NITROGEN REQUIREMENTS AND UREA METABOLISM IN TWO ARBOREAL MARSUPIALS, THE GREATER GLIDER (PETAUROIDES VOLANS) AND THE BRUSHTAIL POSSUM (TRICHOSURUS VULPECULA), FED EUCALYPTUS FOLIAGE[1]

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Maintenance nitrogen requirements (MNRs) were determined in greater gliders fed *Eucalyptus radiata* foliage and in brushtail possums fed *E. melliodora* foliage. Both species had high nitrogen requirements compared with most other marsupial species; the greater glider required 0.56 g truly digestible nitrogen $\cdot$ kg$^{-0.75}$ $\cdot$ day^{-1} and the brushtail possum 0.42 g $\cdot$ kg$^{-0.75}$ $\cdot$ day^{-1} to remain in zero nitrogen balance. The loss of nitrogen as ammonia in the urine was the major reason for the high nitrogen requirement of the greater glider. In contrast, excretion of fecal nitrogen, especially nondietary fecal nitrogen (NDFN), was responsible for the higher MNR of the brushtail possum, compared with previous estimates. This high NDFN excretion was partly attributable to the lack of selective retention of fine particles, including microbial cells, in the hindgut. Both species recycled large proportions of endogenously synthesized urea to the gut, but urea-synthesis rates were low compared with those found in other herbivores fed low-protein diets.

INTRODUCTION

The relatively low nitrogen content of tree foliage, including that of *Eucalyptus* spp., has led several authors to speculate on the ability of small folivores to meet their protein requirements (Hladik 1978; Milton 1979; Ullrey, Robinson, and Whetter 1981; Cork and Pahl 1984). While little is known of the biological value of eucalypt-leaf nitrogen, several factors may reduce its availability to folivores. These include the presence of tannins (Fox and Macauley 1977; Macauley and Fox 1980) and the possibility that nitrogenous compounds are needed for the detoxification of other allelochemicals (Bolliger and Whitten 1940; Martin 1973). However, several species of arboreal marsupials, including the koala (*Phascolarctos*

cinereus) and greater glider (*Petauroides volans*), feed almost exclusively on eucalypt foliage (Marples 1973; Martin 1985). Others, such as the brushtail possum (*Trichosurus vulpecula*), supplement a variable intake of eucalypt foliage with leaves from other species of trees and shrubs, as well as fruits, flowers, and herbage (Kerle 1984). It is not known whether the broader diet chosen by the brushtail reflects a need to consume items of higher nitrogen content.

Braithwaite, Dudzinski, and Turner (1983) showed that high levels of foliage nutrients (particularly nitrogen, phosphorus, and potassium) were closely correlated to the density of arboreal marsupials in hardwood forests in southern New South Wales. Similarly, Degabriele (1981, 1983) has surmised that the abundance of the koala is limited by a shortage of high-nitrogen-content food. If nitrogen is a limiting nutrient for eucalypt-feeding marsupials, they can be expected to possess adaptations for conserving nitrogen. In particular, the recycling of endogenously synthesized urea to the hindgut, the principal site of microbial fermentation in eucalypt-feeding marsupials (Hume 1982), is likely to be important.

This paper describes the estimation of the maintenance nitrogen requirements

(MNRs) of greater gliders and brushtail possums fed eucalypt foliage. The kinetics of urea metabolism in the two species were also examined, using [^{14}C] urea as a tracer. In greater gliders, urea was not the principal nitrogenous excretory product in urine. Therefore, the composition of the urine of the greater glider and some of the factors influencing the types of nitrogenous products found in the urine were examined in more detail.

MATERIAL AND METHODS

MAINTENANCE NITROGEN REQUIREMENTS (MNRs)

Nitrogen intake, excretion, and balance were determined in a series of experiments that included all seasons of the year. A total of 13 adult greater gliders were used, including a core group of five animals (four females, one male) that was common to all eight experiments except one. *Eucalyptus radiata* foliage was the sole diet throughout. Seven adult male brushtail possums were used in a total of five experiments, although a core group of three animals ate the *E. melliodora* foliage most consistently. Details of the animals and their husbandry are given in Foley and Hume (1987).

In each experiment, feed intakes of all animals were stable for at least 10 days prior to a 7-day collection period. Procedures followed in the cutting, storage, feeding, and sampling of the foliage were as described by Foley and Hume (1987). During collection periods, feces were collected daily, weighed, and then stored at −10 C. Urine was collected into plastic bottles containing sufficient glacial acetic acid to maintain pH below 3; the volume was measured, and the urine was then stored at −10 C. The efficiency of urine collection was determined by pouring known volumes of fresh urine onto the collection apparatus and measuring the volumes recovered in the plastic bottle. Recovery was 95%. This was used to adjust urine volumes during collection periods. There was no significant difference between the recovered and original urine in the concentrations of total nitrogen or urea nitrogen.

The MNR was calculated by linear regression of nitrogen balance on nitrogen intake. The MNR was taken as that nitrogen intake that supported zero nitrogen balance (Hume 1986).

UREA KINETICS

The kinetics of [^{14}C] urea were determined in two periods, with five greater gliders and three brushtail possums per period. At the end of a 7-day measurement of nitrogen balance, each animal was injected intramuscularly (at 1400 hours) with about 0.37 MBq [^{14}C] urea. The exact dose was determined by weighing the syringe before and after injection. The decline in specific radioactivity of [^{14}C] urea was followed in urine rather than in plasma, since the low levels of plasma urea in both species would have necessitated the collection of excessively large blood samples. This procedure has been shown to be valid in rabbits (Regoeczi et al. 1965). Since bladder catheterization was not practicable in either species, collection of samples depended on the natural frequency of urination. This varied between four and 12 times per day in the greater gliders and between four and eight times per day in the brushtail possums.

Urine collection bottles were checked every 30 min for 48 h after injection. If urine was present, its volume was measured before being acidified with glacial acetic acid to pH 2–3, and it was stored at −10 C. The collection apparatus was always replaced with a clean unit. Urine volumes were corrected for the volume lost on the collection trays as described above, and the time of urination was taken as the midpoint between collections.

COMPOSITION OF URINARY NITROGEN

Urine samples were collected directly into clean plastic vials from the cloaca of five greater gliders and four brushtail possums feeding on *E. radiata* and *E. melliodora* foliage, respectively. The vials were immediately plunged into liquid nitrogen. These samples were analyzed for total nitrogen, urea, creatinine, allantoin, and uric acid. Blood samples were collected at the same time from the greater gliders by cutting and aspirating a vein on the outer edge of the gliding membrane and from the brushtail possums by cardiac puncture. The plasma was separated by centrifugation and analyzed for urea concentration.

ALTERATION OF GREATER GLIDER URINARY UREA:AMMONIA RATIO

Six greater gliders were randomly allocated to two groups. One group was offered *E. radiata* foliage, the other *Angophora floribunda* foliage. All animals' drinking water was replaced with 60 ml of a 10% glucose solution to ensure that any increases in urinary urea excretion observed were not due to body protein catabolism. Discrete urine samples were collected daily at 1600 hours for 3 days. The treatments were then reversed, and urine was collected for a further 3 days.

ANALYSIS

The dry-matter content of feeds, feed residues, and feces was determined by oven-drying portions to constant weight at 105 C. Separate samples of feed and feed residues were freeze-dried and feces oven-dried at 55 C for chemical analysis. Total nitrogen was determined by the Kjeldahl technique of Ivan, Clack, and White (1974). Total nonstructural carbohydrates were extracted from dried, ground leaf with 0.2 N H_2SO_4, and the extract was analyzed for glucose (Luchsinger and Cornesky 1962). Crude lipid was measured gravimetrically after extraction in 2:1 (v/v) chloroform:methanol (Folch, Lees, and Sloane-Stanley 1957). Essential oils were extracted from frozen leaves by steam distillation (Hughes 1970) in an all-glass apparatus. Total phenolics were extracted from dried, ground leaves with hot 50% aqueous methanol and the extract analyzed for total phenolic content by the method of Folin and Ciocalteau (1927). The methods of Goering and Van Soest (1970) were used to determine fiber and lignin contents. Gross energy was determined in a Gallenkamp adiabatic bomb calorimeter. Amino acids were determined on a Dionex-D300 Amino Acid Analyser.

The urea-nitrogen content of urine and plasma was determined with an automated diacetyl monoxime method (Marsh, Fingerhut, and Miller 1965). Ammonia-nitrogen in urine was determined by steam distillation after addition of saturated sodium tetraborate solution. The concentration of creatinine in urine samples was determined by the method of Folin and Wu (1919) and allantoin by the method of Young and

Conway (1942), using potassium allantoate as a standard. The uric acid content of urine was determined using an automated version of the method described by Brown (1945). Nondietary fecal nitrogen (NDFN) was determined by the method of Mason (1969). NDFN assumes that the only undigested dietary nitrogen in feces is that associated with plant cell walls; the assumption has been shown to be valid in ruminants (Van Soest 1967) and equines (Fonnesbeck 1969) on forage diets. It is preferred to the term metabolic fecal nitrogen (MFN) for herbivores. MFN is assumed to be endogenous in origin, but, in herbivores, a major part of MFN consists of bacterial residues. These must contain nitrogen of both endogenous and exogenous (dietary) origin.

The activity of [^{14}C] in urine was assayed in acidified samples after bubbling CO_2 through the samples to ensure that none of the [^{14}C] label was present as bicarbonate. Preliminary experiments showed that less than 0.1% of added [^{14}C] bicarbonate remained in urine after acidification and CO_2 treatments. Diluted urine (1:10) and injection solutions were counted in scintillation fluid (Chapman and Marcroft 1971) in a Packard Model 3255 Liquid Scintillation Spectrometer. Samples and injection solutions were corrected for quenching by the automatic external standards method.

STATISTICS

Parameters of urea kinetics were calculated using the procedures described by Cocimano and Leng (1967) and Robbins et al. (1974). The specific radioactivity of urinary urea (SR) and the rate of decline in SR were calculated from the linear regression of $\log_e$ SR versus time after equilibration of [^{14}C] urea with the body urea pool. Parameters of nitrogen and urea metabolism were expressed on a metabolic body-mass basis ($kg^{0.75}$) to facilitate comparisons between animals of different species (Kleiber 1961).

RESULTS

COMPOSITION OF *Eucalyptus* FOLIAGE

There were no distinct seasonal trends in levels of any chemical component of either *Eucalyptus radiata* or *E. melliodora*. The

TABLE 1

COMPOSITION OF *Eucalyptus radiata* FOLIAGE EATEN BY GREATER GLIDERS AND
E. melliodora FOLIAGE EATEN BY BRUSHTAIL POSSUMS

| | DRY MATTER (%) | |
COMPONENT	E. radiata	E. melliodora
Organic matter	98.0 ± .4	96.4 ± .3
Total nitrogen	1.9 ± .1	1.6 ± .1
Total nonstructural carbohydrate	8.2 ± .6	9.6 ± .7
Crude lipid	14.3 ± .4	11.0 ± .1
Essential oils	11.0 ± 2.2	1.1 ± .2
Total phenolics	17.5 ± 1.9	26.3 ± 1.2
Neutral-detergent fiber	33.4 ± 1.2	28.7 ± .5
Acid-detergent fiber	31.5 ± 1.6	23.6 ± .5
Acid lignin	16.6 ± 1.1	9.8 ± .5
Gross energy (kJ·g^{-1})	23.8 ± .3	21.0 ± .1

NOTE.—Values for chemical components are means ± SE from eight experiments (*E. radiata*) and five experiments (*E. melliodora*).

values in table 1 are thus the means from eight experiments on greater gliders and five experiments on brushtail possums. Amino acid values (table 2) are from composite samples of the two eucalypt species. The principal difference between the species was the higher essential oil content of *E. radiata*. The total nitrogen contents of the two species were similar, and their amino acid contents were almost identical.

NITROGEN METABOLISM

The higher nitrogen intakes of the greater gliders were principally a reflection of their higher dry-matter intakes compared with those of the brushtail possums (table 3). The major source of nitrogen loss in greater gliders was via the urine, being 48% of nitrogen intake. There were significant ($P < .001$) relationships between urinary nitrogen excretion and nitrogen intake ($y = 0.200 + 0.236x$, $r = .470$, residual standard deviation [RSD] = 0.058) and between fecal nitrogen excretion and nitrogen intake ($y = 0.226 + 0.155x$, $r = .491$, RSD = 0.360) in greater gliders.

In the brushtail possums, fecal nitrogen excretion was the major source of nitrogen loss, being 67% of nitrogen intake. There was a significant ($P < .001$) relationship between fecal nitrogen excretion and nitrogen intake ($y = 0.007 + 0.676x$, $r = .725$, RSD = 0.490) but not between urinary nitrogen excretion and nitrogen intake. Mean nitrogen balance was positive in both species but

negative balances were recorded in some experiments.

The NDFN excretion on a metabolic body-mass basis was similar in the two species, but, because of lower feed intakes by the brushtail possums, NDFN on a dry-matter-intake basis was higher in this species.

The MNRs were estimated from regressions of nitrogen balance on nitrogen intake (fig. 1). On a dietary basis, the MNR of the

TABLE 2

AMINO ACID COMPOSITION OF COMPOSITE SAMPLES OF *Eucalyptus radiata* AND *E. melliodora* FOLIAGE

| | mg·g^{-1} PROTEIN | |
	E. radiata	E. melliodora
Leucine	97	96
Isoleucine	51	52
Valine	65	67
Methionine	13	12
Phenylalanine	65	65
Threonine	51	52
Lysine	62	72
Histidine	23	30
Arginine	68	75
Serine	50	50
Alanine	65	67
Aspartic acid	95	96
Glycine	59	59
Tyrosine	40	43
Cystine	13	15
Glutamic acid	108	109

TABLE 3

NITROGEN INTAKE AND EXCRETION IN GREATER GLIDERS AND BRUSHTAIL POSSUMS FED
Eucalyptus radiata AND *E. melliodora* FOLIAGE, RESPECTIVELY

	Greater Glider ($n = 48$)	Brushtail Possum ($n = 20$)
Mean body mass (kg)	$1.13 \pm .02$	$2.48 \pm .15$
Dry-matter intake	$44.1 \pm .7$	35.5 ± 1.1
Nitrogen intake	$.84 \pm .02$	$.58 \pm .02$
Fecal nitrogen	$.36 \pm .01$	$.39 \pm .02$
Apparent digestibility of nitrogen (%) ...	$57.0 \pm .9$	33.3 ± 1.8
Nondietary fecal nitrogen (NDFN)	$.22 \pm .01$	$.26 \pm .01$
NDFN ($g \cdot kg^{-1}$ DM intake)	$5.0 \pm .1$	$7.4 \pm .1$
Truly digestible nitrogen intake	$.71 \pm .02$	$.44 \pm .00$
Urinary nitrogen	$.40 \pm .01$	$.16 \pm .01$
Nitrogen balance	$+.09 \pm .01$	$+.03 \pm .01$

NOTE.—Values are means $\pm$ SE and are expressed as $g \cdot kg^{-0.75} \cdot day^{-1}$ unless otherwise indicated.

greater gliders was 0.70 $g \cdot kg^{-0.75} \cdot day^{-1}$ and of the brushtail possums 0.56. Estimates of NDFN on a dry-matter-intake basis were used to calculate intakes of truly digestible nitrogen, in the same way that Mitchell and Bert (1954) used MFN. The MNRs calculated on the basis of truly digestible nitrogen were 0.56 $g \cdot kg^{-0.75} \cdot day^{-1}$ for the greater gliders and 0.42 for the brushtail possums.

Although there was a significant relationship between nitrogen balance and digestible-energy intake (greater gliders: $y = 0.450 + 0.882x$, $r = 0.792$ [$P < .01$], RSD = 0.060; brushtail possums: $y = -0.177 + 0.550x$, $r = 0.460$ [$P < .05$], RSD = 0.063), the mean intake of digestible energy by the greater gliders was 0.58 $MJ \cdot kg^{-0.75} \cdot day^{-1}$, the same as their maintenance requirement on *E. radiata* foliage estimated by Foley (1984). This suggests that the greater gliders in the present study were close to energy balance. No estimate of the maintenance energy requirement of brushtail possums is available.

UREA KINETICS

There was no significant relationship between urea-entry rate and nitrogen intake, urea-excretion rate, or urea pool size in either species (table 4). Greater gliders recycled 94% of endogenously synthesized urea or 54 mg urea-N $\cdot kg^{-0.75} \cdot day^{-1}$. Brushtail possums recycled 59% of synthesized urea or 90 mg urea-N $\cdot kg^{-0.75} \cdot day^{-1}$.

URINARY NITROGEN

Approximately 89% of greater glider and 94% of brushtail possum urinary nitrogen was accounted for by urea, creatinine, ammonia, uric acid, and allantoin (fig. 2). Ammonia was the dominant fraction in greater glider urine (78%), but urea accounted for 53% of the urinary nitrogen of the brushtail possums. The ratio of urinary urea concentration to plasma urea concentration (U/P) was 2.9 in the greater gliders and 41.0 in the brushtail possums.

Figure 3 shows the effect of feeding *Angophora floribunda* foliage on the ratio of urea-nitrogen to ammonia-nitrogen in greater glider urine. Animals eating *A. floribunda* excreted more nitrogen as urea ($P < .001$) and less as ammonia ($P < .001$) than did animals fed *E. radiata* foliage. There were no significant differences in the ratio of urea-N:ammonia-N over the 3 days of collection.

DISCUSSION

The greater glider and brushtail possum are both nocturnal arboreal marsupials. Both species use *Eucalyptus* foliage as a major part of their diet, but the brushtail possum does not appear to eat a diet solely of eucalypt leaves. We were interested to know what factors limited the consumption of eucalypt foliage by brushtail possums compared with greater gliders. Arboreal folivores are difficult to maintain in captivity on natural diets, and it has not been possible
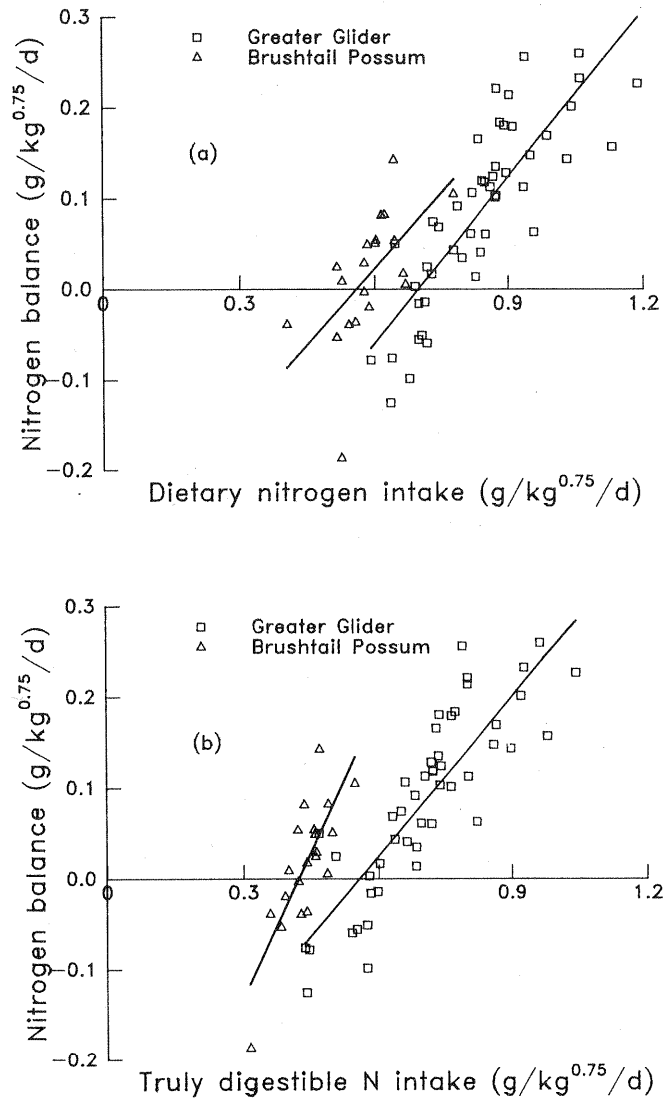
FIG. 1.—a, Regression relationship between nitrogen balance and dietary nitrogen intake in greater gliders and brushtail possums. Regression equations, greater glider: $y = -0.425 + 0.609x$, $r = .832$ ($P < .001$), RSD = 0.055; brushtail possum: $y = -0.312 + 0.558x$, $r = .578$ ($P < .01$), RSD = 0.058. b, Regression relationship between nitrogen balance and truly digestible nitrogen intake in greater gliders and brushtail possums. Regression equations, greater glider: $y = -0.325 + 0.583x$, $r = .849$ ($P < .001$), RSD = 0.052; brushtail possum: $y = -0.542 + 1.071x$, $r = .780$ ($P < .001$), RSD = 0.044.

to maintain strict folivores such as the greater glider on artificial diets. In this study, after observations in the field and preference tests in the animal house (see Foley and Hume 1987), we were able to maintain both arboreal species in metab-

TABLE 4

UREA KINETIC PARAMETERS IN GREATER GLIDERS AND BRUSHTAIL POSSUMS FED *Eucalyptus* FOLIAGE

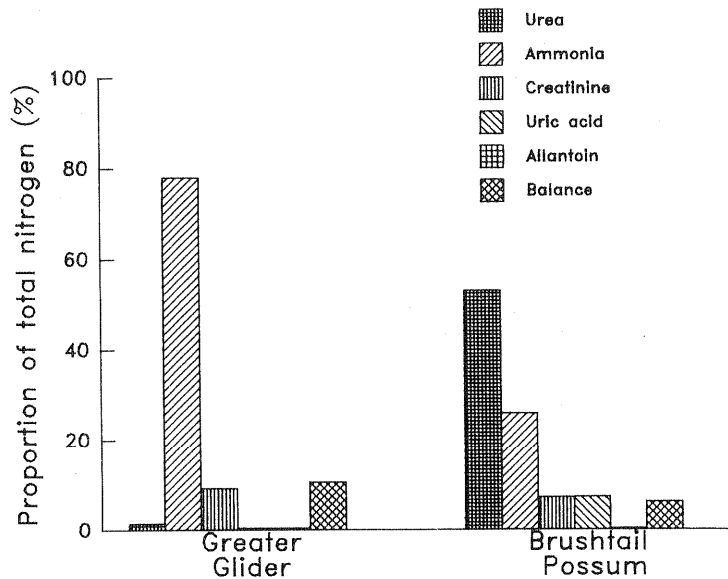|	Greater Glider ($n = 10$)	Brushtail Possum ($n = 6$)
Mean body mass (kg)	$1.10 \pm .02$	$2.45 \pm .10$
Urea pool size (mg N·kg$^{-0.75}$)	18.1 ± 1.7	82.0 ± 6.5
Urea turnover time (min)	475 ± 33	777 ± 71
Urea entry rate (mg N·kg$^{-0.75}$·day^{-1})	57.2 ± 4.2	153.2 ± 6.4
Urea excretion rate (mg N·kg$^{-0.75}$·day^{-1})	$3.6 \pm .3$	62.5 ± 11.4
Urea degradation rate (mg N·kg$^{-0.75}$·day^{-1})	53.5 ± 3.8	91.3 ± 13.2
Urea recycled (%)	$93.5 \pm .8$	59.0 ± 7.2

NOTE.—Values are means $\pm$ SE.

FIG. 2.—Composition of urinary nitrogen of greater gliders and brushtail possums eating eucalypt foliage

olism cages on foliage from single eucalypt species. However, it was not possible to use the same *Eucalyptus* species for both the greater gliders and the brushtail possums. For this reason, the results obtained may be specific not only to *Eucalyptus* foliage diets but to the particular *Eucalyptus* species used. In particular, although the two foliages were similar in levels of most nutrients and in amino acid profiles, *E. radiata* was much higher than *E. melliodora* in essential oil content.

The MNRs of the greater glider on *E. radiata* foliage and of the brushtail possum on *E. melliodora* foliage are greater than those recorded for all other marsupials ex-

cept the red-necked pademelon (*Thylogale thetis*) and the parma wallaby (*Macropus parma*) (Hume 1982, 1986). Among arboreal marsupials, the requirement of the greater glider is almost twice that of the closely related ringtail possum (*Pseudocheirus peregrinus*) when fed a sole diet of *E. andrewsii* foliage (Chilcott and Hume 1984) and of the koala (Cork 1986) when fed *E. punctata* folige. The low requirement of the ringtail possum is largely a result of its practice of caecotrophy (coprophagy) (Chilcott and Hume 1985). These authors calculated that caecotrophy contributed 0.33 g truly digestible nitrogen $\cdot$ kg$^{-0.75}$ $\cdot$ day^{-1}; in the absence of caecotrophy the
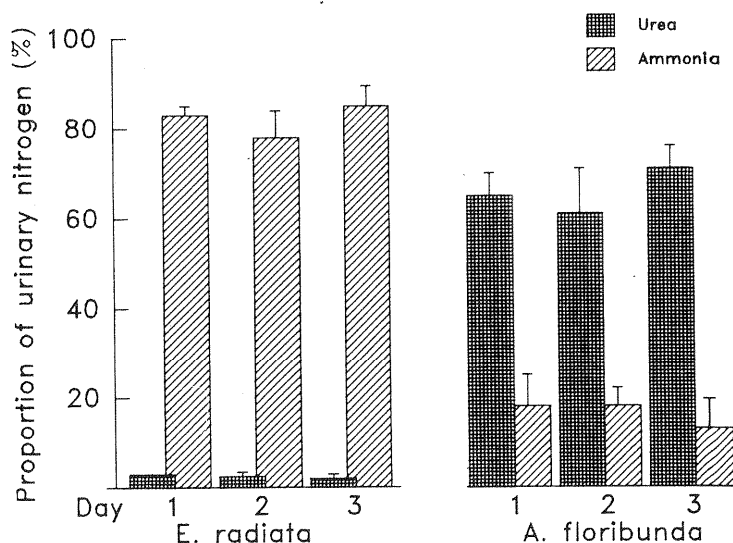

FIG. 3.—Effect of changing the diet of greater gliders from *Eucalyptus radiata* to *Angophora floribunda* on the proportion of urinary nitrogen excreted as ammonia or urea. Values are means ± SE.

MNR of ringtails would be 0.62 g truly digestible $N \cdot kg^{-0.75} \cdot day^{-1}$, close to that of our greater gliders.

High fecal nitrogen losses appear to be a major reason why brushtail possums fed eucalypt foliage have a higher MNR than when fed semipurified diets (Wellard and Hume 1981). On the eucalypt diet, NDFN was two to three times greater than Wellard and Hume's (1981) estimate (table 5). As NDFN consists primarily of bacterial residues produced in the hindgut (Mason 1969, 1971; Van Soest 1982), both the type and level of fiber in the diet will influence the extent of NDFN excretion (Whiting and Bezeau 1957a, 1957b; Wellard and Hume 1981). The fiber source used in Wellard and Hume's (1981) study was highly digestible because of its low lignin content and fine particle size, and this probably explains why NDFN was lower than in the present study. Animals may also reduce their NDFN losses by selectively retaining bacteria in the hindgut (Sperber 1968). The greater glider and koala both selectively retain fine particulate digesta (including bacteria) in the hindgut, whereas the brushtail possum does not (Cork and Warner 1983; Foley and Hume 1987). Hence the higher NDFN excretion by the brushtail on foliage diets compared to other folivores may be due to its lack of a mechanism to selectively retain fluid and fine particles. The loss of NDFN in turn is largely responsible for its high MNR on E. melliodora foliage.

In contrast to the brushtail possum, the high MNR of the greater glider clearly is due to its high nitrogen excretion in the urine. Partitioning of the urinary nitrogen

of the greater glider showed that NH₄-N was the dominant fraction when fed E. radiata foliage, comprising 70%–80% of total urinary nitrogen. The high urea concentrations in urine samples when the animals were fed Angophora floribunda foliage (fig. 3) and the fact that U/P ratios were always greater than unity confirm that the high urinary NH₄-N on the E. radiata diet did not result from hydrolysis of urea during collection.

Urinary NH_4^+ is generally associated with maintenance of body acid-base balance. However, accepted views of mammalian acid-base regulation have recently been challenged with Atkinson and Camien's (1982) argument that mammals must dispose of significant quantities of bicarbonate from dietary sources as well as that produced during protein metabolism. Atkinson and Camien (1982) suggested that urea is the means for disposal of this excess base.

The excretion of detoxified allelochemicals in the urine may also affect acid-base balance. Much of the essential oil fraction of Eucalyptus is detoxified and excreted in the urine as labile glucuronides (Hinks and Bolliger 1957a, 1957b; Eberhard et al. 1975). Conjugation of allelochemicals converts them into strong organic acids (Robinson, Smith, and Williams 1953). For example, the pKa of the monoterpene alcohol isomenthol is about 18, while the pKa of isomenthyl glucuronide is 3.7 (Robinson et al. 1953). Hence, in spite of Atkinson and Camien's (1982) arguments, animals that are producing large amounts of conjugated metabolites in the urine may well have an acid-disposal problem. In Atkinson and

TABLE 5

PARTITIONING OF NITROGEN EXCRETION IN SEVERAL SPECIES OF FOLIVOROUS MARSUPIALS AT SIMILAR LEVELS OF TRULY DIGESTIBLE NITROGEN INTAKE (VALUES IN g $N \cdot kg^{-0.75} \cdot day^{-1}$)

Species	Diet	Truly Digestible Nitrogen Intake	Fecal Nitrogen Excretion	Urinary Nitrogen Excretion	NDFN
Koala [1]	Eucalyptus punctata	.38–.58	.21–.36	.05–.14	.24
Ringtail possum [2]	E. andrewsii	.28–.48	.15–.36	.15–.27	.10
Greater glider [3]	E. radiata	.44–1.04	.26–.44	.27–.57	.22
Brushtail possum [3]	E. melliodora	.36–.55	.28–.51	.11–.24	.26
Brushtail possum [4]	Semipurified (HF)	.30–.70	.08–.19	.07–.18	.10
Brushtail possum [4]	Semipurified (LF)	.26–.72	.03–.06	.10–.44	.05

SOURCES:—1, Cork (1986); 2, Chilcott and Hume (1984); 3, This study; 4, Wellard and Hume (1981).
NOTE.—HF = high fiber; LF = low fiber.

Camien's (1982) scheme, the excretion of acidic conjugated compounds titrates some of the bicarbonate that must be disposed of, and urea production falls accordingly. The conventional view of urinary NH_4^+ is that it results from a combination of NH_3 (arising from the hydrolysis of glutamine in the kidney) and metabolic H^+ and that it reflects a net transfer of acid out of the body.

The hypothesis proposed here to explain the high urinary nitrogen loss of the greater gliders, and hence the high MNR, is that NH_4^+ is excreted in the urine to regulate acid-base balance in connection with the excretion of detoxified allelochemicals. The experiments with Angophora floribunda as the diet showed that the ratio of urinary urea:ammonia was a dietary effect and could be reversed. Since the Angophora leaf contained only traces of terpene and minor amounts of phenolics (W. J. Foley, unpublished), it is probable that this led to a lower excretion of conjugated compounds. Alternatively, A. floribunda may contain more carboxylic acids than E. radiata, which, in Atkinson and Camien's (1982) view, would result in an increased urea excretion.

These alternative explanations could be evaluated by experimental manipulation of the diets of the animals to provide them with known amounts of leaf allelochemicals or carboxylic acids. Concomitant measurements of urinary constituents and blood buffers should give sound data on the extent of perturbation of body acid-base balance resulting from the excretion of conjugation products of leaf terpenes and phenolics.

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