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Responses of the digestive tract of the omnivorous northern brown bandicoot, *Isoodon macrourus* (Marsupialia: Peramelidae), to plant- and insect-containing diets

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Abstract The gastrointestinal tract of omnivores such as bandicoots (Marsupialia: Peramelidae) must be able to process foods as different as invertebrates, fungi and plant material. We studied the mechanisms involved in the utilisation by captive northern brown bandicoots (*Isoodon macrourus*) of insect larvae and milled lucerne (*Medicago sativa*) hay incorporated into a basal diet of a commercial small carnivore mix. Animals on the plant-basal mix digested less dry matter, energy, lipid, fibre and total nitrogen, but consumed 79% more dry matter than those on the insect-basal mix. Consequently intake of digestible energy (i.e. energy absorbed) was not significantly different between diets. Mean retention time (MRT, the mean time a marker remains in the tract) of a large particle marker was shorter on the plant-basal mix, reflecting its higher intake, but MRT of a solute marker was not significantly different between diets. Consequently the solute marker was retained longer than the particle marker on the plant-basal mix, indicating selective retention of solutes and very small particles in the caecum on this diet. This was confirmed by a higher proportion of small particles in the caecum than the distal colon of road-killed *I. macrourus*. Thus the main responses by *I. macrourus* to the plant-basal mix appeared to be an increase in gastrointestinal tract capacity (from radiographic evidence), selective retention of solutes and very small particles in the caecum, and facilitated passage of less tractable large particles through the colon. As a consequence, food intake was higher on the plant-basal mix, which compensated for its lower digestibility, and intake of digestible energy was similar to that on the insect-basal mix. This considerable flexibility of the morphologically rather simple digestive tract of northern brown bandicoots helps to explain their ability to cope with naturally variable diets consisting of mainly invertebrates in summer to much more plant and fungal material in winter, and to survive in nutritionally dynamic environments such as heathlands where there can be dramatic changes in food type and availability following periodic wildfires.

Key words Omnivore · Bandicoot · Food intake · Mean retention time · Hindgut

Abbreviations *Co-EDTA* cobalt-ethylenediaminetetraacetic acid · *Cr-cell walls* chromium-mordanted cell-wall constituents · *CSM* colonic separation mechanism · *MRT* mean retention time · *NDF* neutral-detergent fibre · *PEG* polyethylene glycol (molecular weight 4,000)

Introduction

Bandicoots are small to medium-sized (250 g–3 kg) omnivorous marsupials found in a wide range of habitats, from moist forests in New Guinea to arid off-shore islands of Australia (Strahan 1995). Although quantitative information on diet is not extensive, all bandicoots appear to be opportunistic omnivores, feeding on a wide range of invertebrate, plant and fungal material (Quin 1988; Claridge et al. 1991; Moyle et al. 1995; Gott 1996; Reimer and Hindell 1996). The northern brown bandicoot (*Isoodon macrourus*) is found mainly in grasslands, heath and open woodland habitats throughout its extensive range from the Hawkesbury River in New South Wales, north to Cape York Peninsula in Queensland and west to the Kimberley in the north of Western Australia. Much of its range is prone to wildfire, which results in irregular fluctuations in the nature and availability of food. In addition, at the southern limit of its distribution in New South Wales, the northern brown bandicoot experiences seasonal changes in food supply. Thus, although it appears to prefer invertebrates and their larvae

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when available (in spring and summer), its diet in autumn and winter is likely to contain greater proportions of plant and fungal material (Gott 1996).

Despite likely seasonal shifts in diet, the bandicoot digestive system is relatively simple (Hume 1999), and is typical of that of other mammalian omnivores (Stevens and Hume 1995). Omnivores have a lower gut capacity than herbivores (Parra 1978), with a relatively smaller caecum and colon (Schieck and Millar 1985). These characteristics serve to constrain omnivores in their ability to digest plant material when compared to herbivores. This paper describes several aspects of the digestive tract and its function in northern brown bandicoots given diets containing insect or plant material.

Materials and methods

Animals

Sub-adult and adult northern brown bandicoots (six males, seven females) were caught using cage traps baited with peanut butter on bread on the central coast of New South Wales, approximately 200 km north of Sydney. The study was conducted in winter, the lowest point in the breeding season, and no captured females were carrying pouch young. The bandicoots were housed individually in stainless steel mesh metabolism cages (600 mm × 600 mm × 450 mm high) in the Native Animal House at the University of Sydney. Each cage contained a wooden nest box and rubber matting on the floor. The matting was removed during periods of faecal collection. The room was held at 21.5 ± 2.5 °C on a 12 L:12 D light:dark cycle. Two night lights (each 3 W) were also provided. The animals were initially offered a mixed diet of fruit, minced beef, commercial dry dog food, peanut butter/honey and rolled oats for approximately 2 weeks, then progressively introduced to the two experimental diets. Animals were assigned to the experimental diets at random after stratification for sex and body mass.

Experimental diets

Both experimental diets were based on a commercial small carnivore mix (Wombaroo, Glen Osmond, South Australia) and 4.4% agar to improve physical consistency, and supplemented with either mealworm (*Tenebrio molitor*) larvae or milled lucerne (*Medicago sativa*) hay (1 mm screen) added at 50% and 24% respectively on an air-dry basis. These proportions provided equivalent supplemental dry matter. The small carnivore mix contained, in descending order, meat meal, blood powder, whey and soy protein isolates, wheaten flour, vegetable oils, vitamins and minerals. The chemical composition of the mealworms, the lucerne hay and the small carnivore/agar mix, and of the ingested food, is shown in Table 1.

The mealworm larvae were used to mimic the preponderance of invertebrates in the summer diet of bandicoots, and the milled lucerne hay to mimic the increased plant content of their winter diet (Claridge et al. 1991; Hume 1999). Food and water were both provided ad libitum throughout the study. Cages were cleaned and food refusals (orts) removed and replaced with fresh food during the hour prior to lights out (1800 hours) each day. Animals were initially weighed every 2nd day until body mass stabilised, then every 4 days during non-collection periods, and on the 1st and last days of collection periods. Body mass on the 1st day was used in the statistical analyses.

Food intake and digestibility

The animals were held on the experimental diets for 3 weeks prior to the 7-day collection period. During the collection period, faeces were retained by a mesh screen and urine was collected by a sloping stainless steel tray suspended beneath the metabolism cages into a plastic bottle containing 2 ml glacial acetic acid to maintain urine pH below 3.0 and so prevent microbial growth. All orts, faeces and urine were collected daily, bulked for each animal over the collection period, and stored at −20 °C until analysis.

Rate of passage of digesta markers

At the end of the collection period all animals were offered a small ball of peanut butter, minced beef or avocado containing two inert markers, Co-EDTA (cobalt-ethylenediaminetetraacetic acid, Dojindo, Japan) as a solute marker and Cr-cell walls (chromium-mordanted cell-wall constituents; Udén et al. 1980) as a particle marker. The cell walls were prepared from milled oaten (*Avena sativa*) hay using the neutral-detergent extraction procedure of Van Soest and Wine (1967) but omitting EDTA from the solution. The cell walls were then washed through a stack of five Endecott (London, UK) sieves, and the particles that passed through the 600 μm screen but were retained on the 300 μm screen were labelled with Cr by the mordanting procedure of Udén et al. (1980). Each food ball had 0.5 g Cr-cell walls and 0.1–0.2 g Co-EDTA incorporated into it.

Ten of the animals consumed the markers as a pulse dose (i.e. within 30 min); five on the lucerne diet and five on the mealworm diet. Immediately after marker ingestion, the animals were offered their experimental diets, and collection trays were checked and any faeces present were collected hourly for 12 h, then 4-hourly for 24 h, 6-hourly for 48 h, 12-hourly for 24 h and once after another 24 h (a total of 132 h). Collection time was taken as the mid-point between checking/collection times. Spot checks of the collection

Table 1 Chemical composition (dry-matter basis) of the main dietary ingredients, and of the food actually ingested by northern brown bandicoots (*Isoodon macrourus*). Means ± SD (n = 4). (*MW* mealworm larvae, *NDF* neutral detergent fibre)

	Dietary ingredients			Food ingested		
	Basal mix[1]	MW	Ground lucerne hay	MW-basal mix[2]	Lucerne-basal mix[3]	Significance of difference between foods ingested
Organic matter (%)	90.4 ± 0.1	95.8 ± 0.2	90.5 ± 0.2	95.0 ± 0.2	90.4 ± 0.3	**
Gross energy (kJ · g^{-1})	22.4 ± 0.0	29.1 ± 0.5	21.4 ± 0.2	28.8 ± 0.1	21.7 ± 0.0	**
Total lipid (%)	19.4 ± 5.5	37.5 ± 5.6	14.9 ± 8.0	40.0 ± 12.8	16.5 ± 4.0	*
Total nitrogen (%)	6.1 ± 0.1	7.8 ± 0.1	5.4 ± 0.1	6.9 ± 0.5	5.3 ± 0.2	**
NDF (%)	9.5 ± 1.0	13.7 ± 0.6	20.1 ± 1.5	6.4 ± 2.3	17.7 ± 2.5	**

* $P < 0.05$; ** $P < 0.01$

[1] Basal mix (air-dry) was 95.6% Wombaroo small carnivore mix plus 4.4% agar

[2] MW-basal mix (air-dry) was 42–58% mealworms, reflecting the selection of seven individual animals

[3] Lucerne-basal mix (air-dry) was 24.2% milled lucerne hay mixed uniformly through the basal mix

trays at some intermediate times yielded several additional faecal samples. Urine was collected daily and bulked for each animal over the 132 h. Faeces and urine were analysed for concentrations of Co and Cr by flame atomic absorption spectroscopy (see below).

Transit time was taken to be the collection time when faeces first contained marker. Mean retention time (MRT), the best single overall measure of rate of passage through the entire digestive tract (Warner 1981), was calculated using the equation MRT (h) = $\sum_{=1}^{n} M_i T_i$ divided by the total amount of marker collected, where M is the amount of marker collected in the ith defaecation at time T after dosing, and n is the total number of defaecations collected (Blaxter et al. 1956).

Radiography

In order to study patterns of digesta passage, at the end of the marker collections three of the lucerne-fed animals and two of the mealworm-fed animals were each given an oral dose of 4–5 ml barium sulphate suspension (270–375 g in 100 ml water) as a radio-opaque non-specific bulk digesta marker, by syringe just before lights out at 1800 hours (Hume and Carlisle 1985). Radiographs were then taken using a portable SP 104 X-ray machine. Exposure features were 60 kV, 35 mA, 100 cm focal-film distance, and an exposure time of 0.15 s. Dupont Ultra-Vision medical X-ray film (18 cm × 24 cm and 30 cm × 24 cm) was used, with no intensifying grid.

Ventro-dorsal recumbency views were taken approximately 5 min, then 1, 1.5, 2, 3, 4, 6, 8, 10, 12, 18, 24, 38, 48 and 60 h after dosing. Left-lateral recumbency views were also taken between 1 h and 6 h. The animals were kept inside cotton bags for the intervals between the first three radiographs, but were thereafter returned to their nest boxes between radiographs. At the end of the radiography study all animals were released at their point of capture.

As an index of hindgut capacity, the apparent diameters of the radiographic images of the proximal colon (at the level of the last rib), the distal colon (mid-way between the last rib and the pelvic girdle) and rectum (at the pelvic girdle) were measured manually. It was not possible to measure any similar index of capacity of other parts of the tract because their images were frequently obscured by those of other tract sections. Hindgut diameters were measured four times between 4 h and 24 h after dosing in the two mealworm-fed animals and two of the lucerne-fed animals. Only two estimates were possible in the third lucerne-fed bandicoot (at 4 h and 6 h) because the density of contrast medium after 6 h was too low for accurate measurement.

Digestive tract morphology and particle size distribution

Four road-killed northern brown bandicoots, two from near Townsville, north Queensland, and two from the central coast of New South Wales, were stored frozen, then thawed overnight, weighed, measured and dissected. The actual diets of these animals could not be determined. However, all four bandicoots were collected during autumn or winter, so that the plant/fungal content of their diets was predicted to be at or near a maximum (Claridge et al. 1991; Hume 1999). The gastrointestinal tract from oesophagus to cloaca was removed through a ventral midline incision, cleared of mesenteric attachments, then divided into stomach, small intestine, caecum, proximal colon and distal colon. The junction between proximal and distal colon was not marked by any distinct anatomical feature, so was deemed to be the point at which segmentation of contents commenced as faeces were formed in the distal colon. Each tract segment was measured for length, then weighed before and after removal of its contents. The contents were also weighed, then dried in a forced-draft oven at 50 °C to constant mass. Samples (duplicates wherever possible – each 0.3 g dry matter) were reconstituted by soaking in water overnight, then washed through a stack of Endecott sieves (mesh sizes 1000, 500, 250, 125, 75 and 45 μm). Particles collected on each sieve were dried and weighed, and their masses expressed as proportions of the original sample dry mass. The mass of fine particles (<45 μm mesh) and solutes was determined by difference.

Chemical analyses

Representative duplicate samples of the experimental diets offered, bulked orts and faeces were dried in a forced-draft oven at 50 °C to constant mass to determine dry matter content. Samples of diets offered, orts and faeces (1.0–2.0 g dry matter) were ashed in a muffle furnace for 3 h at 550 °C to determine organic matter content. Further samples (1.0 g dry matter) were analysed for neutral-detergent fibre (NDF) by the method of Van Soest et al. (1991), which included the addition of 50 μl of heat-stable α-amylase (Sigma A3306, USA) to minimise interference by starch. The gross energy content of diets, orts and faeces was determined using a Gallenkamp Autobomb ballistic bomb calorimeter, with benzoic acid as the standard. The determination of the crude lipid content of diets, orts and faeces was based on extraction using a chloroform-methanol-water solvent system (Atkinson et al. 1972). The total nitrogen content of diets, orts, faeces and urine was determined using the semi-micro Kjeldahl method of Clare and Stevenson (1964) and an automated Kjeltec Distillation Unit, using selenium as the catalyst.

For marker analysis, faeces were dried to constant mass at 50 °C, weighed, and then ground with a mortar and pestle. Subsamples (0.2–0.3 g) were digested with 5 ml nitric acid and 1 ml hydrogen peroxide in a high-pressure microwave digestion system (Milestone MLS 1200 Mega Microwave Digestion System, Italy), made up to 100 ml volume, then analysed for concentrations of Co and Cr by flame atomic absorption spectroscopy (Varian model AA/400P). Subsamples (0.2 ml) of the urine bulked over the collection period from each animal were digested using the same method.

Statistical analyses

Parameters of intake, digestibility and nitrogen balance were analysed statistically using analysis of covariance (ANCOVA), with initial body mass as the covariate (Raubenheimer and Simpson 1992). Data were tested for normality using a Shapiro-Wilk W test (Sokal and Rolf 1981). Data for lipid and nitrogen digestibility were arcsine-transformed to achieve normality (Underwood 1997). All analyses were performed using the statistical program JMP (SAS Institute 1995). Prior to ANCOVA, slopes were tested for heterogeneity by using an interaction term which, if not significant, was removed from the ANCOVA (Sokal and Rolf 1981). Intake and nitrogen balance data are presented on a metabolic body mass basis because of the significant difference in initial body mass between diets, and to facilitate comparison with the literature. In the absence of any published exponent for bandicoots, $kg^{0.75}$ was used in this study.

Differences in transit times and mean retention times between the two digesta markers were analysed statistically with paired t-tests (Snedecor and Cochran 1967). Homogeneity of variances were tested using Cochran's test for balanced data (Underwood 1997). Differences between diets were tested using t-tests assuming unequal variances (Snedecor and Cochran 1967). Differences in proportions of small and large particles in the caecum and distal colon of the four road-killed animals were tested using one-way analysis of variance (ANOVA) followed by the Student-Newman Keuls procedure. Differences in apparent diameters of radiographic images of the colon and rectum were tested by Student t-tests (Snedecor and Cochran 1967).

Results

Food intake and digestibility

Although animals were randomly assigned to the two experimental diets after stratification for sex and body mass, at the end of the 3-week pre-collection period

animals on the mealworm-basal mix were significantly heavier (Table 2). However, body mass gain during the 7-day collection period was not significantly different between the two treatments.

The generally lower nutritive value of the plant-basal mix (Table 1) was reflected in lower apparent digestibilities of dry matter, energy, lipid and nitrogen ($P < 0.001$), and a lower digestibility of NDF ($P < 0.05$). However, the bandicoots were able to compensate for the lower energy density of the plant-basal mix by consuming nearly twice as much dry matter ($P < 0.001$) as those on the mealworm-basal mix. As a consequence, intakes of digestible energy (i.e. the amounts of energy absorbed) on the two diets were not significantly different.

Despite its lower ($P < 0.01$) nitrogen concentration (Table 1), the higher dry matter intake of the lucerne-basal mix resulted in higher nitrogen intakes ($P < 0.01$) and, despite a lower apparent digestibility, a significantly higher nitrogen balance as well ($P < 0.05$) when compared to the mealworm-basal mix; urinary nitrogen losses were similar on the two diets.

Rate of passage of digesta

Transit times (time of first appearance of the marker in the faeces) were similar for the two digesta markers, but shorter on the plant-based diet ($P < 0.01$), reflecting its higher daily intake (Table 3). Similarly, the MRT of the particle marker (Cr-cell walls) was shorter on the plant-basal mix ($P < 0.01$).

However, this was not the case for the solute marker (Co-EDTA), for which there was no significant dietary difference in MRT. Consequently there was no significant difference in MRT between the two markers on the mealworm-basal mix; however on the lucerne-basal mix, the MRT of Co-EDTA was 2.7 times longer than that of Cr-cell walls ($P < 0.001$).

Although no particle marker appeared in the urine, considerable quantities of the solute marker were detected, equivalent to 16.6 ± 2.8% of the total dose in the lucerne-basal mix animals, and 26.6 ± 3.2% in the mealworm-basal mix animals.

Radiography

Filling and emptying of gastrointestinal tract compartments were visualised radiographically, and cannot readily be quantified. Nevertheless, it is possible to make some general statements about patterns observed in the five bandicoots used in this part of the study. No differences between the two diets were evident in the time taken for the contrast medium to clear the stomach. In the small intestine, contrast medium reached its maximum density at 2 h on both treatments, with complete clearance by 10 h. Similarly, there were no differences between the two diets evident in filling patterns of the caecum/proximal colon and distal colon with contrast medium. However, the contrast medium cleared from the caecum/proximal colon more rapidly on the lucerne-basal mix, and completely cleared from the hindgut

Table 2 Intake and digestibility, and nitrogen balance, by northern brown bandicoots (*I. macrourus*) offered a basal mix with either MW or milled lucerne hay added. Means ± SD; *NS* not significant

Parameter	MW-basal mix ($n = 7$)	Lucerne-basal mix ($n = 6$)	Significance of difference
Body mass			
Initial (g)	1365 ± 351	977 ± 274	*
Gain ($g \cdot day^{-1}$)	6 ± 4	1 ± 4	NS
Dry matter			
Intake ($g \cdot day^{-1}$)	23.9 ± 4.3	33.8 ± 10.4	*
($g \cdot kg^{-0.75} \cdot day^{-1}$)	19.0 ± 2.3	34.2 ± 5.6	***
Apparent digestibility (%)	92.7 ± 0.8	67.2 ± 3.1	***
Digestible intake ($g \cdot kg^{-0.75} \cdot day^{-1}$)	17.8 ± 2.2	23.1 ± 4.0	NS
Energy			
Gross intake ($kJ \cdot kg^{-0.75} \cdot day^{-1}$)	548 ± 68	741 ± 21	**
Apparent digestibility (%)	94.4 ± 0.4	73.5 ± 2.0	***
Digestible intake ($kJ \cdot kg^{-0.75} \cdot day^{-1}$)	517 ± 63	545 ± 93	NS
Lipid			
Intake ($g \cdot kg^{-0.75} \cdot day^{-1}$)	7.5 ± 2.0	5.8 ± 2.0	NS
Apparent digestibility (%)	97.9 ± 1.3	78.8 ± 13.9	***
Nitrogen			
Intake ($g \cdot kg^{-0.75} \cdot day^{-1}$)	1.32 ± 0.20	1.82 ± 0.26	**
Apparent digestibility (%)	91.6 ± 0.8	81.5 ± 1.8	***
Urinary output ($g \cdot kg^{-0.75} \cdot day^{-1}$)	1.09 ± 0.17	1.01 ± 0.12	NS
Balance ($g \cdot kg^{-0.75} \cdot day^{-1}$)	+0.11 ± 0.10	+0.46 ± 0.27	*
NDF			
Intake ($g \cdot kg^{-0.75} \cdot day^{-1}$)	1.2 ± 0.4	6.1 ± 1.6	***
Digestibility (%)	62.1 ± 21.9	39.5 ± 10.0	*

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 3 Whole-tract transit times and mean retention times of a solute marker (Co-EDTA) and a particle marker (Cr – mordanted cell walls) and apparent diameters of the proximal colon, distal colon and rectum in northern brown bandicoots (*I. macrourus*) offered a basal diet with either MW or milled lucerne hay added. Means ± SD; *NS* not significant

	MW-basal mix ($n = 5$)	Lucerne-basal mix ($n = 5$)	Significance of difference between diets
Transit time (h)			
Co-EDTA	5.2 ± 0.6	1.1 ± 0.6	***
Cr-cell walls	6.5 ± 1.0	1.9 ± 1.2	**
Significance of difference between markers	NS	NS	
Mean retention time (h)			
Co-EDTA	27.3 ± 6.4	27.4 ± 5.3	NS
Cr-cell walls	26.9 ± 4.0	10.0 ± 5.2	**
Significance of difference between markers	NS	***	
Apparent diameter (mm)[1]			
Proximal colon	6.2 ± 0.2	9.4 ± 0.6	**
Distal colon	4.7 ± 0.2	7.3 ± 0.6	**
Rectum	7.2 ± 1.2	7.8 ± 1.4	NS

** $P < 0.01$; *** $P < 0.001$

[1] Measured from radiographs taken 4–24 h after dosing, $n = 2$ for MW-basal mix, $n = 3$ for lucerne-basal mix

between 24 h and 38 h, compared with 48–56 h on the mealworm-basal mix.

Both the proximal colon and the distal colon were wider ($P < 0.01$) on the plant-based diet than the mealworm-based diet, but rectal widths were similar, at least in the small sample size of five animals tested. This difference in colon diameter between the two diets is highlighted in Figs. 1 and 2, which are radiographs of the hindgut taken at times of maximum density of contrast medium in one animal (body mass 1.85 kg) on the mealworm-basal mix (10 h after dosing) and one animal (1.47 kg) on the lucerne-basal mix (4 h after dosing), respectively. The earlier time of maximum density in the colon on the lucerne-basal mix than the mealworm-basal mix correlates with the earlier clearance of contrast medium from the entire tract on the plant diet.

Digestive tract morphology and particle size distribution

The gastrointestinal tract of the northern brown bandicoot is shown in Fig. 3. The small intestine was the dominant section of the tract, both in terms of length and fresh tissue mass (Table 4). The dry matter percent of tract contents from four road-killed animals was relatively uniform in the stomach, small intestine, caecum and proximal colon, but tended to increase in the distal colon (Table 4).

The distribution along the gastrointestinal tract of particle sizes, grouped into three size classes (large, those retained on 1,000 μm and 500 μm sieves; medium, those that passed through the 500 μm sieve but were retained on the 250 μm and 125 μm sieves; and small, those that passed through the 125 μm sieve), in the four road-killed bandicoots is shown in Fig. 4. The proportion of small particles was higher ($P < 0.05$) in the caecum (64.4 ± 11.1%) than the distal colon (37.4 ± 8.8%).

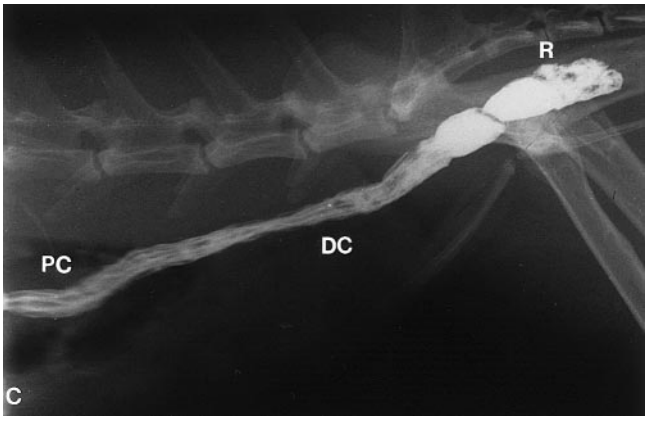

Fig. 1 Left lateral radiograph of the hindgut of a northern brown bandicoot (body mass 1.85 kg) on the mealworm-basal mix taken 10 h after dosing with barium sulphate, the time of maximum density of the contrast medium. (*C* caecum, *DC* distal colon, *PC* proximal colon, *R* rectum)

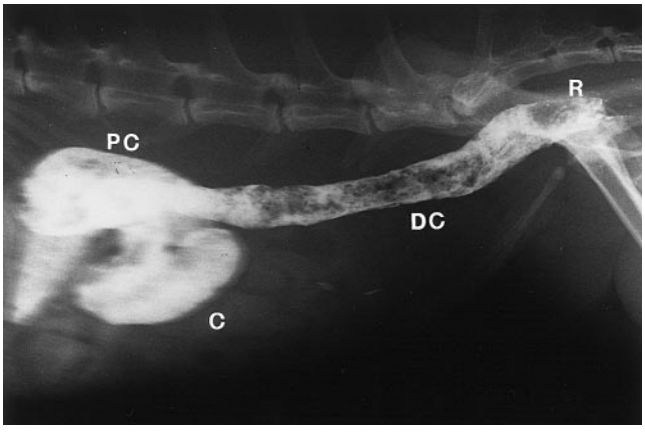

Fig. 2 Left lateral radiograph of the hindgut of a northern brown bandicoot (body mass 1.47 kg) on the lucerne-basal mix taken 4 h after dosing with barium sulphate, the time of maximum density of the contrast medium

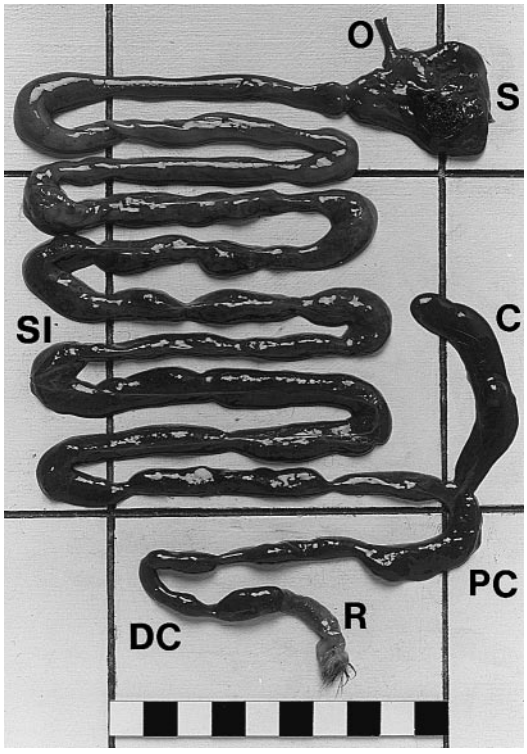

Fig. 3 Gastrointestinal tract of the northern brown bandicoot (*Isoodon macrourus*). (*O* oesophagus, *S* stomach, *SI* small intestine). Scale bar = 10 cm

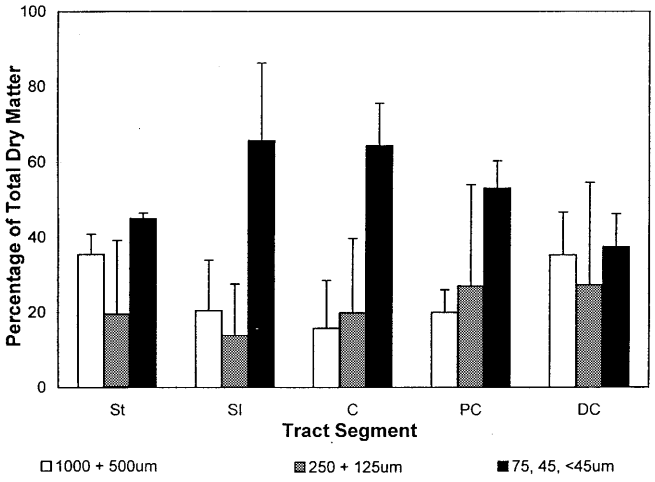

Fig. 4 Distribution of three size classes of particles along the gastrointestinal tract of four northern brown bandicoots road-killed in autumn/winter. *White bars* large particles (those retained on 1,000 μm and 500 μm sieves); *grey bars* medium particles (those that passed through the 500 μm sieve but were retained on 250 μm and 125 μm sieves); *black bars* small and very small particles (those that passed through the 125 μm sieve)

Discussion

Results from the several parts of this study support the notion that the gastrointestinal tract of the northern brown bandicoot, although relatively simple in its morphology (Fig. 3), has the capacity to process considerable amounts of plant material. The main responses to the inclusion of plant material in the basal mix were an increase in tract capacity, as suggested by the radiographic study, and selective retention of solutes and very small particles of digesta, with relatively rapid elimination of large particles; this allowed an increase in food intake such that the intake of digestible energy was maintained at the level of the insect-based diet.

The basal mix of a commercial small carnivore diet and agar was used with the northern brown bandicoots to ensure adequate dry matter intakes on both experimental diets. In a previous study with long-nosed bandicoots (*Perameles nasuta*; Moyle et al. 1995) the animals performed poorly on a diet of shredded sweet potato alone and lost body mass at the rate of $10\ g \cdot day^{-1}$. In the present study the animals on the milled lucerne hay and small carnivore mix maintained body mass. Nevertheless, the level of incorporation of plant material into the basal mix (24% air-dry) was sufficient to reduce the nutritional quality of the complete diet significantly below that of the insect-basal mix, in which mealworm larvae were included at a rate equivalent to the level of inclusion of the milled lucerne on a dry matter basis. Thus the lucerne-basal mix was significantly lower in total lipid and gross energy, lower in total nitrogen, but higher in fibre content (Table 1).

These differences in chemical composition were sufficient to result in significantly lower digestibilities of all

Table 4 Morphometrics of the digestive tract, and the dry matter percent of its contents, of the northern brown bandicoot (*I. macrourus*). Values are means ± SD (n = 4), with the percentage of total tract length, tissue mass and fresh digesta mass in parentheses

Parameter	Stomach	Small intestine	Caecum	Proximal colon	Distal colon
Length (cm)	6.1 ± 1.3 (4.1 ± 1.0)	105 ± 12 (70.4 ± 5.5)	8.8 ± 1.5 (5.9 ± 1.0)	9.9 ± 3.5 (6.6 ± 2.3)	19.1 ± 5.4 (13.0 ± 4.3)
Mass of fresh tissue (g)	3.9 ± 1.2 (18.2 ± 4.7)	13.6 ± 8.4 (56.4 ± 5.8)	0.9 ± 0.7 (3.6 ± 1.1)	1.3 ± 0.6 (6.2 ± 2.7)	3.7 ± 1.9 (15.5 ± 4.3)
Mass of fresh digesta (g)	9.7 ± 8.6 (27.0 ± 17.4)	17.3 ± 15.9 (43.6 ± 30.2)	2.0 ± 1.0 (8.1 ± 6.7)	2.4 ± 1.8 (7.2 ± 3.7)	3.4 ± 3.3 (14.1 ± 16.9)
Dry matter percent of contents	29.2 ± 3.7	24.2 ± 4.1	29.8 ± 3.1	30.2 ± 1.8	35.5 ± 5.2

constituents listed in Table 2 in bandicoots on the lucerne-basal mix. However, the digestive tract of *I. macrourus* had the capacity to accommodate the increased bulk of the lucerne-basal mix, allowing the animals to completely compensate for the lower nutritional quality of the plant material, with greater intakes of dry matter and gross energy, so that intakes of digestible energy were similar on the two diets.

The intakes of digestible energy on which both groups of *I. macrourus* maintained body mass (517 $kJ \cdot kg^{-0.75} \cdot day^{-1}$ and 545 $kJ \cdot kg^{-0.75} \cdot day^{-1}$ on the mealworm- and lucerne-basal mix respectively) must be close to the maintenance energy requirement for the species in captivity. Similarly, captive adult *P. nasuta* on a mealworm diet ad libitum ingested 511 $kJ \cdot kg^{-0.75} \cdot day^{-1}$ (Moyle et al. 1995). The only other estimates of the digestible energy requirement for maintenance of captive omnivorous or carnivorous marsupials are those of Green and Eberhard (1979) for the Tasmanian devil (*Sarcophilus harrisii*) and the eastern quoll (*Dasyurus viverinus*), both of which required 545 $kJ \cdot kg^{-0.75} \cdot day^{-1}$ for body mass balance. These are in good agreement with the intakes recorded for the captive bandicoots. At the dry matter intakes needed to meet their maintenance energy requirements, both groups of northern brown bandicoots were in positive nitrogen balance, so it is not possible to estimate a maintenance nitrogen requirement for the species; a series of diets of lower nitrogen content but of similar digestible energy content would be needed for this purpose (Hume 1999).

Two responses of the gastrointestinal tract allowed the bandicoots to ingest and process the 79% greater dry matter intake on the plant-basal mix compared to the insect-basal mix (Table 3). The first appeared to be an increase in digestive tract capacity, especially the hindgut, in the lucerne-basal mix animals. This difference is evident in the radiographs of two animals in Figs. 1 and 2, and is supported by the significantly greater apparent diameters of the colon in the radiographs from a total of five animals. Similar increases in the capacity of the hindgut have been reported in small herbivores such as voles and lemmings when switched to diets of higher fibre content (Gross et al. 1985; Lee and Huston 1993). Hammond (1993) showed that this was a phenomenon that also occurred in the field; in prairie voles (*Microtus ochrogaster*) the capacity of the hindgut was significantly greater in winter when their diet consisted mainly of senescent grasses relatively high in fibre content.

The second response of the bandicoots to the lucerne-basal mix was the significantly longer MRT of the solute marker than the large particle marker. This is strongly indicative of the presence of a colonic separation mechanism (CSM) (Björnhag 1987, 1994), resulting in the selective retention of fluid, solutes and very small particles (including bacteria) in the caecum of these animals. As well as concentrating fermentation in the caecum, a CSM facilitates the elimination of larger, less tractable particles from the tract, thereby minimising gut fill and permitting a higher rate of food intake (Stevens and Hume 1995). This is a digestive strategy found in several groups of small mammalian herbivores including lagomorphs, some rodents, and folivorous marsupial possums (Cork et al. 1999). It has also been demonstrated in another omnivore, the long-nosed bandicoot (Moyle et al. 1995). The presence of a CSM in these two species of bandicoots is likely to be an important factor in their ability to cope with a naturally variable diet which contains predominantly invertebrates in summer but greater proportions of plant and fungal material in winter, and to exploit nutritionally unpredictable habitats such as regenerating heathlands after wildfire (Stoddart and Braithwaite 1979; Quin 1988).

The absence of a significant difference in the MRTs of the two digesta markers on the insect-basal mix may reflect the need for a certain minimal level of indigestible dietary residues in the hindgut to provide a matrix of sufficient physical resistance for the CSM to be effective. Results from Björnhag (1989) support such a need; when the diet of rabbits was finely ground, there was no selective retention of the solute marker PEG (polyethylene glycol), whereas there was strong selective retention on the same diet when coarsely ground. The finding in our study of a significantly greater proportion of very small particles and solutes in the caecum than the distal colon of four animals road-killed in autumn and winter (Fig. 4) suggests that a CSM is operative in free-living northern brown bandicoots.

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