J Comp Physiol B (1995) 164:552–560

Journal of Comparative Physiology B Biochemical, Systemic, and Environmental Physiology

Digestive performance and selective digesta retention in the long-nosed bandicoot, *Perameles nasuta*, a small omnivorous marsupial

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Accepted: 15 September 1994

Abstract. Bandicoots are opportunistic omnivores that feed on invertebrates, fungi and both epigeal and hypogeal plant parts. We examined the performance of the digestive tract of the long-nosed bandicoot (*Perameles nasuta*) in terms of intake and total digestibility, patterns of excretion of inert digesta markers, and likely sites of digesta retention, on two diets designed to mimic part of their natural plant and insect diets. On the insect diet (mealworm larvae), bandicoots virtually maintained body mass at a digestible energy intake of 511 kJ · $kg^{-0.75}$ · day^{-1} and were in strongly positive nitrogen balance. In contrast, on the plant diet (shredded sweet potato), bandicoots ate only one-third as much digestible energy, lost 7% body mass, and were in negative nitrogen balance. Mean retention times of two particle markers on the plant diet (27.5 and 27.0 h) were more than double those on the insect diet (12.4 and 11.2 h), and on both diets the mean retention time of the fluid digesta marker was greater than those of the particle markers, indicating consistent selective retention of fluid digesta in the gut. It was seen radiographically than in mealworm-fed bandicoots major sites of digesta retention were the distal colon and rectum, whereas in the sweet potato-fed animals the caecum and proximal colon were principal sites. It was concluded that retention of plant material in the caecum and proximal colon (the main sites of microbial digestion) and the preferential retention of fluid digesta (together with bacteria and small feed particles) in the caecum were important factors in the ability of bandicoots to switch between insect and plant foods, depending on relative availabilities, and thus to exploit nutritionally unpredictable environments.

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Abbreviations: ADF, acid-detergent fibre; bm, body mass; Co-EDTA, cobalt-ethylenediaminetetra-acetic acid; CWC, cell wall constituents; DE, digestable energy; dm, dry matter; EUN, endogenous urinary nitrogen; ICP, inductively-coupled plasma atomic emission spectroscopy; MFN, metabolic faecal nitrogen; MRT, mean retention time; NDF, neutral-detergent fibre; ww, wet weight

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Key words: Omnivory – Digestibility – Nitrogen balance – Mean retention time – Digesta retention sites – Radiography – Hindgut – Bandicoot, *Parameles nasuta*

Introduction

The long-nosed bandicoot is a small (800–1000 g) polyprotodont marsupial that is distributed along the east coast of mainland Australia. It is still relatively common in a range of forested and heathland habitats (Stodart 1983; Ashby et al. 1990; Gordon et al. 1990; Menkhorst and Seebeck 1990). Its polyprotodont dentition suggests that it is primarily insectivorous but there are few published accounts of the diet of *Perameles nasuta*.

Recently, Moyle (1992) established that in Sydney Harbour National Park, *P. nasuta* was opportunistically omnivorous. The five most abundant diet categories in scats collected through a 6-month period (February–August 1992) were adult beetles (Coleoptera), fungi, monocotyledonous leaves, monocot roots, and larval coleopterans. Similarly, Claridge et al. (1991) concluded that *P. nasuta* in forested habitats relied heavily on plant material as well as adult and larval beetles.

Several authors have recently used modelling approaches to suggest that mammals below a bm of 1–3 kg should not be able to rely on microbial fermentation of plant material in their digestive tract as a primary source of metabolizable energy (Cork 1994). However, some small mammalian herbivores, notably voles (Rodentia) with bm usually less than 100 g, overcome the disadvantage for a herbivore of being small by separating large particles from fluid and small particles in their proximal colon, selectively retaining the latter in a capacious caecum (Hume et al. 1993), thereby concentrating digestive effort on the most fermentable substrates. This enhances overall digestive performance (Hume et al. 1993).

Like voles, long-nosed bandicoots (bm about 1 kg) also fall below the theoretical lower limit of body size for

Table 1. Composition (% of dry matter) of experimental diets offered to long-nosed bandicoots

	Diet		Significance of difference between diets
	Mealworm	Sweet potato	
Dry matter (% of moist sample)	37.2±0.4	21.7±0.2	**
Total nitrogen	9.0±0.1	0.5±0.0	**
Crude lipid	22.2±0.7	1.2±1.1	**
Gross energy ($kJ \cdot g\ dm^{-1}$)	25.6±0.7	17.1±0.3	**
Fibre (NDF[a])	14.8±0.9	12.7±0.1	*
Fibre (ADF[b])	5.7±0.0	5.5±0.1	n.s.

Means ± standard errors
[a] NDF = neutral-detergent fibre;
[b] ADF = acid-detergent fibre
n.s. not significant; * $P<0.05$; ** $P<0.01$

herbivory. In contrast, apart from most myrmecophagous mammals, insectivores are much smaller than 1 kg bm (Eisenberg 1981). Thus, on theoretical grounds, bandicoots may be predicted to utilize both plant and insect foods. The digestive tract of *P. nasuta* reflects its mixed diet; it is relatively short and simple (Hume 1982) but the short proximal colon and caecum are both expanded relative to those of specialized insectivores (Stevens 1988).

In this paper we examine the performance of the digestive tract of the long-nosed bandicoot in terms of total digestibility, and of patterns of excretion of inert markers used to track the fluid and particulate phases of ingested food, on two diets designed to mimic natural plant and insect diets.

Materials and methods

Animals. Twelve non-reproductive adult long-nosed bandicoots, six of each sex, were caught in wire cage traps baited with peanut butter on bread (Heinsohn 1966) at North Head in Sydney Harbour National Park, New South Wales. The animals were transported to the laboratory in cotton bags inside the traps, and transferred to individual stainless-steel metabolism cages, each 60 cm × 30 cm × 40 cm high and fitted with a wooden nest box containing fresh bedding straw. The bandicoots were maintained at 21.5±2.5 °C in a 12 h light:12 h dark cycle with dim night light (photon flux 0.62 $\mu E \cdot m^{-2} \cdot s^{-1}$ at the source), and were offered a maintenance diet of variable proportions of bread, minced beef, dried fruit, oats, peanut butter and honey (Collins 1977; Broughton and Dickman 1991). The bandicoots were initially weighed weekly to monitor changes in body mass during adjustment to cages and the maintenance diet. When a stable body mass had been reached, the animals were weighed every two weeks to minimise handling stress.

Experimental diets. The two experimental diets were live mealworm (*Tenebrio molitor*) larvae and raw white sweet potato (*Ipomoea batatas*). Mealworms were cultured in a mixture of bran and sweet potato, but the larvae were fasted for 24 h before being offered to the bandicoots to prevent ingestion by the bandicoots of plant fibre in the mealworm gut. The fasted larvae were then cooled in a freezer for 20 min to reduce activity and thereby prevent escape from the feeding bowls.

The sweet potato was used to mimic the natural tuberous dietary components of long-nosed bandicoots (Claridge et al. 1991; Moyle 1992). Sweet potato has been used as a major diet component for captive long-nosed bandicoots, common brushtail possums (*Trichosurus vulpecula*), grey cuscus (*Phalanger orientalis*) and several other marsupial and eutherian species (Collins 1977). The sweet potato offered to all bandicoots was supplemented with a multi-vitamin mix (Pentavite, Roche, New South Wales) when bulky, white faeces were produced by some of the animals. The same type of faeces are produced by rats on an uncooked potato starch diet, when a B-vitamin deficiency leads to ingestion of faeces (refection) (Fridericia et al. 1927).

On the basis of intakes of the maintenance diet, 50 g (ww) of mealworms and 85 g (ww) of sweet potato offered daily was sufficient to ensure feeding ad libitum. Fresh water was always available ad libitum, and feeding took place at 1900 hours, the start of the dark phase.

The composition of the two experimental diets is shown in Table 1. The levels of total nitrogen (crude protein), crude lipid (ether extract) and gross energy were all significantly higher in the mealworms than in the sweat potatoes. Although the level of neutral-detergent fibre (NDF) of mealworms was also higher ($P<0.05$) than that of sweet potatoes, the NDF of mealworms is composed of chitin rather than cellulose, hemicellulose and lignin (Van Soest and Wine 1967). Because chitin is a structural polymer constructed largely of carbohydrate, it is included in the definition of NDF in this paper.

Six animals (three male) were offered the mealworm larvae and four animals (two male) the shredded sweet potatoes supplemented with the multi-vitamin mix. Initially, six bandicoots were offered sweet potatoes, but two were removed from the experiment after losing more than 10% of bm. The animals were changed from the maintenance diet to their respective experimental diets over a period of 7 days, then kept on these for a further 30 days prior to a collection period of 5 days. The bedding straw and the floors of the nest boxes were removed as the diet was changed in order to clear the gut of any ingested bedding material and to prepare the animals for collection of faeces and urine.

Intake and digestibility. For the collection period, the flat trays suspended beneath the metabolism cages were replaced with sloping trays which collected the faeces on stainless-steel mesh but allowed the urine to flow through into a plastic bottle containing 1 ml glacial acetic acid. The acid kept the pH of collected urine below 3.0, and thus prevented loss of nitrogen as ammonia and discouraged bacterial growth. Urine was collected prior to feeding and stored at −20 °C until analysis, when it was bulked for each animal over the collection period and the total volume measured. Faeces were also collected prior to feeding, weighed, and stored at −20 °C until analysis, when they were dried at or below 50 °C to constant weight (48 h). This temperature was shown by Robertson (1978) to avoid formation of Maillard polymers and thus artifact fibre. Spilled and uneaten food was treated in a similar manner to faeces.

Rate of passage of digesta. At the end of the 5-day collection period for measuring intake and digestibility, rate of passage of three components of digesta was measured on the two diets. All food was removed from the cages, then all ten animals were given a pulse dose of three inert markers in 10 g minced beef; all animals ate the dose within 1 h. The markers used were Co-EDTA, which associates almost exclusively with the fluid component of the digesta (Udén et al. 1980), chromium mordanted to large particles of cell-wall constituents (Cr-CWC) (Udén et al. 1980), and ytterbium mor-

danted to medium particles of CWC (Yb-CWC) (Ellis and Beever 1984). The cell walls were prepared from ground oaten (*Avena sativa*) hay using the neutral-detergent fibre (NDF) procedure of Van-Soest and Wine (1967). The cell walls were then washed through a stack of Endicott (London, UK) screens, and the large particle fraction was taken to be those particles that passed through the 600 μm screen but were retained on the 300 μm screen. The medium particle fraction was particles that passed through the 150 μm screen but were retained on the 75 μm screen. Fine particles (those that passed through the 75 μm screen) and dissolved solutes have been shown by Sakaguchi and Hume (1990) to move with fluid digesta in common brushtail (*Trichosurus vulpecula*) and common ringtail (*Pseudocheirus peregrinus*) possums.

After marker ingestion (2000–2100 hours) the animals were returned to their test diets and faeces were collected hourly for 12 h, and subsequently every 4 h for 24 h, then every 6 h for 48 h. Excretion times were taken to be the mid point of each collection interval. Urine was collected at the same time and bulked for each animal to determine absorption of markers from the gut and subsequent excretion through the kidneys. Faeces and urine were stored at −20 °C until analysed.

Radiography. Three animals were continued on the mealworm diet and two on the sweet potato diet after the rate of passage study in order to observe sites of digesta retention along the gut radiographically. Barium sulphate [X-Opaque-HD, M.C.I. (Aust) Pty, Melbourne, Australia] was used to outline various sections of the digestive tract and as a non-specific bulk digesta marker (Hume and Carlisle 1985). Radio-opaque particles, prepared by cutting radio-opaque threads from surgical gauze (Ray-Tec X-ray detectable swabs, Johnson and Johnson, Sydney) into 2-mm lengths, were used as a large particle marker (Hume and Carlisle 1985).

Bandicoots on the mealworm diet were dosed with the contrast media by injecting ten mealworms with a total of 2–5 ml of a slurry containing 300 g barium sulphate per 70 ml water and by inserting ten particles into two other mealworm larvae. Only the marked mealworms were offered initially, and when these had been eaten the bandicoots were offered their usual diet. Bandicoots on the sweet potato diet were given 3 ml of the barium sulphate slurry and 20 particles in a small amount of minced beef homogenised with shredded sweet potato. All doses were fully ingested.

Radiographs were taken with a portable X-ray machine at 60 kV, 35 mA and 95 cm focal-film distance on Dupont Cronex 10T medical X-ray film (24 cm × 30 cm) with no intensifying grid. Views were taken in left lateral recumbency (0.15-s exposure) and dorsoventral recumbency (0.20-s exposure). Animals were restrained by hand using lead-lined gloves and apron, and were returned to their nest boxes between exposures. Plates were taken just prior to normal feeding time (1900 hours), then at 5 and 25 min, then 1, 2, 3, 4, 5, 6, 8, 12, 20, 24 and 38 h after ingestion of the contrast media.

All bandicoots were released to point of capture at the end of the experiments.

Analytical. The dm content of feed, feed residues, faeces and digesta was determined by oven drying at 95 °C to constant mass (24 h). The gross energy content of feed, feed residues, faeces and urine was determined in a Gallenkamp ballistic bomb calorimeter, using benzoic acid as the standard. Feed, faeces and standards were compressed into tablets, although some samples were too dry for effective compression and so instead were carefully packed into the base of the crucible. Urine was prepared by freeze-drying 5.0 ml onto 0.2 g cellulose fibre (cotton wool) directly in the crucibles and correcting for the heat of combustion of the cotton wool.

The total nitrogen content of feed, feed residues, faeces and urine was determined by a semi-micro Kjeldahl method (Ivan et al. 1974) using a selenium catalyst, approximately 0.1 g dm and 0.2 ml urine. The crude lipid (ether extract) content of feed, feed residues and faeces was determined by Soxhlet extraction with petroleum ether. The NDF content of feed, feed residues and faeces was determined by the method of Van Soest and Wine (1967) with the addition of 50 ml heat-stable α-amylase (Sigma A3306) to remove starch (Van Soest et al. 1991) and the omission of sodium sulphite, as the diets were considered to be relatively low in tannins (Hanley et al. 1992). Decalin, a naphthalene compound, was also omitted (Golding et al. 1985), and thus care had to be taken to avoid excessive foaming during refluxing. ADF content of the residues from the NDF determinations was analysed by the method of Van Soest (1963).

Concentrations of the three metals used as digesta markers (Co, Cr and Yb) were determined on digests of collected faeces by inductively-coupled plasma atomic emission spectroscopy (ICP). The faeces were dried to constant mass at 95 °C and the total mass recorded. Each sample was then ground in a mortar and pestle, homogenised, and a 2-g subsample digested in a 100-ml volumetric flask with 10 ml concentrated nitric acid followed by 5 ml hydrogen peroxide. The digest was then made up to 100 ml for ICP analysis. Subsamples (2 ml) of urine were digested in the same way.

Calculations and statistical analysis. Transit time of each marker was taken as the time of first appearance of that marker in the faeces (Warner 1981). MRT, the best single overall measure of passage time through the entire digestive tract (Warner 1981), was calculated using the equation:

$$\mathrm{MRT(h)} = \frac{\sum_{i=1}^{n} M_i - t_i}{\sum_{i=1}^{n} M_i}$$

where M is the amount of marker excreted in the ith defaecation at time t after dosing, and n is the total number of defaecations (Blaxter et al. 1956).

Statistical comparisons between unpaired intake and digestibility means were made using Student's t-test. To facilitate comparisons among individuals of different bm, metabolic parameters were expressed in terms of metabolic bm ($kg^{0.75}$) (Kleiber 1961). Differences between MRT of digesta markers within animals were tested by paired t-tests (Snedecor and Cochran 1967), and differences between diets were tested by one-factor analysis of variance, at the 5% and 1% levels of confidence. Homogeneity of variances was tested using Bartlett's test for unbalanced data (Zar 1974).

Results

Intake and digestibility

Bandicoots on the mealworm diet virtually maintained bm through the collection period, but those on the sweet potato diet lost approximately 7% of bm ($P<0.01$) (Table 2). This was because of both a lower intake of dm ($P<0.05$) – and thus gross energy ($P<0.05$) – and a lower digestibility of the dm ($P<0.05$) and gross energy ($P<0.01$) of the sweet potato than of the mealworms. Consequently the intake of DE on the sweet potato diet was only one-third of that of the mealworm diet ($P<0.01$; Table 3). The apparent digestibilities of the crude lipid and crude protein (total nitrogen) of the plant diet were also lower ($P<0.01$) than those of the animal diet.

Nitrogen intake on the sweet potato diet was only 5% of that on the mealworm diet ($P<0.01$). Faecal nitrogen was similar on the two diets, and on the sweet potato diet exceeded nitrogen intake. Consequently, apparent digestibility of nitrogen was negative on the plant diet, but it was positive and high on the animal diet ($P<0.01$). In contrast to faecal losses, nitrogen excretion in the urine was lower ($P<0.01$) on the sweet potato diet than on the

Table 2. Body mass changes, and intakes and digestibilities of dry matter, fibre and crude lipid in long-nosed bandicoots

	Diet		Significance of difference between diets
	Mealworm	Sweet potato	
Body mass			
Mean (g)	795 ±42	710 ±65	n.s.
Change ($g \cdot day^{-1}$)	−2 ±1	−10 ±1	**
Dry matter			
Intake ($g \cdot day^{-1}$)	18.3±0.2	13.6±1.0	**
($g \cdot kg^{-0.75} \cdot day^{-1}$)	21.9±0.7	17.7±1.3	*
Apparent digestibility (%)	89.8±0.6	64.5±10.5	*
Fibre			
Intake of NDF[a] ($g \cdot kg^{-0.75} \cdot day^{-1}$)	3.4± 0.1	2.2±0.2	**
Digestibility of NDF (%)	70.5±1.5	65.4±3.3	n.s.
Intake of ADF[b] ($g \cdot kg^{-0.75} \cdot day^{-1}$)	1.2± 0.0	1.0±0.1	**
Digestibility of ADF (%)	51.6±2.9	46.7±6.7	n.s.
Crude Lipid (Ether extract)			
Intake ($g \cdot kg^{-0.75} \cdot day^{-1}$)	4.9±0.2	0.2±0.0	**
Apparent digestibility (%)	96.9±0.2	70.7±3.4	**

Means ± standard errors
[a] NDF = neutral-detergent fibre;
[b] ADF = acid-detergent fibre
n.s. not significant; * $P<0.05$; ** $P<0.01$

Table 3. Intake and balance of energy and nitrogen in long-nosed bandicoots

	Diet		Significance of difference between diets
	Mealworm (n=6)	Sweet potato (n=4)	
Energy			
Intake of GE ($kJ \cdot kg^{-0.75} \cdot day^{-1}$)	560 ±19	302 ±23	**
Apparent digestibility of GE (%)	91.3 ±0.6	61.3 ±14.7	*
Intake of DE ($kJ \cdot kg^{-0.75} \cdot day^{-1}$)	511 ±16	176 ±39	**
Metabolizability of DE (%)	92.3 ±0.4	92.4 ±3.8	n.s.
Intake of ME ($kJ \cdot kg^{-0.75} \cdot day^{-1}$)	472 ±14	167 ±40	**
Nitrogen			
Intake ($g \cdot kg^{-0.75} \cdot day^{-1}$)	2.00±0.10	0.08±0.17	**
Faecal excretion ($g \cdot kg^{-0.75} \cdot day^{-1}$)	0.18±0.02	0.19±0.05	n.s.
Apparent digestibility (%)	90.8 ±0.7	−60.8 ±12.6	**
Urinary excretion ($g \cdot kg^{-0.75} \cdot day^{-1}$)	0.78±004	0.12±0.04	**
Balance ($g \cdot kg^{-0.75} \cdot day^{-1}$)	+1.00±0.30	−0.20±0.06	**

Means ± standard errors
GE: gross energy; DE: digestible energy;
ME: metabolizable energy
n.s.: not significant; * $P<0.05$; ** $P<0.01$

mealworm diet, but it was still higher than nitrogen intake on the plant diet. Thus, nitrogen balance was negative on the sweet potato, while on the mealworms it was strongly positive ($P<0.01$).

Digestibility of fibre (both NDF and ADF) was similar on the two diets (Table 2), despite the differences in composition of the fibre from the two sources.

Rate of passage of digesta markers

Figure 1 shows representative marker excretion curves from one animal on the mealworm diet and one on the sweet potato diet. On each diet, there were no significant differences in transit times (times of first appearance of the marker in the faeces) among the three markers, but transit times on the plant diet (20.6 ± 4.2 h) were three times those on the animal diet (7.7 ± 0.6 h).

MRTs of the medium and large particle markers were similar. MRTs of the particle markers on the plant diet were more than twice those on the animal diet ($P<0.01$), but the MRT of the fluid marker (Co-EDTA) did not differ significantly between the two diets. On both diets the MRT of Co-EDTA was greater ($P<0.01$) than those of the particle markers, indicating selective retention of the fluid phase of the digesta in the gut.

Minimal quantities of the fluid marker (0.1 ± 0.2% of the dose) and no particle marker were detected in the urine. Thus, although Udén et al. (1980) reported absorption of Co-EDTA from the gut of rabbits there was no evidence for this in bandicoots; the small amount of the water-soluble Co-EDTA found in the urine could easily have resulted from contamination of urine by faeces in the collection tray.

Radiography

Results from all animals and all times were used in the interpretation of results, but only selected radiographs taken at 5 min, 30 min, 8 h and 12 h are shown here. Radiographs taken before the administration of radio-opaque media allowed identification of the caecum and colon by the presence of gas, which shows up dark

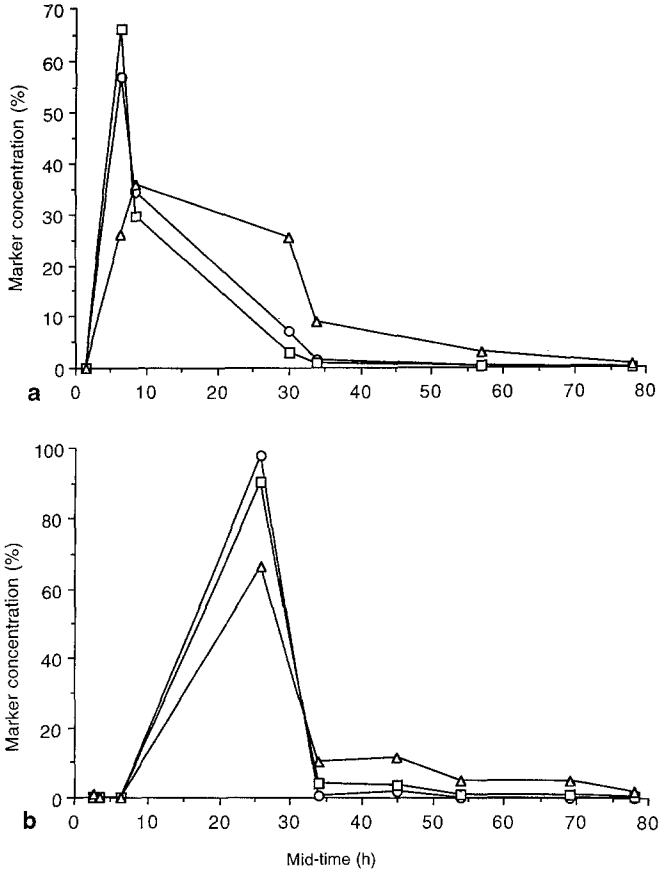

Fig. 1a, b. Concentration in dry faeces (as % of total marker) of Co (*triangles*), Cr (*squares*) and Yb (*circles*) versus time after dosing in one bandicoot on the mealworm diet (**a**) and one bandicoot on the sweet potato diet (**b**). *Co* (as Co-EDTA) represents the fluid phase of digesta together with small particles; *Cr* (as Cr-mordanted cell walls) represents large (300–600 mm) particles; *Yb* (as Yb-mordanted cell walls) represents medium (75–150 mm) particles

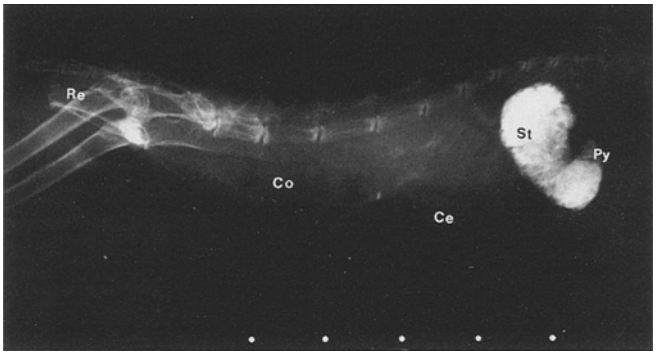

Fig. 2. Left lateral recumbent radiograph of a bandicoot 5 min after dosing with barium sulphate and radio-opaque particles. At this stage there was no difference between the mealworm and sweet potato diets. *Ce*=caecum; *Co*=colon; *Py*=pylorus; *Re*=rectum; *St*=stomach. Scale: 2 cm between points

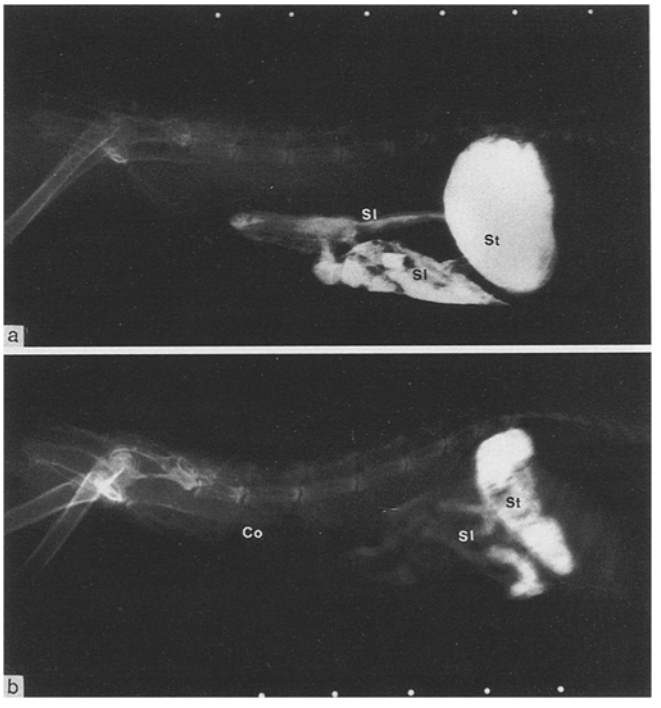

Fig. 3a, b. Left lateral recumbent radiograph of bandicoots on the mealworm diet (**a**), and the sweet potato diet (**b**), 30 min after dosing with barium sulphate and radio-opaque particles. *Co*=colon; *SI*=small intestine; *St*=stomach. *Scale*: 2 cm between points

(Fig. 2). At 5 min after dosing, the stomach was clearly outlined and the position of the pylorus easily identified (Fig. 2).

Between 5 and 30 min some barium sulphate had left the stomach, and the small intestine was clearly outlined, especially in the animals on the mealworm diet (Fig. 3).

Although quantification of radiographic results is not possible, the difference between diets alluded to above became more apparent with time after dosing. In the mealworm-fed animals, little barium sulphate remained in the stomach at 4 h, and although most was still in the small intestine, the caecum and colon were clearly outlined. At 8 h, only the ileum of the small intestine was discernable, and digesta in the caecum and proximal colon, and faecal pellets in the distal colon and rectum were heavily marked (Fig. 4). By 12 h, all barium sulphate had left the ileum, the caecum and proximal colon were only partially outlined, and barium sulphate had accumulated in faecal pellets in the distal colon and rectum (Fig. 5).

In contrast, in the sweet potato-fed bandicoots the caecum was less completely outlined at 4 h, and barium sulphate had not reached the distal colon at 8 h (Fig. 4), nor the rectum at 12 h (Fig. 5). All barium sulphate appeared to have been excreted by 24 h on both diets.

Radio-opaque particles (indicated by arrowheads in Figs. 4, 5) were difficult to identify if much barium sulphate was present at the same time. Thus, rate of flow of particles out of the stomach could not be determined. Particles were visible in the small intestine and colon of sweet potato-fed animals 4 h after dosing, and were discernable in the colon at 8 and 12 h (Figs. 4, 5). In the mealworm-fed animals, some particles had already been excreted by 12 h, but a few particles still remained in the colon 24 h after dosing.

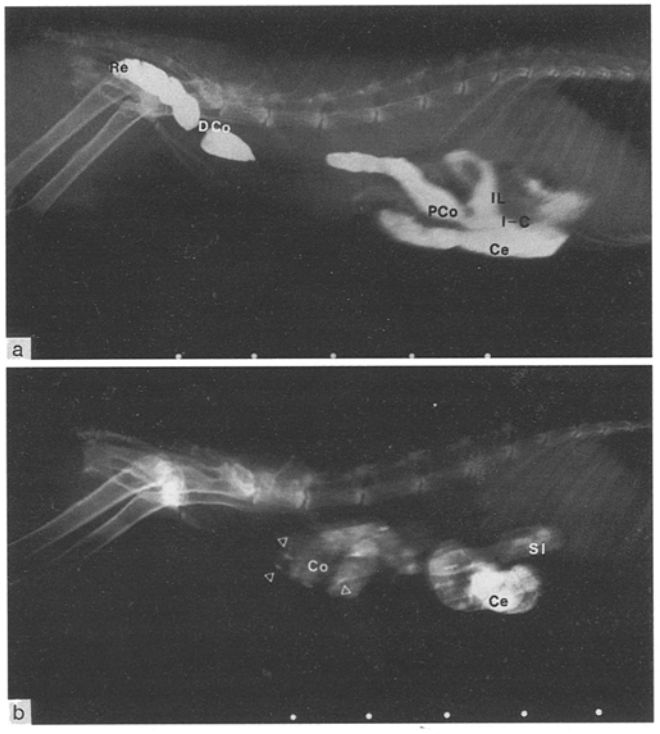

Fig. 4a, b. Left lateral recumbent radiograph of bandicoots on the mealworm diet (**a**), and the sweet potato diet (**b**), 8 h after dosing. *Co* = colon; *DCo* = distal colon; *IL* = ileum; *I-C* = ileo-colonic junction; *PCo* = proximal colon; *Re* = rectum; *SI* = small intestine. *Scale*: 2 cm between points

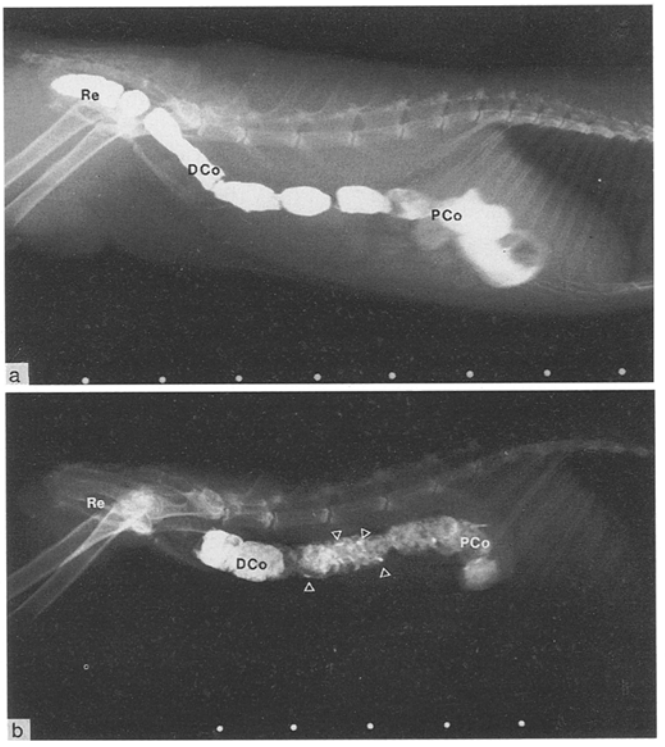

Fig. 5a, b. Left lateral recumbent radiograph of bandicoots on the mealworm diet (**a**), and the sweet potato diet (**b**), 12 h after dosing. *DCo* = distal colon; *PCo* = proximal colon; *Re* = rectum. *Scale:* 2 cm between points

Discussion

The higher quality of the mealworm versus the sweet potato diet suggested by their respective compositions (Table 1) was confirmed by animal performance. Bandicoots virtually maintained bm on the mealworm diet, with a digestible energy intake of 511 kJ · $kg^{-0.75}$ · day^{-1}. Thus, this intake must be close to the maintenance energy requirement for this species in captivity. A similar value (545 kJ · $kg^{-0.75}$ · day^{-1}) was reported by Green and Eberhard (1979) for the maintenance digestible energy requirement of two carnivorous marsupials in captivity, the Tasmanian devil (*Sarcophilus harrisii*) and the eastern quoll (*Dasyurus viverrinus*). The only other estimates of maintenance energy requirement for captive marsupials are for three herbivores: 456 kJ · $kg^{-0.75}$ · day^{-1} for the red kangaroo (*Macropus rufus*), 414 for the euro (*M. robustus erubescens*) (Hume 1974), and 326 for the rufous hare-wallaby (*Lagorchestes hirsutus*) (Bridie et al. 1994). All are less than our value for the long-nosed bandicoot and Green and Eberhard's (1979) values for the Tasmanian devil (*Sarcophilus harrisii*) and the largely insectivorous eastern quoll (*Dasyurus viverrinus*). The supposition in the literature (Stodart 1983) that the long-nosed bandicoot is primarily insectivorous rather than herbivorous, is supported by our data.

In contrast to the mealworm diet, on the sweet potato diet the bandicoots lost bm, and DE intakes were well below maintenance levels (Table 3). The animals were also in substantial negative nitrogen balance. Nitrogen losses via faeces and urine both exceeded nitrogen intake, and both were also greater than endogenous losses predicted on the basis of published values. For most marsupials, EUN (the minimum nitrogen loss in the urine) is about 60 mg · $kg^{-0.75}$ · day^{-1} (Hume 1982); for the sugar glider (*Petaurus breviceps*), a small (130 g) omnivore that feeds on insects and plant exudates, EUN is only 25 mg · $kg^{-0.75}$ · day^{-1} (Smith and Green 1987). Because nitrogen intake was so low on the sweet potato diet, urinary nitrogen losses on this treatment should be close to EUN, and thus comparable with published EUN values. However, urinary nitrogen loss by the bandicoots on the sweet potato diet was 120 mg · $kg^{-0.75}$ · day^{-1}. This high value was undoubtedly due largely to catabolism of skeletal muscle to meet essential energy needs (Levey and Karasov 1989), the excess nitrogen being excreted via the kidneys as urea.

Faecal nitrogen excretion in the long-nosed bandicoots on the sweet potato diet (equivalent to 1100 mg · 100 g dm^{-1} intake) was also much higher than published values for MFN, the minimum nitrogen loss in the faeces. In the sugar glider MFN is 87 mg · 100 g dm^{-1} intake (Smith and Green 1987). It is higher in herbivorous marsupials (240–410 mg · 100 g dm^{-1} intake), because of greater losses associated with microbial biomass and sloughed mucosal cells from the gut. The high faecal nitrogen excretion by the bandicoots fed sweet potato (as high as by the mealworm-fed animals) could be due to the resistance of the uncooked sweet potato starch to enzymatic digestion in the small intestine (Englyst et al. 1992).

Table 4. Transit time (h) and mean retention time (h) of three digesta markers in long-nosed bandicoots

	Diet		Significance of difference between diets
	Mealworm ($n=6$)	Sweet potato ($n=4$)	
Transit time (h)			
Co-EDTA	7.7±0.6	20.6±4.2	**
Yb-CWC	7.8±0.7	20.6±4.2	**
Cr-CWC	7.7±0.6	20.6±4.2	**
Sign. of diff. between Co-EDTA and the two particle markers	n.s.	n.s.	
Mean retention time (h)			
Co-EDTA	23.6±3.1	33.1±1.9	n.s.
Yb-CWC	12.4±1.8	27.5±1.5	**
Cr-CWC	11.2±1.6	27.0±1.9	**
Sign. of diff. between Co-EDTA and the two particle markers	**	**	

Means±standard errors
Co-EDTA represents fluid digesta and small particles (<75 μm); Yb-CWC represents medium particles (75–150 μm); Cr-CWC represents large particles (300–600 μm)
n.s.: not significant; * $P<0.05$; ** $P<0.01$

Undigested starch would be fermented in the hindgut, leading to increased faecal nitrogen output in the form of bacterial biomass (Mathers and Dawson 1991). The source of this faecal nitrogen is presumably from tissue degradation.

The finding that the fibre (both NDF and ADF) of the two diets was uniformly readily digestible, despite differences in chemical composition of the two fibre sources, suggests that both larval invertebrate chitin and the cell walls of tuberous plant roots are potentially rich sources of digestible energy to the omnivorous long-nosed bandicoot. Indeed, results from the rate of passage study indicate that the digestive tract of the long-nosed bandicoot is flexible in its response to plant and animal diets. On the mealworm diet, the short transit time of all three markers (7.7 h), the rapid increase in marker concentration in the faeces to a peak at 8 h (Fig. 1), and the complete elimination of the particle markers by 30 h, correspond closely with the findings of Griffiths (Waring et al. 1966), who fed different species of termites as passage markers to the northern brown bandicoot (*Isoodon macrourus*) and examined collected faeces for undigested exoskeletons. Marker termites first appeared in the faeces 7 h after ingestion, reached a peak concentration at 9 h, and were completely eliminated by 29 h (Hume 1982). In contrast, on the sweet potato diet, transit times of all markers were nearly three times those on the mealworm diet, and peak marker concentrations occurred more than three times later than on the mealworms.

The value of using a fluid marker in conjunction with particle markers is well illustrated by the present results. In the mealworm-fed animals, the MRT of the fluid marker was double that of the particle marker. This indicates that, relative to the passage of particles such as insect exoskeletons, fluid digesta – and small particles of food and bacteria (Sakaguchi and Hume 1990) – are selectively retained in the bandicoot gut (Table 4). Selective retention of fluid digesta in the hindgut of small herbivores has several advantages (Björnhag 1987): it maintains a high concentration of microorganisms for maximal rates of fermentation in the caecum, and increases the digestive efficiency of an animal by eliminating the large digesta particles relatively rapidly (Cork and Warner 1983; Chilcott and Hume 1985), allowing a more concentrated digestive effort on the fluid and fine, potentially more fermentable particles (Bjorndal et al. 1990) in the caecum (Björnhag 1981; Hume et al. 1993). These advantages are likely to be important for bandicoots; selective retention of fluid and fine particles allows utilisation of an omnivorous diet with a high fibre content. Without selective excretion of large particles, the animals may be unable to process enough plant and invertebrate material to satisfy their relatively high mass-specific energy requirements (Hulbert and Dawson 1974).

Importantly, on the sweet potato diet, although MRTs of the particle markers were much greater than those of the mealworm-fed animals, there was still selective retention of the fluid marker, i.e. longer MRTs (Table 4), indicating that the separation mechanism resulting in selective retention of fluid and fine particulate digesta is a consistent feature of the gut of the long-nosed bandicoot, independent of diet (although the actual mechanisms involved are as yet unclear). Thus, the digestive tract of bandicoots is likely to be more adaptable to diets of different qualities than might be predicted from their rather simple morphology (Hume 1982) alone.

The greater MRTs of the particle markers on the sweet potato diet are probably due partly to the lower feed intakes on the plant diet (Stevens 1988). However, it is also probable that gut capacity was greater on the plant than the animal diet; Gross et al. (1985) and Hammond and Wunder (1991) have demonstrated that prairie voles (*Microtus ochrogaster*) respond to lower quality food by increasing gut capacity, especially the caecum and colon. Similar responses were recorded in three other species of voles by Lee and Houston (1993). Although it is not known empirically whether gut capacity changed in the bandicoots in our study, radiographic evidence suggests that gut volume was greater on the sweet potato diet. This would be consistent with the increases in caecal mass observed in rats after ingestion of raw potato starch (Calvert et al. 1989).

Differences between the two diets in the sites of digesta retention were suggested by the radiographic study. It appears that a major site of digesta retention in the mealworm-fed animals was the distal colon and rectum in the

form of faecal pellets. Bandicoots are considered strictly nocturnal (Stodart 1983), and our animals rarely defaecated during the light phase. Thus, rate of passage of digesta through the small intestine and the caecum and proximal colon (the region of microbial fermentation) was probably considerably more rapid than suggested by MRTs. MRT is a measure of rate of passage from mouth to anus or cloaca, and thus is the net effect of differential passage and retention in all parts of the gut. It is clear from Figs. 4 and 5 that a substantial amount of marked digesta spent at least 4 h longer in the rectum on the mealworm compared with the sweet potato diet.

In contrast to the mealworm-fed animals, the main site of digesta retention in the bandicoots on sweet potato appeared to be the caecum and proximal colon, rather than the distal colon and rectum (Figs. 4, 5). Thus, not only was there slower passage of digesta, especially medium and large particles, on the lower quality plant diet but the digesta also spent more time exposed to microbial attack in the caecum and proximal colon. The demonstrated flexibility of the bandicoot digestive tract is probably an important factor in the ability of these small marsupials to exploit nutritionally unpredictable habitats such as regenerating heathlands (Stoddart and Braithwaite 1979; Quin 1988; Moyle 1992).

Acknowledgements. We thank Nazaneen Soran for skilled technical assistance, Andrew Krockenberger for general advice, Andrew Wood for advice on radiographic techniques, Irene Schouten for advice on ether extractions and bomb calorimetry, Caroline Tibbles for help with bandicoot husbandry, and Allen Lyngkuist for logistical support. The bandicoots were held under the provisions of Licence A158 from the National Parks and Wildlife Service of New South Wales, and the study was supported by the Australian Research Council.

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