PASSAGE OF DIGESTA MARKERS IN TWO SPECIES OF ARBOREAL FOLIVOROUS MARSUPIALS—THE GREATER GLIDER (PETAUROIDES VOLANS) AND THE BRUSHTAIL POSSUM (TRICHOSURUS VULPECULA)[1]

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Retention times of markers of particulate (^{103}Ru-P) and fluid (^{51}Cr-EDTA) digesta were measured in greater gliders fed *Eucalyptus radiata* foliage and brushtail possums fed mostly *E. melliodora* foliage. Mean retention times (MRT) were long (ca. 50 h), in common with findings in other arboreal folivores, but there was no evidence of differential passage of either digesta marker in either species. Nonetheless, there were more fine digesta particles (<0.075 mm) in the cecum of the greater glider than in the feces, suggesting that fine particles were selectively retained in the hindgut. In contrast, all parts of the digestive tract of the brushtail possum contained a similar proportion of fine particles. The retention times of an alternative particle marker (^{51}Cr-mordanted large particles) were less than half those of ^{103}Ru-P, indicating that coarse digesta particles were excreted relatively rapidly from the hindgut of the greater glider and that ^{103}Ru-P was biased toward selectively retained fine particles. Selective retention of fine particles in the cecum of the greater glider may reduce the gut-filling effects of a high-fiber diet and may partly explain why this species eats a diet composed entirely of eucalypt foliage compared with the broader diet of the brushtail possum.

INTRODUCTION

The utilization of highly fibrous foods by herbivores is usually thought to depend on extended retention of digesta, allowing maximum opportunity for microbial fermentation. However, not all herbivores attempt to maximize digestion of the cell wall fraction of their diets. Some species, such as the giant panda (*Ailuropoda melanoleuca*) (Dierenfeld et al. 1982) and the horse (*Equus caballus*) (Janis 1976), appear to sacrifice maximal fiber digestibility for an increased intake of total digestible nutrients. In the giant panda in particular, digesta passage is rapid, allowing little time for degradation of plant fiber.

On the other hand, several arboreal folivores, including the koala (*Phascolarctos cinereus*) (Cork and Warner 1983) and three-toed sloth (*Bradypus variegatus*) (Montgomery and Sunquist 1978), retain digesta for long times, yet fiber digestibility is low. In the koala this may be due to the highly lignified nature of its *Eucalyptus* foliage diet or, alternatively, to the fact that the extended retention of particulate digesta recorded by Cork and Warner (1983) did not accurately reflect that of fiber because of selective retention of fine digesta particles. Whatever the reason, it is likely that interactions between feed intake and digesta passage will be more crucial in small herbivores such as the greater glider (1–1.5 kg) and brushtail possum (2–3 kg) because of relatively high mass-specific energy requirements.

The greater glider (*Petauroides volans*) and brushtail possum (*Trichosurus vulpecula*) are folivorous marsupials, and both are hindgut fermenters. In the greater glider, the cecum alone is enlarged, whereas in the brushtail possum both the cecum and proximal colon serve as a fermentation chamber (Hume 1982). Greater gliders feed almost exclusively on eucalypt leaf (Marples 1973) and are found only in the eucalypt forests and woodlands of eastern Australia. Although eucalypt foliage is an

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important part of the diet of the brushtail possum, at least in southeastern Australia, it is invariably supplemented with foliage from other species of trees and shrubs as well as with fruits, herbs, and grasses; the brushtail possum also has the widest distribution of any Australian marsupial (Kerle 1984).

Previous studies on digestion and digesta passage in the brushtail possum have been based on semipurified diets (Wellard and Hume 1981). Apart from the preliminary report by Hume, Foley, and Chilcott (1984), nothing has been published on digestive function in the greater glider. This paper reports on investigations into retention times and patterns of excretion of digesta markers in greater gliders and brushtail possums fed sole diets of *Eucalyptus* foliage.

MATERIAL AND METHODS

ANIMALS AND HUSBANDRY

Greater gliders were caught by hand during logging operations in forests dominated by New England blackbutt (*Eucalyptus andrewsii*) (Forest Type 161: Forestry Commission of N.S.W. 1965) in northern New South Wales. Brushtail possums were caught in wire-cage traps in woodland dominated by *E. caligninosa, E. melliodora, E. viminalis,* and *Angophora floribunda,* near Armidale.

Animals of both species were maintained in wire mesh metabolism cages (80 × 60 × 30 cm) in an air-conditioned room. Lighting was on a 12L:12D cycle, with a gradual change in intensity over 40 min to simulate dawn and dusk. Each metabolism cage was equipped with a perch and drinking water container. A plastic measuring cylinder was attached to the outside of the cage door and stems of branchlets pushed through the mesh so that they stood in water to maintain freshness. Greater gliders were also provided with a small wooden nest box fixed to an upper corner of the cage. A wire-mesh floor allowed any feces and urine voided in the box to be collected. Nest boxes provided for the brushtail possums were not used and so were removed.

Feces and urine were collected with a fine mesh screen and plastic-covered sloping tray under the cage. The efficiency of urine collection was determined by placing known volumes of freshly voided urine on the screens and trays and measuring the volume collected. This was 94%, and measured volumes were corrected accordingly. Animals of both species were weighed at the beginning and end of each period.

DIET AND FEEDING

After initial capture, both species were offered foliage from all the eucalypt species present in the areas in which they were captured. Greater gliders showed a strong preference for *E. radiata* foliage, while brushtail possums initially ate only minor amounts of all species offered. In the field, brushtail possums were observed feeding on *E. melliodora* leaf, and although foliage from these particular trees was eaten only sparingly in the animal house, *E. melliodora* seemed to offer the best prospect of forming the basis of a single-species diet. Branches of *E. radiata* and *E. melliodora* were collected in the field weekly, packed into plastic bags, transported to the University of New England campus, and stored until use at 8 C, with the cut ends standing in water to maintain freshness.

Since both species are nocturnal, fresh foliage was offered to each animal during the midafternoon, while the animals were resting. The following routine was adopted: The mass of uneaten leaves was measured and a sample taken for determination of dry-matter content. Sufficient small branchlets of fresh foliage were then stripped from larger branches for each animal plus some for a control and for determination of dry matter. The weight change of control branches was always less than 1%, and so corrections for water gain or loss in fed branches during each 24-h period were not necessary.

EXPERIMENTAL DESIGN

Three experiments were conducted to measure the passage of markers of various digesta fractions through the gut and the proportions of particles of different sizes in different parts of the gut of both species.

MARKERS

Both fluid and particulate digesta fractions were labeled. The complex of ^{51}Cr with ethylene diamine tetra-acetic acid (^{51}Cr-EDTA) associates principally with the fluid phase of digesta (Downes and McDonald 1964); ^{103}Ru-labeled Tris(1,10-

phenanthroline)-ruthenium (II) chloride complexed with phenanthroline (^{103}Ru-P) has a strong affinity for particulate digesta (Tan, Weston, and Hogan 1971). The degree of absorption of each marker from the gut was assessed by measuring the activity of ^{51}Cr and ^{103}Ru in urine. No assessment was made of possible retention of markers in animal tissues; this was found not to occur in another folivorous marsupial, the koala, by Cork and Warner (1983).

An alternative particle marker, ^{51}Cr-mordanted plant cell walls, was used in a later experiment with greater gliders. *E. radiata* foliage was ground and sieved to obtain 0.5–1.0 mm particles, 10 g of which were extracted with neutral detergent solution (Goering and Van Soest 1970) for 3 h, washed under running water for 3 days, and extracted with acetone. The particles were mordanted with chromium by the method of Uden, Collucci, and Van Soest (1980) but with the addition of $Na_2{}^{51}Cr_2O_7 \cdot 2H_2O$ (7.4 MBq/g original dry matter). Feces containing ^{51}Cr mordant were homogenized in distilled water and hot neutral detergent solution and centrifuged at 15,000 *g* for 15 min to test whether the marker stayed attached to the particles. Samples of urine were also counted to assess whether the marker was absorbed from the gut. In all experiments, feces and urine were collected and stored until background levels were reached to avoid radioactive contamination of the experimental area.

Retention times of digesta markers.—Five mature greater gliders (one male, four females) and six mature male brushtail possums were used. The greater gliders were fed solely on the mature foliage of *E. radiata* as described above. Three of the brushtail possums were offered a diet of 75% *E. melliodora,* 10% *E. viminalis,* 10% *E. saligna,* and 5% *Angophora floribunda* foliage. This mixed diet was necessary since feed intakes were variable when *E. melliodora* was the sole diet offered prior to the experiment. In a second experiment, three brushtail possums were offered *E. melliodora* foliage alone. Ten observations of the overall (mouth to anus) rate of passage of ^{103}Ru-P (0.1 MBq, 0.1 mg Ru) and ^{51}Cr-EDTA (0.3 MBq, 0.2 mg Cr) were made in greater gliders and seven (four on the mixed diet) were made with brushtail possums. The markers were administered as a pulse dose to the back of the mouth of each animal at about 1700 hours, just prior to feeding. Since not all the marker administered was swallowed the dose of marker was taken as the amount of each marker excreted during the subsequent 300 hours. By this time, fecal marker concentrations were less than 0.2% of peak values.

Feces collection trays were checked every 2 h for the first 72 h after dosing, then at 0600, 1800, and 2000 hours for the next 7 days and at 0600 and 1800 for the final 4 days. All fecal pellets were collected, weighed, and stored at −10 C. Urine was collected daily, bulked for each animal, and stored at −10 C.

Digesta particle size distribution.—Samples of digesta were collected from the stomach and hindgut of three greater gliders and three brushtail possums fed *E. radiata* and *E. melliodora* foliage, respectively, as part of the experiments on essential oil metabolism described by Foley (1984). These samples were stored in 10% formalin. The samples were fractionated through five screens (1.0, 0.5, 0.25, 0.125, and 0.075-mm mesh size) (Evans et al. 1973). The dry matter recovered on each sieve (and the residual) was expressed as a proportion of total dry matter recovered.

Retention of mordanted large particles in greater gliders.—Five mature greater gliders (one male, four females) were used. Approximately 0.5 g ^{51}Cr-mordanted large (0.5–1.0 mm) particles were administered as a pulse dose by stomach tube to prevent them from being chewed. At 1630 hours, the animal was sedated with Ketalar (Parke-Davis: 0.5 ml/kg), and the tube (0.8 mm O.D.) was lubricated with glycerine and passed down the esophagus into the stomach. The mordanted particles were flushed through the tube with 3–5 ml water. This was followed with 2 ml of a solution of ^{103}Ru-P (0.1 MBq) and a further 2–3 ml water. Sedation lasted 20–25 min, and all animals behaved normally after this time. There were no significant differences in the intake of dry matter in the weeks preceding and after sedation. Feces and urine samples were collected as described above.

ASSAY OF RADIOISOTOPES

Samples of feces were packed to a constant height in tared plastic gamma counting tubes. The activities of ^{51}Cr and ^{103}Ru

were assayed simultaneously by the method of Tan et al. (1971) in a Packard Autogamma Spectrometer (Model 3002, Packard Instrument Co., Illinois). Equivalent volumes of urine were treated similarly. Feces samples were then dried to constant weight at 60 C. After correction for background radiation, the results were expressed as counts/min/g dry matter (cpm).

STATISTICAL

The mean retention time (MRT) of all radioisotope markers was calculated from the formula: $MRT = (\Sigma m_i t_i)/\Sigma m_i$ (Warner 1981), where m_i is the amount of marker, m, excreted at time t_i, and t_i is the time in hours of fecal excretion after dose administration, taken as the midpoint time of the period during which the feces were collected.

The time for excretion of 5% (t_5), 50% (t_{50}), 95% (t_{95}), and 99% (t_{99}) of each marker was calculated from the relationship between percentage of dose remaining in the gut and time. The time at which marker concentration began to rise steeply was designated t_0 and the time at which the marker concentration was a peak, t_{max}.

Since no feces were usually excreted by either species during the light phase (0600–1800 hours), no attempt was made to apply a complete compartmental analysis to the data on fecal marker concentrations. However, it was clear that much of the variation in fecal concentration of ^{103}Ru-P and ^{51}Cr-EDTA beyond t_{max} could be accounted for by a single exponential function. Hence equations of this form were fitted to data beyond $t = 100$ h, and the inverse of the slope of this equation was designated t_{exp} (the fractional turnover rate). This was taken to be an estimate of the MRT of marker in the largest gut compartment (Warner 1981).

However, two exponential functions were needed to account for variation in the fecal concentration of the ^{51}Cr mordant beyond t_{max}. The first curve was fitted after removal of the effect of the second curve by a graphical curve-peeling method (Rescigno and Segre 1966). The two curves were postulated to represent physically distinct pools (see below). Comparisons between means were made using Student's t-test (Snedecor and Cochran 1967).

RESULTS

MARKER BEHAVIOR

In all experiments with greater gliders, only 2%–3% of the total fecal ^{51}Cr-EDTA counts and less than 0.2% of the total ^{103}Ru-P counts were detected in urine. There was a similar amount (1%–3%) of ^{51}Cr-EDTA counts in the urine of the brushtail possums but less than 0.1% of the ^{103}Ru-P counts when this species was fed solely on *E. melliodora*. No estimate of marker absorption was made when the brushtail possums were fed the mixed foliage diet.

Only 0.1% of the ^{51}Cr-cell wall mordant marker appeared in the urine. Homogenization of fecal samples, followed by high-speed centrifugation, showed that negligible counts were present in the supernatant. This eliminated the possibility that the marker occurred in a soluble form in the feces. These two pieces of evidence suggested that the ^{51}Cr remained attached to plant particles during passage through the gut. Less than 0.1% of ^{103}Ru-P was detected in urine when it was dosed simultaneously with ^{51}Cr mordant.

EXPERIMENT 1—MARKER EXCRETION AND RETENTION TIMES

Figures 1 and 2 show the pattern of fecal excretion of ^{103}Ru-P and ^{51}Cr-EDTA in one greater glider and one brushtail possum, respectively. In both species, the curves showed an initial rapid rise in fecal marker concentration followed by a prolonged period of steady decline.

Retention times in both species were long (tables 1, 2). There were no significant differences in any parameters of digesta passage between the brushtail possums when fed the mixed foliage diet and when fed *E. melliodora* foliage only. In the brushtail possums, there were no significant differences in MRT, t_5, t_{50}, t_{95}, and t_{99}, or t_{exp} between the two markers. However, t_{exp} of both ^{51}Cr-EDTA and ^{103}Ru-P was lower ($P < .001$) than the respective MRTs.

In the greater gliders there was no significant difference in either t_5 or the MRTs between the two markers. However, there was a trend toward greater separation of the two markers with increasing proportional excretion times. Thus, while the t_5 excretion times were similar, the t_{50} ($P < .05$), t_{95} ($P < .01$), and t_{99} ($P < .01$) ex-

cretion times were greater for ^{51}Cr-EDTA than for ^{103}Ru-P. The fractional turnover rate of both markers was lower ($P < .01$) than their respective MRTs.

EXPERIMENT 2—PARTICLE SIZE DISTRIBUTION (FIGS. 3, 4)

There were more fine (<0.075 mm) particles in the stomach and cecum of the greater gliders (fig. 3) than in the stomach, cecum, and proximal colon of the brushtail possums (fig. 4). Although the feces of each species contained similar proportions of fine particles, those of the brushtail possums contained more coarse (>0.50 mm) material. In fact, there were more large digesta particles in all gut segments of brushtail possums than of greater gliders. There was a greater ($P < .001$) proportion of fine (<0.075 mm) particles in the cecum of the greater glider compared with the feces, but the proportion of fine particles was similar in all digesta samples from the brushtail possum.

EXPERIMENT 3—EXCRETION OF TWO PARTICLE MARKERS

Plots of marker excretion versus time for both particle markers in one greater glider are shown in figure 5. The terminal portion of the log-transformed ^{103}Ru-P excretion curve was linear ($r = .993$), but the ^{51}Cr-

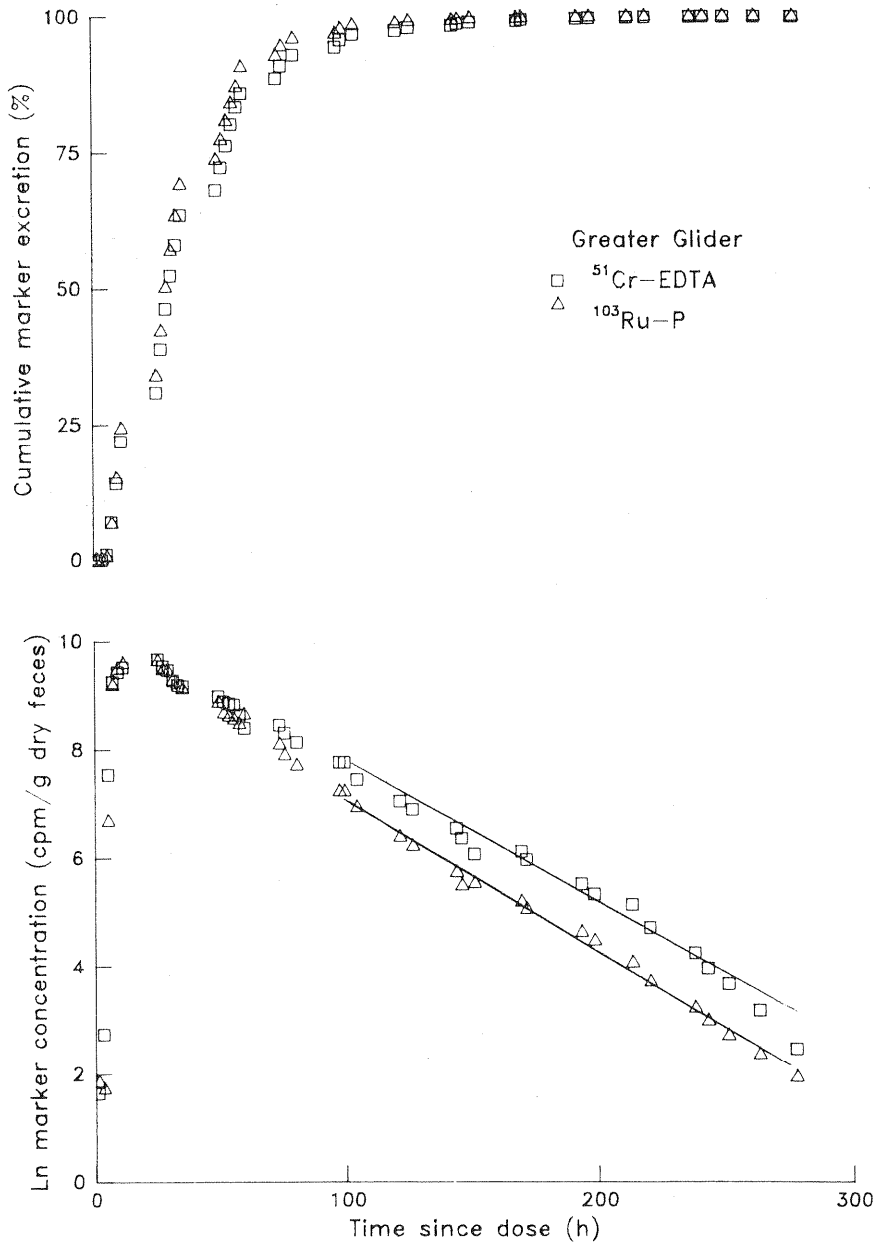

FIG. 1.—Cumulative fecal excretion and change in fecal concentration of ^{51}Cr and ^{103}Ru with time in one greater glider following an oral dose of ^{51}Cr-EDTA and ^{103}Ru-P. Regression lines fitted to curves (>100 h): ^{51}Cr: $y = 10.38 - .026x$; $r = .986$ ($P < .001$), RSD = .247; ^{103}Ru: $y = 9.86 - .028x$; $r = .997$ ($P < .001$), RSD = .137.

cell wall mordant excretion curve was curvilinear, with two distinct components. The first component, which accounted for about 99% of the dose, had a higher ($P < .001$) slope than the second component. The second component suggested a minor pool turning over slowly. The slope of this second component was not significantly different from that of the terminal portion of the ^{103}Ru-P excretion curve.

The computed MRT of the ^{51}Cr-cell wall mordant (table 3) was less than half that recorded for the ^{103}Ru-P marker ($P < .001$). Although the t_5 was similar, there was increasing divergence between the two markers at t_{50}, t_{95}, and t_{99}, with the ^{51}Cr-cell wall mordant being excreted more rapidly.

DISCUSSION

The times that both fluid and particle digesta markers were retained in the gut of both species were long compared with nearly all other herbivores, irrespective of body size, diet, or habitat (Warner 1981). This is remarkable in view of the small body sizes of the greater glider and brushtail possum. Long retention times seem to be a common feature of all arboreal folivores

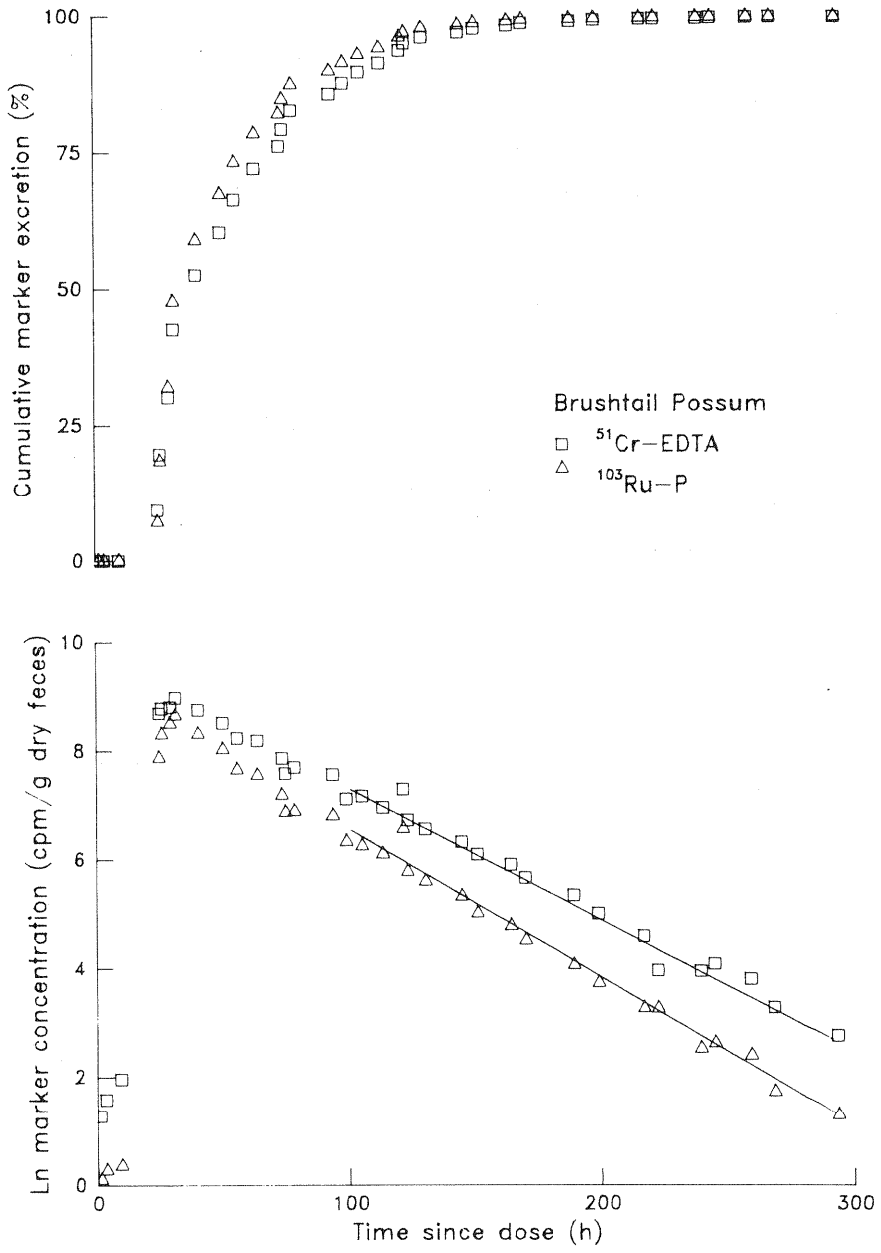

FIG. 2.—Cumulative fecal excretion and change in fecal concentration of ^{51}Cr and ^{103}Ru with time in one brushtail possum following an oral dose of ^{51}Cr-EDTA and ^{103}Ru-P. Regression lines fitted to curves (>100 h): ^{51}Cr: $y = 9.69 - .024x$; $r = .991$ ($P < .001$), RSD = .193; ^{103}Ru: $y = 9.22 - .027x$; $r = .993$ ($P < .001$), RSD = .198.

TABLE 1

MEASURES OF THE RETENTION OF SINGLE ORAL DOSES OF ^{51}Cr-EDTA AND ^{103}Ru-P IN GREATER GLIDERS

	MARKER	
	^{51}Cr-EDTA	^{103}Ru-P
t_0	9 ± 2	7 ± 3
t_5	8 ± 1	7 ± 1
t_{max}	18 ± 8	18 ± 7
MRT	50 ± 2	46 ± 2
t_{exp}	40 ± 2	32 ± 2
t_{50}	33 ± 1	27 ± 2
t_{95}	128 ± 5	105 ± 4
t_{99}	192 ± 7	161 ± 6

NOTE.—Body mass (kg) 1.05 ± .05. Estimated by total fecal collection (n = 10). Mean ± SE. Values in hours.

studied (Montgomery and Sunquist 1978; Milton 1981). In the case of the brushtail possum, MRTs are similarly long on artificial diets (Wellard and Hume 1981). Among the more folivorous marsupials, in the larger koala (8 kg) the MRT of fluid digesta is more than 200 h but that of the particulate digesta marker is only 100 h (Cork and Warner 1983). In the ringtail possum (*Pseudocheirus peregrinus*) (700-g body mass) there is also a marked separation of fluid and particulate digesta markers (Chilcott and Hume 1985). In this species the practice of cecotrophy (coprophagy) probably increases the difference in MRT between the two markers. In contrast, there was little evidence of differential passage of either digesta marker in either the greater glider or the brushtail possum.

Wellard and Hume (1981) also found no significant difference between the MRTs of ^{51}Cr-EDTA and ^{103}Ru-P in their study of brushtail possums and concluded that there was no selective retention in this species. The present data on particle size distribution in the brushtail possum gut support this conclusion. However, in the case of the greater glider, there was a significantly higher proportion of very fine particles in the cecum than in the feces, suggesting that selective retention of fine particles occurred in this organ. Fine particles consist mainly of bacterial and cellular debris and usually flow in suspension with fluid digesta (Björnhag 1972, 1981).

The lack of agreement between the data on marker MRTs and those on particle size distributions in greater gliders may be due to nonideal behavior of the two markers. For example, small amounts of ^{51}Cr-EDTA have been shown to bind to particles in the rumen of sheep (Warner 1969). However, a more likely explanation involves the nature of attachment of ^{103}Ru-P to particulate digesta. Ruthenium-103-P attachment depends on available surface area (Tan et al. 1971), and this results in a bias of the marker toward fine particles (Dixon, Kennelly, and Milligan 1983; Cork and Warner 1983; Egan et al. 1983; Dixon and Milligan 1985). This bias may also result from the migration of marker between digesta particles in the gut (Faichney and Griffiths 1978). Hence, if the majority of marker was attached to fine particles, and these flow in a suspension with fluid digesta (Björnhag 1972, 1981), any separation of digesta that occurs may not be evident from MRTs of ^{103}Ru-P and ^{51}Cr-EDTA.

However, the MRT of ^{51}Cr-mordanted large particles in the greater glider was less than half that of ^{103}Ru-P administered simultaneously. Chromium mordants are the most tenaciously bound and hence unquestionable particle marker (Ellis et al. 1982). This result therefore confirmed that large particles are eliminated more rapidly than fine particles and that there is a selective retention mechanism operant in the hindgut of the greater glider. There were

TABLE 2

MEASURES OF THE RETENTION OF SINGLE ORAL DOSES OF ^{51}Cr-EDTA AND ^{103}Ru-P IN BRUSHTAIL POSSUMS

	MARKER	
	^{51}Cr-EDTA	^{103}Ru-P
t_0	10 ± 3	10 ± 2
t_5	11 ± 2	12 ± 2
t_{max}	32 ± 3	32 ± 2
MRT	51 ± 3	49 ± 2
t_{exp}	33 ± 3	30 ± 2
t_{50}	32 ± 2	32 ± 2
t_{95}	109 ± 6	107 ± 4
t_{99}	163 ± 9	159 ± 6

NOTE.—Body mass (kg) 2.35 ± .15. Estimated by total fecal collection (n = 7). Mean ± SE. Values in hours.

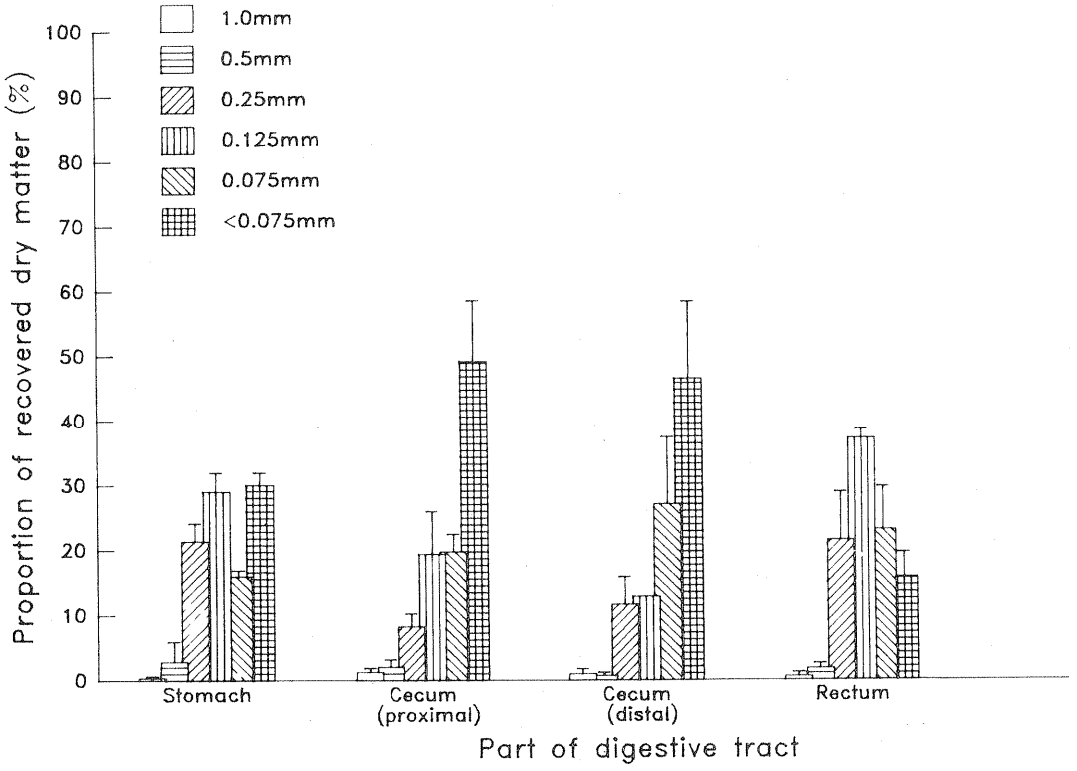

FIG. 3.—Proportions of digesta retained on sieves of different sizes from various gut segments of greater gliders. Mean ± SE of three animals.

two components of the excretion curve of the ^{51}Cr mordant. The first of these, which accounted for more than 99% of the dose, undoubtedly represented the excretion of large particles. The second component, only 0.5% of the dose, may have represented fine particles that were missed during sieving but were selectively retained in the

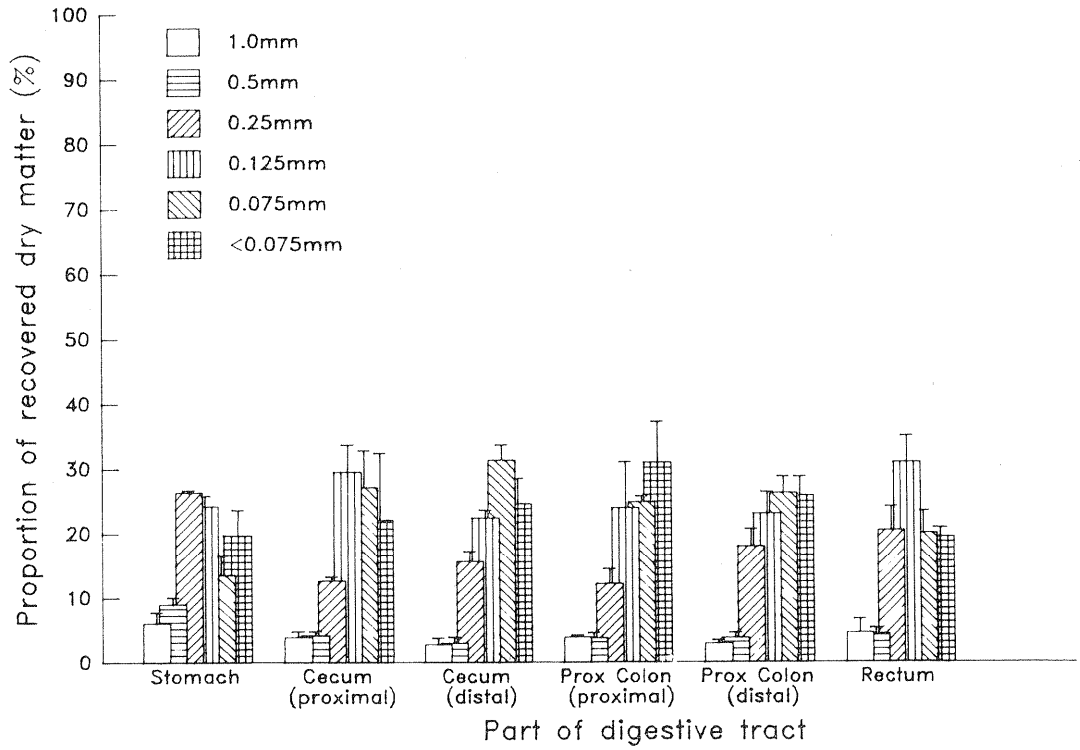

FIG. 4.—Proportions of digesta retained on sieves of different sizes from various gut segments of brushtail possums. Mean ± SE of three animals.

cecum. This conclusion is supported by the lack of significant difference between t_{exp} of this second component and t_{exp} of the ^{103}Ru-P curve (table 3). Thus particulate digesta flow in the greater glider involves the simultaneous turnover of at least two digesta pools.

While the mechanism of selective retention of fine particles was not investigated here, the present results showing the occurrence of a separation mechanism in the hindgut of the greater glider, but not of the brushtail possum, are consistent with other data on hindgut function in these species. Rübsamen et al. (1983) found that there was a large net influx of water into the proximal colon of the greater glider but not of the brushtail possum. Earlier, Björnhag (1972) had proposed that selective retention of fine particles in the rabbit cecum oc-

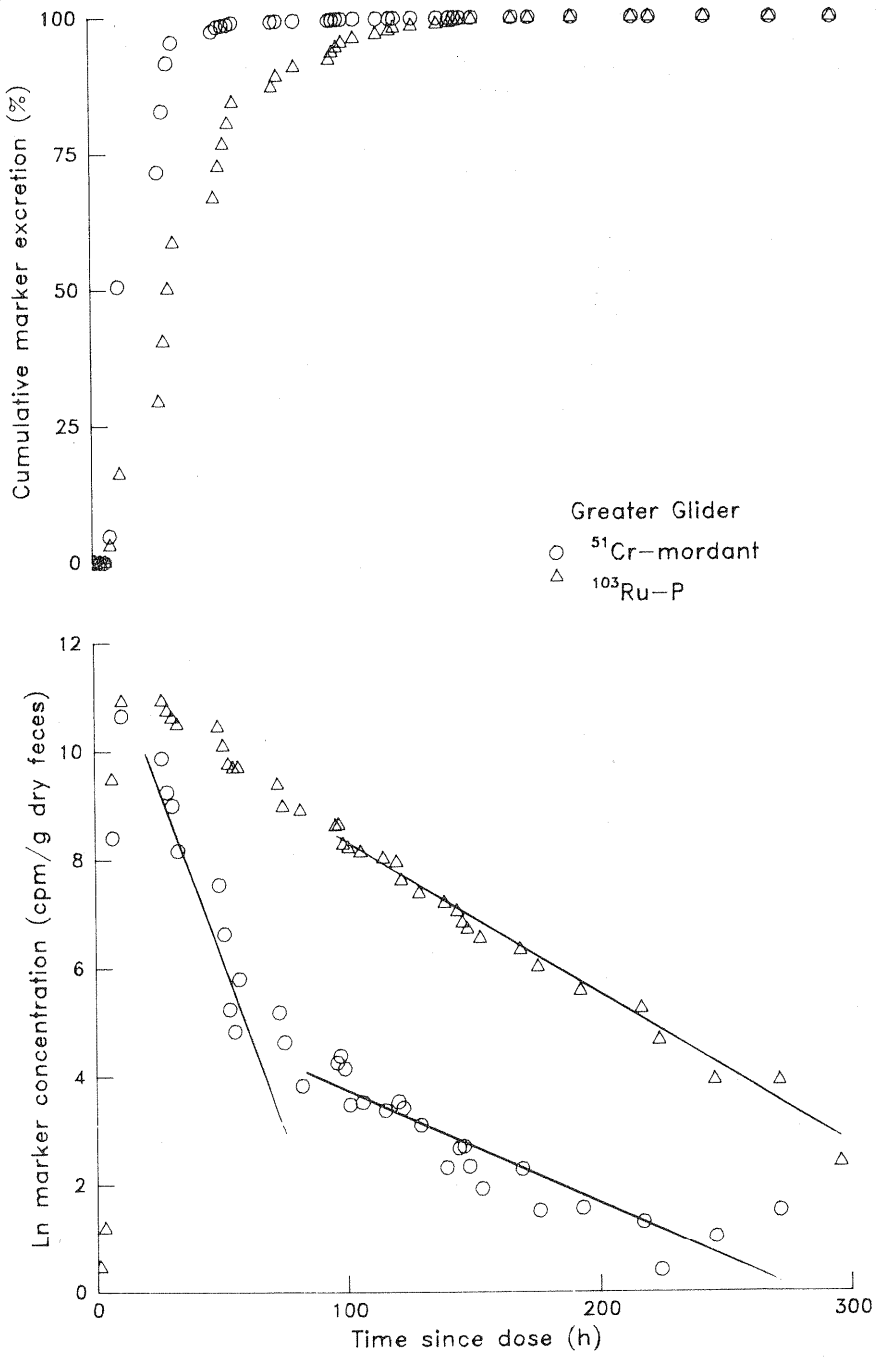

FIG. 5.—Cumulative fecal excretion and change in fecal concentration of ^{51}Cr and ^{103}Ru with time in one greater glider following an oral dose of ^{51}Cr-mordanted particles and ^{103}Ru-P. Regression lines: ^{51}Cr: (component 1 corrected for component 2) $y = 12.63 - .129x$; $r = .916$ ($P < .001$), RSD = 1.123; (component 2) $y = 5.84 - .021x$; $r = .927$ ($P < .001$), RSD = .515; ^{103}Ru: $y = 11.12 - .028x$; $r = .993$ ($P < .001$), RSD = .201.

TABLE 3

MEASURES OF THE RETENTION OF SINGLE ORAL DOSES OF A ^{51}Cr MORDANT OF *Eucalyptus radiata* CELL WALLS AND ^{103}Ru-P IN GREATER GLIDERS

	MARKER	
	^{51}Cr-mordant	^{103}Ru-P
t_0	9 ± 1	9 ± 1
t_5	5 ± 1	9 ± 1
t_{max}	20 ± 9	24 ± 6
MRT	23 ± 2	50 ± 3
t_{exp}^1	8 ± 1	...
t_{exp}^2	43 ± 3	38 ± 2
t_{50}	13 ± 1	34 ± 2
t_{95}	42 ± 4	120 ± 9
t_{99}	62 ± 6	180 ± 14

NOTE.—Body mass (kg) 1.14 ± .05. t_{exp}^1 and t_{exp}^2 are estimates of the MRT in the cecum of the two particle fractions represented by the two exponents of the ^{51}Cr-mordant excretion curve. Mean ± SE. Values in hours.

curred by retrograde transport from the proximal colon to the cecum, effected by retropulsive movements in the proximal colon together with the "rinsing" effect of fluid secreted into the proximal colon. While our results are consistent with this hypothesis, further work is needed to determine the mechanisms and controls of the separation process. Selective retention of fine particles provides several advantages for small herbivores. Since the majority of fine digesta particles are probably bacteria (Björnhag 1972; Sperber, Björnhag, and Ridderstrale 1983), selective retention may reduce fecal nitrogen losses in arboreal folivorous marsupials. The little evidence available on fecal nitrogen losses in arboreal marsupials supports this idea, since the loss of nondietary fecal nitrogen in brushtail possums is 20%–40% higher than in greater gliders (Foley 1984).

A second advantage of selective retention of fluid and fine particles may be to reduce the gut-filling effects of a bulk of indigestible fiber. That is, animals with a separation mechanism may effectively extend the upper limit of food intake without having to decrease overall digesta retention times. In view of this idea, it is interesting that brushtail possums have lower intakes of preferred eucalypt foliage than other folivorous marsupials (36 g dry matter $kgW^{-0.75} \cdot day^{-1}$ vs. 42–44 in koalas, greater gliders, and ringtail possums; Hume et al. 1984). Although the comparison is confounded by the different eucalypts fed to each species, the variation in intake cannot be explained by differences in body size or basal metabolic rate.

However, if the gut-filling effect of indigestible fiber is a major limit to food intake in the brushtail possum, it is unclear why this species seems unable to increase the rate of turnover of the whole hindgut contents. There are three possible reasons why this option may not be available to marsupials that feed on eucalypt foliage. The importance of short-chain fatty acids (SCFA) in electrolyte and water conservation in the hindgut is well established (Stevens 1978; Rübsamen et al. 1983); increasing the rate of turnover of digesta contents may lead to a lower rate of SCFA production and hence a lowered capacity for creating the osmotic gradients necessary for water reabsorption. Second, increasing the intake of readily digestible nutrients may involve a concomitant increase in the intake of eucalpyt leaf allelochemicals, and the energy cost of detoxification may exceed the energy gain from digestible nutrients. Third, O'Brien, Lomdahl, and Sanson (1986) have shown that microorganisms from the cecum of the ringtail possum can degrade complexes between tannins and leaf cytoplasts. Nothing is known of the kinetics of this process or its occurrence in other eucalypt foliage feeders, but it is likely to be slow and hence require long digesta retention times.

Clearly, further research is required to quantify the extent of digestion of plant cell walls and the contribution of SCFA to the energy balance of the greater glider and brushtail possum before arguments such as these can be considered further.

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