22. PHYSIOLOGICAL MECHANISMS OF FOLIAGE DIGESTION IN THE GREATER GLIDER AND RINGTAIL POSSUM (MARSUPIALIA: PSEUDOCHEIRIDAE)

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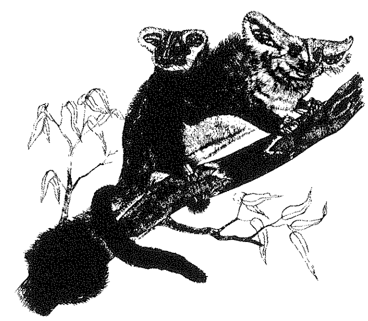
The diet of both the Greater Glider and Ringtail Possum is largely *Eucalyptus* foliage. Arboreal folivores appear to have low field metabolic rates (i.e. low total energy requirements) and therefore low feed intakes. These are adaptations advantageous to animals feeding on tree foliage which is generally of low nutritive value. Low feed intakes also mean that the ingestion of secondary compounds (xenobiotics) such as essential oils and phenolics is minimised.

Both pseudocheirids are hindgut fermenters, with a large caecum. The rate of passage of digesta through the gut is slow, and fluid digesta (along with fine particles) are selectively retained in the caecum, the less digestible coarse particles being eliminated relatively rapidly. The Ringtail Possum is coprophagic, or more specifically caecotrophic (i.e. soft faeces of high nutritive value derived from caecal contents are ingested from the cloaca). Caecotrophy increases the mean retention time of fluid digesta, maximises the digestibility of fibre in fine particles, and salvages caecal microbial products such as B-vitamins and protein. Consequently the maintenance nitrogen requirement of the Ringtail Possum is much lower than that of the non-coprophagic Greater Glider.

These metabolic and digestive adaptations are assessed in relation to the utilization by the Greater Glider and Ringtail Possum of *Eucalyptus* foliage as a principal or even sole source of nutrients.



Key Words: Field Metabolic Rate, Digestibility, *Eucalyptus* Foliage, Rate of Passage, Coprophagy.

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INTRODUCTION

ALTHOUGH *Eucalyptus* foliage is an abundant food resource, particulary in the tall open forests, and open forests of southeastern Australia, its utilization by arboreal folivorous marsupials is potentially limited by two sets of factors. The first of these is the presence of secondary compounds (xenobiotics); the second is a generally low nutritive value. The relative importance of these two potential limitations to utilization of *Eucalyptus* foliage is as yet imperfectly understood.

The Greater Glider *(Petauroides volans)* eats mainly the foliage of a number of *Eucalyptus* species, but does include some buds and flowers in its diet as well (Marples 1973). The Common Ringtail Possum *(Pseudocheirus peregrinus)* is equally as folivorous as the Greater Glider, but includes more non-eucalypt species in its diet (Thomson and Owen 1964). Both animals are of small body size; the mature weight of *P. volans* is about 1000-1200 g, that of *P. peregrinus* only 700 g. Diets containing high levels of lignified fibre are usually associated with animals of large body size. Such animals have high gut volume to body weight ratios and relatively low mass — specific metabolic rates and nutrient requirements (Hume and Warner 1980, Van Soest 1982). The question arising then is how such small animals as the Greater Glider and Ringtail Possum are adapted to the utilization of *Eucalyptus* foliage as their main or even sole source of nutrients.

ENERGETIC CONSIDERATIONS

Basal Metabolic Rate

McNab (1978) concluded that a low basal metabolic rate (BMR) was characteristic of folivorous mammals, marsupial and eutherian alike. The mean BMR of five eutherians classified by McNab (1978) as arboreal folivores was only 53% of that predicted from Kleiber's (1961) equation. Likewise the mean BMR of three marsupial folivores was only 59% of that predicted for eutherians, and 84% of that predicted for marsupials on the basis of Dawson and Hulbert's (1970) equation, although the BMR quoted by McNab (1978) for *Pseudocheirus* is higher than Kinnear and Shield's (1975) estimate, on which McNab's (1978) value is based. However, more recently it has been shown that the BMR of other eutherian folivores such as the Howler Monkey *(Alouatta palliata)* may not be below that expected

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for a eutherian (Milton *et al.* 1979). Similarly the BMR of other marsupial folivores is not necessarily less than that expected for a marsupial. This includes the two pseudocheirids covered in this review. In fact, Kinnear and Shield's (1975) reported BMR for the Ringtail Possum of 2.54 $W.kg^{-0.75}$ is close to the marsupial "mean" (Dawson and Hulbert 1970) of 2.33 $W.kg^{-0.75}$. Foley (1984) found a similar value for the Greater Glider (Table 1).

Field Metabolic Rate

Although comparisons of BMR are of physiological interest, it is the total energy cost of free existence, or field metabolic rate (FMR) which is of much greater ecological significance. Among marsupials FMR has been measured in two carnivores (*Antechinus* spp.), two omnivores, the Sugar Glider *(Petaurus breviceps)* and Leadbeater's Possum *(Gymnobelideus leadbeateri)*, and two arboreal folivores, the Koala and Greater Glider (Table 1). In the carnivores and omnivores the ratio of FMR to BMR is relatively high, while in the two arboreal folivores it is low. In eutherian folivores such as the Sloth *(Bradypus tridactylus)* and the Howler Monkey the ratio is similarly low. Thus it seems that a low FMR rather than a low BMR is a characteristic of folivorous mammals, at least in those so far studied.

Low energy and nutrient requirements are probably important adaptations to the relatively low nutritive value of *Eucalyptus* foliage. In contrast, carnivores and omnivores utilize much more readily digestible diets, and thus energy availability is not usually such a major limiting factor.

Xenobiotics

Another consequence of low enegy requirements, and therefore of relatively low feed intakes, is that the ingestion of xenobiotics is minimised. The xenobiotics most commonly associated with *Eucalyptus* foliage are the essential oils (Southwell 1978), but phenolic compounds are also present in significant amounts (Fox and Macauley 1977). Although it is likely that the folivorous marsupials have evolved with the enzymes required to detoxify and conjugate eucalypt xenobiotics, there is a metabolic cost incurred in these processes. Thus it is advantageous for folivores to minimise their intake of leaf material, and thus their ingestion of xenobiotics.

DIGESTIVE PHYSIOLOGY

Both the Greater Glider and Ringtail Possum are hindgut fermenters (Hume 1982). The digestive tracts of the two species are shown in Fig. 1. Both are characterised by a relatively small and simple stomach, but by a well developed caecum; there is little enlargement of the proximal colon, so that the hindgut fermentation is virtually confined to the caecum. This is in contrast to the Koala and the Brushtail Possum *(Trichosurus vulpecula)* in which both the caecum and proximal colon are enlarged to form an extensive fermentation chamber (Hume 1982,

Table 1. Basal and field metabolic rates of arboreal folivores compared with other groups of marsupials. Metabolic rates in $W.\ kg^{-0.75}$.

	BMR	FMR	FMR/BMR	Reference
Carnivores				
Antechinus stuartii	3·30	14·85	4·5	1
Antechinus swainsonii	2·33	9·87	4·2	2
Omnivores				
Petaurus breviceps	2·31	10·86	4·5	3
Gymnobelideus leadbeateri	2·10	12·15	5·8	4
Folivores				
Phascolarctos cinereus	1·75	4·55	2·6	5
Petauroides volans	2·37	6·64	2·8	6

1 Nagy, Seymour, Lee and Braithwaite (1977); 2 Cowan, O'Riodan and Cowan (1974); 3 Smith (1980); 4 Smith, Nagy, Fleming and Green (1982); 5 K. A. Nagy and R. W. Martin, personal communication; 6 Foley (1984).

A low FMR can be expected to confer several advantages on arboreal folivores. The first is that, related to a low FMR and therefore low maintenance requirements for energy, requirements for other nutrients such as water and protein may also be expected to be low. This has been shown to be the case for water in the Koala (Degabriele *et al.* 1978) and for nitrogen in the Ringtail Possum (Chilcott and Hume 1984a).

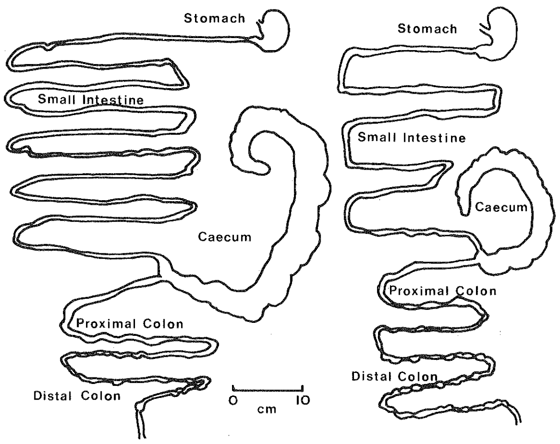

Fig. 1. The digestive tract of the Greater Glider *(Petauroides volans)* (left) and the Ringtail Possum *(Pseudocheirus peregrinus)* (right).

Cork and Hume 1983). The muscles of the walls of the caecum of the Greater Glider and Ringtail Possum are organised into longitudinal bands, taeniae, between which are found non-permanent sacculations or haustra. Sequential contractions of the wall result in movement of the haustra and mixing and propulsion of the digesta.

In our studies of the nutrition and digestive physiology of the Greater Glider and Ringtail Possum we have been able to maintain each species on a sole diet of *Eucalyptus* foliage for periods of up to three years. However, their food preferences are highly specific, and consequently the diet was not common between the two species, being *E. radiata* for the Greater Glider and *E. andrewsii* for the Ringtail Possum. The possibility therefore exists that an unknown part of any differences found between the two folivores may be dietary in origin. Table 2 contains data on a number of aspects of the digestive physiology of the two pseudocheirids.

Foliage Intake and Digestibility

Daily dry matter intakes by both the Greater Glider and Ringtail Possum were lower on a metabolic body weight basis than those recorded for most species of macropodine marsupial fed chopped lucerne hay (Hume 1982). The apparent digestibility of the dry matter of eucalypt leaves (59%) was similar to that of the chopped lucerne hay by the macropodines (55 to 62%). Thus the lower dry matter intakes of the pseudocheirids reflect lower energy requirements of the two arboreal folivores, at least in captivity. Although the apparent digestibility of dry matter was similar between the two pseudocheirids, digestibility of both neutral-detergent fibre and acid-detergent fibre was higher in the Ringtail Possum.

Rate of Passage of Digesta

Both the low dry matter intakes and the large size of the caecum of the two pseudocheirids can be used to explain the slow rate of passage of digesta through the gut in the two species. The mean retention time (MRT) (i.e. the average time spent by each digesta fraction within the gut) of fluid (marked with ^{51}Cr-EDTA) in both species was longer than values recorded in much larger herbivores such as sheep and goats (38-39 h) (Van Soest 1982) and Eastern Grey Kangaroos, *Macropus giganteus* (14 h) (Dellow 1982); in general smaller animals exhibit shorter MRT's.

Long MRT's have also been reported in two other folivorous marsupials, the Brushtail Possum, *Trichosurus vulpecula,* fed semi-purified diets (Wellard and Hume 1981) and the Koala fed *E. punctata* foliage (Cork and Warner 1983). Long MRT's thus appear to be characteristic of arboreal folivorous marsupials, and are likely to be an important adaptation to the poorly digestible *Eucalptus* foliage on which they feed. That is, for the animals to extract sufficient nutrients from eucalypt leaves the foliage must

Table 2. Digestion and digesta passage in the Greater Glider and Ringtail Possum.

	Greater Glider	Ringtail Possum
Body weight (kg)	1·1	0·7
Diet	*E. radiata*	*E. andrewsii*
Dry matter intake ($g/kg^{0·75}/d$)	44	42
Apparent digestibility of dry matter (%)	59	59
Digestibility of neutral-detergent fibre (%)	34	45
Digestibility of acid-detergent fibre (%)	32	44
Mean retention time (h):		
Fluid digesta (^{51}Cr-EDTA)	54	70
Particulate digesta (^{103}Ru-Phenanthroline)	51	37
Maintenance nitrogen requirement ($mg/kg^{0·75}d$)	560	290 (620)*

* Estimate in the absence of caecotrophy.

remain in the digestive tract for extended periods of time. The alternative strategy, of increasing leaf intake and reducing passage time, may not be available to them because of the increased load of xenobiotics that higher feed intakes would entail.

Selective Retention of Fluid Digesta

The other important feature of the MRT data in Table 2 is that clearly in the Ringtail Possum there is selective retention of fluid (and fine particles), with more rapid elimination of coarse particles (marked with ^{103}Ru-Phenanthroline); fine particles (which are potentially more digestible because of their greater surface area:volume ratio) tend to move with fluid digesta (Van Soest 1982). Although there was little difference in the MRT of fluid and particulate digesta in the Greater Glider, the distribution of particles of different sizes along the gut showed that selective retention of fine particles also occurs in this folivore (Foley 1984). That is, ^{103}Ru-Phenanthroline tends to overestimate the MRT of particulate digesta because it migrates from small to larger particles as particles are digested (Van Soest 1982).

The particle size distribution data referred to above also suggest that in both the Greater Glider and the Ringtail Possum selective retention of fine particles (and fluid) occurs in the caecum. In the Koala selective retention also occurs, but both the caecum and proximal colon are involved (Cork and Warner 1983). Thus selective retention in the hindgut of the potentially most digestible parts of the digesta appears to be another adaptation to the utilization of *Eucalyptus* foliage by arboreal marsupials.

Coprophagy

The Ringtail Possum, the smallest arboreal folivore among the Marsupialia, was found to possess a further digestive adaptation, coprophagy (ingestion of faeces). This was clearly demonstrated by direct observation and by fitting captive animals with plastic collars which prevented them from taking caecotrophes (soft faeces of high nutritive value derived for caecal contents) from the cloaca (Chilcott and Hume 1984). The nutritional consequences of coprophagy (or more specifically "caecotrophy") to the Ringtail were quantitated, and were considered to be two-fold. First, recycling of fine digesta particles through the gut, by increasing substantially the time available for microbial fermentation of this fibre in the caecum, maximises fibre digestibility. This is thought to at least partly explain the higher fibre digestibilities in the Ringtail than in the Greater Glider, in which coprophagy has not been observed (Table 2). Caecotrophy also tends to increase the MRT of fluid digesta; this explains the difference in fluid MRT's found between the two pseudocheirids (Table 2).

The second significant advantage of caecotrophy is the recycling of microbial products (e.g. protein and B-vitamins), synthesised in the caecum, which would otherwise be lost to the animal. The relatively low maintenance nitrogen requirement of the Ringtail Possum (Table 2) is directly related to caecotrophy. Chilcott and Hume (1985) have calculated that, in the absence of caecotrophy, the maintenance nitrogen requirement of the Ringtail would be doubled to be similar to that of the Greater Glider. The lower requirement of the Ringtail means that this species can subsist on *E. andrewsii* foliage which is of lower nitrogen content (1.1%) than the *E. radiata* foliage (1.9% nitrogen) consumed by the Greater Glider in our studies.

CONCLUSIONS

Adaptations to folivory include both metabolic (energetic) and digestive factors. Tree foliage, particulary *Eucalyptus* spp., is of generally low nutritive value. It is therefore advantageous for animals utilizing foliage as their principal or sole source of nutrients to be frugal in their expenditure of energy. Some folivorous mammals exhibit low basal metabolic rates, but more importantly most have low total energy expenditures. Low field metabolic rates are reflected in low feed intakes, which offer an added advantage in that the ingestion of xenobiotics contained in the foliage of many tree species is minimised.

Digestive adaptations to folivory in the Greater Glider and Ringtail Possum include considerable development of the hindgut, primarily the caecum, into a fermentation chamber, low levels of foliage intake, slow rates of passage of digesta through the gut, and selective retention in the caecum of fluid and fine particulate digesta. Selective retention increases the oppurtunity for fermentation of the potentially more digestible components of the diet, the less digestible coarse particles being eliminated relatively rapidly.

In the Ringtail Possum the combination of selective retention of digesta in the caecum with caecotrophy further increases the oppurtunity for microbial degradation of fine particles, as well as salvaging products of the microbial fermentation such as protein and B-vitamins which would otherwise be lost to the animal.

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