11.9
Rate of digesta passage (h)							
Transit time, Co-EDTA	10.5	10.5	10.5	4.5	10.5	1.5	8.0 ± 4.0
Transit time, Cr-cell walls	31.5	31.5	52.5	82.5	58.5	58.5	52.5 ± 19.3
Mean retention time, Co–EDTA	85.5	79.8	82.4	93.2	73.0	92.8	84.5 ± 7.8
Transit time, Cr-cell walls	100.4	80.9	90.1	159.9	114.1	107.6	108.3 ± 27.7

[A]Lactating female
[B]Neutral-detergent fibre (plant cell walls)



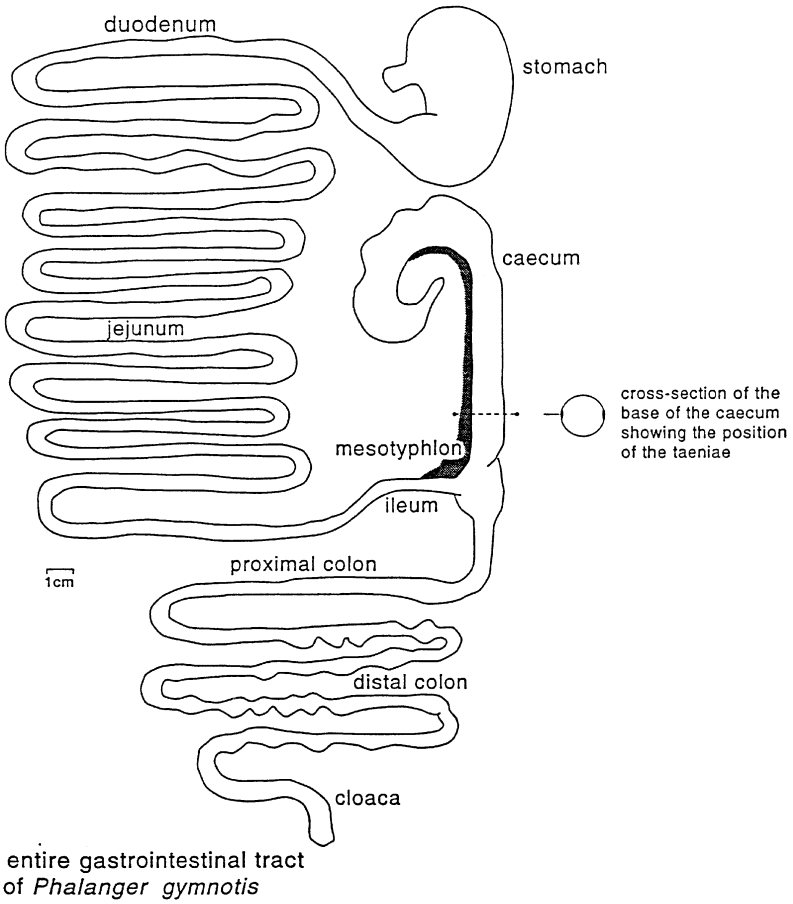


Fig. 1. The gastrointestinal tract of *Phalanger gymnotis*, including detail of gastric morphology and a cross-section of the base of the caecum showing the position of the taeniae.

Table 2. Digestive tract morphometrics and digesta composition in *Phalanger gymnotis* (the ground cuscus)

Values are means ± s.d.; n.a., not available

Variable	Stomach	Small intestine	Caecum	Proximal colon	Distal colon, cranial	Distal colon, caudal
Length (% total gut)	2.0 ± 0.3	71.5 ± 3.4	5.2 ± 0.6	6.3 ± 1.3	15.1 ± 1.8	
Tissue mass (% total gut)	21.0 ± 2.7	51.3 ± 3.5	11.1 ± 0.6	7.6 ± 1.1	9.0 ± 1.2	
Mass contents (% total gut)	35.6 ± 8.3	24.5 ± 4.2	18.7 ± 4.0	9.7 ± 2.3	11.5 ± 3.9	
Dry-matter contents (%)	14.2 ± 0.6	15.2 ± 1.9	16.1 ± 0.2	15.5 ± 2.2	29.2 ± 2.4	34.9 ± 6.6
Total nitrogen (% of dry matter)	1.38 ± 0.32	1.24 ± 0.24	5.05 ± 0.13	4.39 ± 0.48	5.10 ± 0.25	5.08 ± 0.20
Particle sizes (% of total dry matter)						
Large (>500 µm)	32.5 ± 3.4	n.a.	10.7 ± 2.7	n.a.	15.7 ± 2.6	15.5 ± 3.7
Medium (125–500 µm)	12.2 ± 6.8	n.a.	11.9 ± 1.6	n.a.	12.0 ± 3.0	12.2 ± 2.5
Small (< 125 µm)	55.4 ± 6.1	n.a.	77.2 ± 3.2	n.a.	73.5 ± 3.5	72.3 ± 3.4
Short-chain fatty acids						
Total (mmol L^{-1})	7.8 ± 9.1	n.a.	75.1	87.2	n.a.	n.a.
Individual acids (molar %)						
Acetate	n.a.	n.a.	67.7	65.6	n.a.	n.a.
Propionate	n.a.	n.a.	22.6	23.3	n.a.	n.a.
n-Butyrate	n.a.	n.a.	9.1	8.4	n.a.	n.a.
Isobutyrate	n.a.	n.a.	0	0.5	n.a.	n.a.
Isovalerate	n.a.	n.a.	0.6	2.3	n.a.	n.a.

Over half the dry matter in the stomach was in the small (<125 μm) particle fraction (Table 2). This proportion increased to over three-quarters in the caecum ($P < 0.001$). There was no significant difference between the caecum and distal colon in proportions of small or medium particles, although the distal colon had a higher ($P < 0.05$) proportion of large particles (Table 2).

The concentration of total short-chain fatty acids (SCFAs) in the stomach was low and variable; too low for accurate determination of the molar proportions of the individual acids (Table 2). Total SCFA concentrations in the caecum and proximal colon were approximately 10-fold higher than stomach values. Hindgut SCFAs consisted mainly of acetic acid (67%), propionic acid (23%) and butyric acid (9%) (Table 2).

There was negligible production of SCFAs in one animal (No. 4). Fermentation rates in the other three animals are shown in Table 3. The individual acids were produced in molar proportions similar to their initial concentrations. Total calculated SCFA production was equivalent to 4.8% of the animals' intake of digestible energy.

Table 3. Fermentation rates in *Phalanger gymnotis* (the ground cuscus)
SCFA, short-chain fatty acid

Variable	Cuscus No.			Mean ± s.d.
	2	3	5	
Body mass (kg)	2.69	2.80	1.95	2.48 ± 0.46
Contents of caecum/proximal colon (g)	49.0	67.5	47.1	54.5 ± 11.3
SCFA production (mmol L^{-1} h^{-1})				
Acetic	18.3	15.5	24.0	19.3 ± 4.3
Propionic	5.7	6.2	9.2	7.0 ± 1.9
Butyric	2.1	2.8	2.7	2.5 ± 0.4
Valeric	0.2	0.3	0.9	0.5 ± 0.4
Total	26.3	24.8	36.8	29.3 ± 6.5
Daily SCFA production				
mmol	26.5	33.8	34.4	31.6 ± 4.4

Discussion

The results from all three parts of this study are consistent with the highly frugivorous dietary habits described for the ground cuscus by Flannery (1994). The unilocular stomach is clearly capable of considerable expansion to accomodate bulky foods. It was the largest digestive-tract region in terms of mass of contents, even at the end of the 24-h feeding cycle. The low concentration of SCFAs (Table 2) is indicative of only limited microbial activity in the stomach, which is as expected because of the lack of any structure limiting the mixing of hydrochloric acid throughout the stomach. The thick muscular wall of the pylorus together with the well-developed pyloric sphincter suggests that digesta retention in the stomach may be significant. We wonder whether these features are related to the high oil content of the seeds (and leaves) of many of the food plants of the ground cuscus. The most powerful inhibitors of gastric emptying are lipids of 12–18 carbon atoms (Argenzio 1993).

The long small intestine may also be related to the slow rate of lipid digestion, but could also be explained by the high content of non-structural carbohydrates in fruit. Of the four species of New Guinean phalangerids examined by Hume *et al*. (1993), *P. gymnotis* had the longest small intestine (62% of total tract length *v.* 40–51%), holding 22% of total tract contents *versus* 7–9% in the other three, more folivorous, species. Conversely, *P. gymnotis* had the shortest caecum (7% *v.* 11–12% of total tract length), which held only 18% of total tract contents *versus* 34–59%.

In the feeding study, the high digestibilities of the dry matter and energy of the largely fruit diet contrasted with the low and variable plant-cell-wall digestibility. Microbial fermentation of the cell-wall fraction made only a minor contribution to the energy economy of the animal. The 5% contribution to digestible-energy intake made by SCFAs in *P. gymnotis* in this study contrasts with the 15% contribution in *T. vulpecula* on a foliage-only diet (Foley *et al.* 1989). Although rates of SCFA production (16–24 mmol L^{-1} h^{-1}) (Table 3) were similar to those measured by Foley *et al.* (1989) in *T. vulpecula* on foliage (15–23 mmol L^{-1} h^{-1}), the low plant-cell-wall intake of *P. gymnotis* in this study placed an upper limit on the contribution of cell walls to SCFA production. Probably only half of the total SCFAs produced came from structural carbohydrates, the remainder coming from the fermentation of non-structural polysaccharides and even some sugars. Microbial fermentation of plant cell walls may be of greater importance in free-living *P. gymnotis* forced to consume more foliage at times when fruit is not readily available. Hindgut fermentation, even though of minor importance in this study, provides for dietary flexibility in the wild.

Although nitrogen levels in the caecum and colon in this study were comparable to those reported by Hume *et al.* (1993) in formalin-preserved wild specimens of *P. gymnotis*, levels in the stomach were lower [1.4 *v.* 3.3% (Hume *et al.* 1993)]. This difference can be used to suggest that the natural diet of *P. gymnotis* contains more foliage, as foliage is generally higher in protein than is fruit (Milton 1993). Alternatively, fruits selected by wild *P. gymnotis* may be relatively high in protein. More information is needed on the range of dietary items consumed by free-living New Guinean possums.

Although dry-matter intake by *P. gymnotis* in this study was low compared with *T. vulpecula* fed eucalypt foliage [29 *v.* 36 g $kg^{-0.75}$ day^{-1} (Foley and Hume 1987*b*)], dry-matter and energy digestibilities were high (90 and 87%, respectively, *v.* only 51 and 46% in *T.vulpecula*). Consequently, intake of digestible energy (DE) was higher in *P. gymnotis* (409 *v.* 340 kJ $kg^{-0.75}$ day^{-1}). More-comparable performance is seen in *T. vulpecula* fed a low-fibre honey-based diet (Wellard and Hume 1981), viz. a DE intake of 385 kJ $kg^{-0.75}$ day^{-1}, but a low intake of dry matter (26 g $kg^{-0.75}$ day^{-1}) with high digestibilities of both dry matter and energy (92 and 91%, respectively). These intakes can be compared with the estimate by Harris *et al.* (1985) of 370 kJ DE $kg^{-0.75}$ day^{-1} to maintain captive *T. vulpecula* in energy balance.

Other features of digestive-tract function were also similar to those of *T. vulpecula*. For instance, there was no evidence for selective retention of solutes and small particles in the caecum, based on the similarity in MRTs for the solute and large particle markers. Similarly, there was no difference in total nitrogen concentrations between caecum and distal colon, suggesting that microbial cells are not selectively retained in the caecum. This serves to separate both phalangerid marsupials from the two pseudocheirids in which digesta passage has been studied; both the common ringtail possum (*Pseudocheirus peregrinus*) and the greater glider (*Petauroides volans*) have been shown to have a colonic separation mechanism that results in selective retention of solutes and small particles (including microbial cells) in the caecum and facilitates the clearance of larger digesta particles from the hindgut (Chilcott and Hume 1985; Foley and Hume 1987*a*).

The relatively long MRTs in *P. gymnotis* (85 and 108 h for the solute and large particle marker, respectively) may be related to the physical nature of the largely fruit diet they selected. In *T. vulpecula*, MRTs were shorter on a natural foliage diet (51 and 49 h) (Foley and Hume 1987*a*) than on the honey-based diet of Wellard and Hume (1981) (64 and 71 h). The more intimate association of fibre with other components of the natural foliage diet may have a greater stimulatory effect on gut motility. The low level of indigestible residue in the fruit in the present study probably was not effective in stimulating gut motility, a statement supported by the long transit time of more than 48 h.

The lower proportion of large particles in the caecum than in the distal colon (Table 2) was not seen in *T. vulpecula* by Foley and Hume (1987*a*). It is, however, consistent with the observations of Hume *et al.* (1993) on formalin-preserved specimens of *P. gymnotis* and three other New Guinean phalangerids, suggesting that formalin preservation was not responsible for

the observed pattern of particle-size distributions in those specimens. This possible difference between New Guinean phalangerids and *T. vulpecula* can be explored only through comparative studies based on greater numbers of both New Guinean and Australian species. A recent study of Australian folivorous possums by Crowe and Hume (1997) suggested that Australian phalangerids are a much more uniform group in their digestive physiology than the New Guinean phalangerids examined by Hume *et al.* (1993).

To our knowledge this study is the first involving controlled feeding of a New Guinean possum, and provides valuable *in vivo* data for comparison with earlier studies based on preserved museum specimens. As it is the only such study on a phalangerid other than the common brushtail possum, it also has allowed comparisons within this marsupial family. Results from the study are consistent with reports that the natural diet of *P. gymnotis* is based largely on fruit rather than on foliage.

Acknowledgments

We are particularly grateful to the Australian Reptile Park for access to their animals and for the provision of experimental facilities. We are also indebted to Mrs Nazaneen Soran for expert technical assistance, to Dr G. L. R. Gordon, CSIRO Division of Animal Production, for the SCFA analyses, and to Dr G. J. Faichney and Dr T. F. Flannery for their comments on a draft of the manuscript. The study was supported by an ARC Small Grant.

References

Argenzio, R. A. (1993). Gastrointestinal motility. In 'Duke's Physiology of Domestic Animals'. (Eds M. J. Swenson and W. O. Reece.) pp. 336–348. (Cornell University Press: Ithaca.)

Blaxter, K. L. (1962). 'The Energy Metabolism of Ruminants.' (Hutchinson: London.)

Blaxter, K. L., Graham, N. McC., and Wainman, F. W. (1956). Some observations on the digestion of food by sheep and on related problems. *British Journal of Nutrition* **10**, 69–91.

Bulmer, R. N. H., and Menzies, J. I. (1972). Karam classification of marsupials and rodents (1). *Journal of Polynesian Sociology* **82**, 86–107.

Carrol, E. J., and Hungate, R. E. (1954). The magnitude of the fermentation in the bovine rumen. *Applied Microbiology* **2**, 205–214.

Chilcott, M. J., and Hume, I. D. (1985). Coprophagy and selective retention of fluid digesta: their role in the nutrition of the common ringtail possum, *Pseudocheirus peregrinus*. *Australian Journal of Zoology* **33**, 1–15.

Crowe, O., and Hume, I. D. (1997). Morphology and function of the gastrointestinal tract of Australian folivorous possums. *Australian Journal of Zoology* **45**, 357–368.

Flannery, T. F. (1994). 'Possums of the World.' (Geo: Sydney.)

Foley, W. J., and Hume, I. D. (1987*a*). Passage of digesta markers in two species of arboreal folivorous marsupials — the greater glider (*Petauroides volans*) and the brushtail possum (*Trichosurus vulpecula*). *Physiological Zoology* **60**, 103–113.

Foley, W. J., and Hume, I. D. (1987*b*). Digestion and metabolism of high-tannin *Eucalyptus* foliage by the brushtail possum (*Trichosurus vulpecula*) (Marsupialia: Phalangeridae). *Journal of Comparative Physiology B* **157**, 67–76.

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. *Physiological Zoology* **62**, 1126–1143.

Harris, P. M., Dellow, D. W., and Broadhurst, R. B. (1985). Protein and energy requirements and deposition in the growing brushtail possum and Rex rabbit. *Australian Journal of Zoology* **33**, 425–436.

Hume, I. D., Jazwinski, E., and Flannery, T. F. (1993). Morphology and function of the digestive tract in New Guinean possums. *Australian Journal of Zoology* **41**, 85–100.

Kerle, J. A. (1984). Variation in the ecology of *Trichosurus*: its adaptive significance. In 'Possums and Gliders'. (Eds A. P. Smith and I. D. Hume.) pp. 115–128. (Australian Mammal Society: Sydney.)

Menzies, J. I., and Pernetta, J. C. (1986). A taxonomic revision of cuscuses allied to *Phalanger orientalis* (Marsupialia: Phalangeridae). *Journal of Zoology (London) (B)* **1**, 551–618.

Milton, K. (1993). Diet and primate evolution. *Scientific American* **269**, 70–77.

Ottenstein, D. M., and Bartley, D. A. (1971). Separation of free acids C2–C5 in dilute aqueous solution column technology. *Journal of Chromatographic Science* **9**, 673–681.

Sakaguchi, E., and Hume, I. D. (1990). Digesta retention and fibre digestion in brushtail possums, ringtail possums and rabbits. *Comparative Biochemistry and Physiology A* **96**, 351–354.

Snedecor, G. W., and Cochran, W. G. (1989). 'Statistical Methods.' 8th Edn. (Iowa State University Press: Ames, Iowa.)

Udén, P., Colucci, P. E., and Van Soest, P. J. (1980). Investigation of chromium, cerium and cobalt as markers in digesta rate of passage studies. *Journal of the Science of Food and Agriculture* **31**, 625–632.

Van Soest, P. J., Robertson, J. B., and Lewis, B. A. (1991). Methods of dietary fibre, neutral detergent fibre, and non-starch polysaccharides in relation to animal nutrition. *Journal of Dairy Science* **74**, 3583–3597.

Warner, A. C. I. (1981). Rate of passage of digesta through the gut of mammals and birds. *Nutrition Abstracts and Reviews, Series B* **51**, 789–820.

Wellard, G. A., and Hume, I. D. (1981). Digestion and digesta passage in the brushtail possum, *Trichosurus vulpecula* (Kerr). *Australian Journal of Zoology* **29**, 157–166.

Willis, J. C. (1955). 'A Dictionary of Flowering Plants and Ferns.' (Cambridge University Press: Cambridge.)

Manuscript received 13 August 1997; revised and accepted 29 September 1997