

Energy and Water Metabolism in Free-living Greater Gliders, *Petauroides volans*

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Abstract

Water flux and metabolic rate were measured using a low-level, doubly-labelled water technique in eight free-living greater gliders, *Petauroides volans* which were maintaining constant body masses at about 1 kg in eucalypt forest near Maryborough, Queensland. Mean water influx was 88.0 ± 3.2 mL d⁻¹ and mean metabolic rate was 25.1 L CO₂ d⁻¹ or 520 kJ d⁻¹. These arboreal folivores have field metabolic rates and water influx rates that are 96% and 71% respectively of those predicted for a herbivorous marsupial of their body mass. Assuming that faecal energy losses were 43% of gross energy intakes and that urinary energy losses were 15% of digestible energy intakes, the gross energy intake of the animals was about 1130 kJ d⁻¹. Animals would need to eat between 45 and 50 g of dry matter daily to satisfy these energy requirements. Based on these results, a preliminary energy budget for greater gliders has been proposed.

Introduction

Energetic studies can provide insights into the nutritional constraints faced by small arboreal folivores. Foliage diets usually contain low levels of protein but are rich in lignified fibre and allelochemicals (Cork *et al.* 1983). Allelochemicals such as terpenes and phenols must be detoxified and excreted; this is an energetically expensive process (Hinks and Bolliger 1957). The combination of low nutrient content and high allelochemical levels, together with the small body size dictated by life in the trees, has led several authors (for example McNab 1978) to suggest that arboreal folivores live close to the limits of their energy budgets. This is not always reflected in a low basal metabolic rate as suggested by McNab (1978). The three-toed sloth, *Bradypus variegatus*, and the koala, *Phascolarctos cinereus*, which both have lower basal rates than expected (McNab 1978; Degabriele and Dawson 1979), also have notably low field metabolic rates (Nagy and Montgomery 1980; Nagy and Martin 1985). On the other hand, in the howler monkey, *Alouatta palliata*, low field metabolic rates (Nagy and Milton 1979) are not coupled with a basal rate lower than would be predicted (Milton *et al.* 1979). Adaptations to minimise energy expenditure should be reflected in low field metabolic rates rather than low basal metabolic rates.

The greater glider, *Petauroides volans*, is a small (0.9–1.7 kg) arboreal marsupial which feeds almost exclusively on the leaves of *Eucalyptus* trees (Marples 1973; Kehl and Borsboom 1984). It has a standard metabolic rate close to that predicted for a marsupial of this body

mass (Foley 1987). Previous studies of the energetics of greater gliders highlighted the large losses of energy in the urine as a major factor limiting metabolisable energy intake on a diet of *E. radiata* foliage (Foley 1987). Nevertheless, captive greater gliders were able to maintain energy balance on *E. radiata* foliage as a sole diet.

The present study was undertaken to gain more reliable data than those currently available (Marples 1973) on the energy expenditure and water metabolism of free-living greater gliders. We used the doubly-labelled water technique (Nagy 1983), but in contrast to many previous studies the level of isotope employed and consequently the cost was much lower. Details of this technique and a validation experiment using greater gliders will be presented elsewhere.

Materials and Methods

Study Area

The study area was located in the Wongi State Forest, near Maryborough, south-eastern Queensland (25°28'S., 152°38'E.). The vegetation consists of mixed eucalypt forest known colloquially as 'wallum' and forms part of the Colton land system described by Coaldrake (1961). Structurally, the vegetation is an open, grassy, mature forest with a canopy height of 14 to 24 m tall and a density of 90–150 stems per hectare. The predominant overstorey trees included *Eucalyptus umbra*, *E. intermedia*, *E. drepanophylla*, *Angophora costata* and *Melaleuca quinquenervia*. Soils are dense clay loams which may be water-logged in summer. The annual rainfall is 1200 mm with a pronounced summer peak. Mean summer maximum temperature is 29.5°C and mean winter minimum temperature is 10.1°C.

Water Turnover

Eight greater gliders (six males, two females) were caught three times over a 14 day period commencing on 12 July 1982. Rain fell on five nights throughout the study but the days were generally fine. Temperatures at night ranged from 0–14°C and in the day from 18–26°C. Animals were caught at night by cutting the branch on which they were sitting with a rifle shot (Kehl and Borsboom, 1984). Animals were then weighed and fitted with a small (7–10 g) reflective collar and 150 MHz radio transmitter (A.V.M. Instruments, Illinois) and a reflective tail tag. A blood sample (2 mL) was taken for measurement of isotope background levels by cutting and aspirating a vein on the ventral surface of the gliding membrane. The animals were then injected intraperitoneally with 0.501 mL of water containing 24 MBq of tritium (³H) and 38.3 atom % ¹⁸O. The precise injection volumes were determined by later weighing an equivalent volume of distilled water. Animals were kept in open-weave bags for 4 h to allow the isotope to equilibrate with the body water pool. A second blood sample was then taken and the animal released into the tree where it was captured. Blood samples were stored in heparin-coated vials at 4°C. All animals were recaptured twice, usually five and ten days after injection and blood samples taken as described above.

The tritium content of water distilled from blood samples were determined by liquid scintillation spectrometry and oxygen-18 content by isotope ratio mass spectrometry. Full details of the methods used will be described later. Validation experiments in captive greater gliders (Nagy, Foley, Kaplan, D. Meredith and M. Minagawa, unpublished) showed that CO₂ production as estimated by KOH absorption was on average 8% greater than estimates made by the doubly-labelled water method. Although this error was significant, we suggest that at least part of the error arose from difficulties in correcting the total CO₂ produced, for the contribution of CO₂ from foliage used to feed the greater gliders in the validation experiment. We conservatively estimate that field measurements of CO₂ production by greater gliders are accurate to within ±10% but they may very likely be better than this.

Rates of CO₂ production and water flux were calculated from the isotope data using the equations described by Nagy (1980) and Nagy and Costa (1980) and assuming that any change in the volume of body water occurred linearly through time. Body water volumes were estimated at the time of injection from oxygen-18 dilution space and body water volumes at subsequent recaptures, were assumed to be the same proportion of body mass as at injection.

Diet

The diet of greater gliders in forest adjacent to the study area was determined by dusk to dawn observations of the time spent feeding on particular tree species (by six animals). Samples of the leaves consumed by these animals were collected by shooting down the branch. Greater gliders may be able to increase their food intake per unit time by feeding extensively on young leaves of lower fibre content since presumably less time is required for mastication. However, as there were no young leaves on any of the three species utilised during the study, we have assumed that the proportion of time spent feeding

is representative of the amount of each species ingested. The dry matter (DM), energy and total nitrogen content of the diet was determined as described by Foley (1987).

Statistical Analysis

To enable comparisons to be made between this and other studies, values have been expressed per $\text{kg}^{0.58}$ for metabolic rate (Nagy 1987), per $\text{kg}^{0.67}$ for feeding rate (Nagy 1987) and per $\text{kg}^{0.60}$ for water flux (Nagy and Peterson 1988).

Results

Body Mass and Body Water

The mean mass of all animals was 1.02 kg which is at the lower end of the range of body masses of adult greater gliders at Wongi (Kehl and Borsboom 1984). Although some animals lost minor amounts of body mass during the measurements, the mean value (-0.23% change per day, 95% confidence interval, -0.69 to $+0.23$) was not significantly different from zero and so we have assumed that the animals were close to energy balance. Body water volumes averaged $71.6 \pm 1.1\%$ of body mass.

Table 1. Body mass, metabolic rate and water flux in free-living greater gliders at Wongi near Maryborough, Qld

Animal	Measurement Interval (days)	Body mass		Metabolic rate		Water influx rate	
		Mean (g)	Change ($\% \text{ d}^{-1}$)	($\text{mL CO}_2 \text{ g}^{-1} \text{ h}^{-1}$)	($\text{L CO}_2 \text{ d}^{-1}$)	($\text{mL kg}^{-1} \text{ d}^{-1}$)	(mL d^{-1})
Males							
1	4.8	903	+0.12	0.997	21.6	91.0	82.2
1	5.0	913	+0.33	1.061	23.2	90.0	82.2
2	4.7	1040	+0.31	0.992	24.8	79.3	82.5
2	5.1	1045	-0.10	1.098	27.5	83.3	87.0
4	4.9	1085	-1.33	0.890	23.2	90.0	97.7
4	5.0	1070	+0.74	1.004	25.8	76.4	81.7
5 ^A	4.8	1070	+1.55	1.013	26.0	110.0	117.7
5	5.0	1055	-2.09	1.283	32.5	78.7	83.0
6	5.9	1100	+0.62	0.934	24.7	80.5	88.6
6	4.9	1100	-0.84	1.204	31.8	83.5	91.9
7	4.9	1130	-0.45	0.829	22.5	92.2	109.2
7	5.0	1100	-0.64	0.957	25.3	79.7	87.7
Mean		1051	-0.15	1.022	25.7	86.2	90.5
SE		21	0.29	0.036	1.0	2.7	3.2
Females							
3	4.9	860	-0.48	1.111	22.9	87.5	75.3
3	5.1	835	-0.71	1.052	21.1	76.0	63.5
8 ^B	4.8	1030	-0.51	0.884	21.9	91.8	94.6
8	5.0	1010	-0.20	1.094	26.5	81.8	82.6
Mean		934	-0.48	1.035	23.1	84.3	79.0
SE		50	0.10	0.052	1.2	3.4	6.5
Overall mean		1018	-0.23	1.025	25.1	85.7	88.0
SE		24	0.22	0.030	0.8	2.1	3.2

^A Animal landed in creek during capture and so weight changes may not be reliable.

^B Carrying small (≈ 45 mm) pouch young.

Metabolic Rate and Water Flux

There was no significant difference between mean water influx and efflux rates and so animals were assumed to be in water balance. Similarly there was no significant relationship (least squares linear regression analyses) between mass-specific water influx rates and either

mass-specific CO₂ production or changes in body mass. Additionally, mass-specific CO₂ production rates were not correlated with daily body mass changes.

The caloric equivalent of CO₂ must be used to convert CO₂ production rates to energy expenditures. However, the caloric equivalent of CO₂ varies depending on the nutrients metabolised (Blaxter 1962). This problem can be overcome by estimating the proportions of protein and lipid metabolised from different diets. However, the partition of *Eucalyptus* foliage into these categories is complicated by a lack of knowledge of the composition of each broad fraction. For example, 'crude lipid' consists of a mixture of potentially available fatty acids and essential oils and waxes which provide minimal metabolisable energy (Foley 1987). Experiments with captive greater gliders (Foley 1984, 1987) showed that except during starvation, the respiratory quotient remained close to 1.0 irrespective of the level of feeding. Therefore in the present study we used a conversion factor of 21.2 kJ 1 CO₂⁻¹ to reflect the respiratory quotients observed in captive greater gliders. Data derived from the field CO₂ production rates on this basis are presented in Table 2. The calculated metabolic rates are 547 kJ d⁻¹ for males and 492 kJ d⁻¹ for females.

Table 2. Metabolic rate, feeding rate and water influx in free-living greater gliders

	Units	Males (1.05 kg)	Females (0.94 kg)
Field metabolic rate	(kJ d ⁻¹)	547	492
	(kJ kg ^{-0.58} d ⁻¹)	531	512
Feeding rate	(kJ d ⁻¹)	1129	1016
	(kJ kg ^{0.58} d ⁻¹)	1097	1057
	(g dry matter d ⁻¹)	50	45
	(g kg ^{-0.67} d ⁻¹)	48	47
	(g fresh matter d ⁻¹)	103	92
Water intake	(mL d ⁻¹)		
	Preformed	53	47
	Metabolic	17	15
	Difference	21	17
	Total	91	79
Total	(mL kg ^{-0.60} d ⁻¹)	88	82

Diet and Feeding Rates

During the two week study period, greater gliders fed predominately on *Eucalyptus umbra*, with smaller quantities of *E. intermedia*, *E. exserta*, *E. drepanophylla* and *Melaleuca quinquenervia* also being consumed. Table 3 gives the estimated proportion of each species in the diet based on the proportion of time spent feeding in each. These figures are similar to those reported by Kehl and Borsboom (1984) for greater gliders in the same area when during 21 h of feeding observations, *E. umbra* made up 55% of the diet, *E. intermedia* 13%, *E. drepanophylla* 11%, *M. quinquenervia* 11%, *E. trachyphloia* 6% and others including *E. exserta* 4%.

Since Kehl and Borsboom (1984) recorded high variability in both the numbers and range of tree species fed on during any one night, the relatively small differences between their diet figures and those observed here probably result from the short, single-season sample in this study. Errors resulting from a species mix different from our typical diet will have relatively little effect on calculated feeding rates because there was little variation in the gross energy content of the different species (22–24 kJ g DM⁻¹). Feeding rates were derived from the field metabolic rates which can be regarded as the metabolisable energy intake necessary for maintenance of energy balance. Allowances then need to be made for the likely energy loss in the excreta and feeding rate calculations will be sensitive to these estimates as well.

Manganese has been used as an indigestible marker in koalas (Nagy and Martin 1985) to determine faecal energy losses in similar calculations. However, 14% of the manganese of *E. radiata* leaves was digested by captive greater gliders (Foley, unpublished). Lignin is also

positively digested (Foley 1987) and acid-insoluble ash (another widely used natural marker substance) was present in the leaves in levels too low ($<0.01\%$) to allow accurate measurement. Therefore we have assumed that faecal energy losses of free-living greater gliders at Wongi are similar to those of greater gliders fed *E. radiata* foliage (43% of gross energy intake; Foley 1987). This value is within the range of values reported in koalas (Cork *et al.* 1983) and ringtail possums, *Pseudocheirus peregrinus* (Chilcott and Hume 1984).

However, urinary energy losses of greater gliders fed *E. radiata* leaf were large, 45% of the digested energy. This is probably due to the excretion of large amounts of essential oils and their metabolites from the oil-rich *E. radiata* leaves (Foley 1987). The oil content of the diet of greater gliders at Wongi was probably only a quarter of that of *E. radiata* (9–13% DM; Foley *et al.* 1987) with *Melaleuca quinquenervia* being the richest in oils (3% DM) and *E. umbra* having the lowest levels (1.0% DM; Barker and Smith 1920). Hence it seems reasonable to assume that the urinary energy losses of animals in the field would be proportionally lower than those fed *E. radiata* foliage. On this basis we have assumed urinary energy losses were 15% of digestible energy intake, which is similar to values reported for koalas (Cork *et al.* 1983) and ringtail possums (Chilcott and Hume 1984). Under-estimation of urinary energy losses will result in an under-estimation of feeding rates. We have ignored the loss of energy in the methane produced during fermentation; Foley (1987) has shown that this is less than 0.5% of the total gross energy intake.

When these figures were applied to the energy expenditures, digestible energy intakes were estimated to be 644 kJ d⁻¹ for males and 579 kJ d⁻¹ for females. This in turn indicates a gross energy intake of 1129 kJ and 1016 kJ for males and females respectively (Table 2). Because the diet contained 22.8 kJ gross energy g DM⁻¹, the calculated feeding rate was between 45 and 50 g DM d⁻¹ (Table 2) and 0.44–0.49 g of nitrogen d⁻¹.

Table 3. Estimated time spent feeding on leaves of different tree species by greater gliders at Wongi and the proportions of water, nitrogen and gross energy contributed by each species

Intake per 100 g dry matter represents the amount of each nutrient that a greater glider eating 100 g of this average diet would obtain from each different tree species. The composition of each species can be determined by dividing the value given for each nutrient by the proportion that it occurred in the diet. For example, *E. umbra* contained $(0.64 \times 100/70) = 0.98\%$ nitrogen

Species	Time spent feeding (%)	Intake per 100 g dry matter		
		Water (g)	Nitrogen (g)	Gross energy (kJ)
<i>Eucalyptus umbra</i>	70	72.6	0.64	1600
<i>E. intermedia</i>	10	11.1	0.12	220
<i>E. exserta</i>	5	5.1	0.07	113
<i>E. drepanophylla</i>	5	5.1	0.06	107
<i>Melaleuca quinquenervia</i>	10	11.3	0.08	240
Total	100	105.2	0.97	2280

Water Influx

The mean water influx rate of 88 mL d⁻¹ can be partitioned between preformed water in the leaves, the water produced during the oxidation of nutrients and the remaining water (primarily drinking water). On this basis, preformed water in the leaves (51 mL d⁻¹) was the major route of water intake (58%). We have based our calculation of metabolic water production to reflect primarily the oxidation of carbohydrate (that is 0.03 g water kJ ME⁻¹; Schmidt-Nielsen 1983). This source provided 16 mL d⁻¹ or 18% of total intake. The remainder (21 mL d⁻¹) must have resulted from animals licking dew and rainwater from the surface of the leaves or grooming water from their fur.

Table 4. Energy budget for a free living greater glider (1 kg body mass) at Wongi in winter

The metabolism value is the field metabolic rate. This has then been partitioned into the categories listed below based on the values presented in the text. The residual is the portion of energy expenditure unaccounted for in the above categories

	Energy flux (kJ kg ⁻¹ d ⁻¹)	Percentage of intake	Percentage of metabolism
Intake:			
Gross energy of food	1075	100	—
Output:			
Faeces	462	43	—
Urine	92	9	—
Metabolism	521	48	100
Basal energy loss	205	—	39
Heat increment	38	—	6
Thermoregulation	33	—	7
Activity	118	—	23
Travel costs	10	—	2
Residual	117	—	23

Discussion

Energetics of Arboreal Folivores

Do greater gliders have relatively low field energy requirements as might be expected for an arboreal folivore? (McNab 1978). The field metabolic rate of a 1 kg greater glider (521 kJ d⁻¹, Table 4) is 96% of the value of 544 kJ d⁻¹ predicted for a 1 kg herbivorous marsupial (equation 28 in Nagy 1987). Thus, greater gliders have field metabolic rates that are virtually identical to other plant-eating marsupials based on data for four species of terrestrial herbivores and three species of marsupial herbivores) and herbivorous marsupials as a group have already been shown to have lower field metabolic rates than non-herbivorous marsupials (Nagy 1987). However, greater gliders consumed food at a rate (47.5 g DM kg⁻¹ d⁻¹, Table 2) that was 39% higher than that predicted for a 1 kg herbivorous marsupial (34.2 g kg⁻¹ d⁻¹). This relatively high food requirement probably reflects the low digestibility and metabolisability of eucalypt leaf. The water influx rate of a 1 kg greater glider (85 mL kg⁻¹ d⁻¹) is only 71% of the value of 119 mL kg⁻¹ d⁻¹ predicted for a herbivorous marsupial (equation 8 in Nagy and Peterson 1988) and again, herbivorous marsupials have been shown to have significantly lower water influx rates than non-herbivorous marsupials. The relatively dry diet consumed by the greater gliders (51% water; calculated from Table 3) is probably responsible for this surprisingly low water influx rate.

Another way to make comparisons of field metabolic rate among species is to calculate the ratio of the field metabolism to basal or standard metabolism (SMR). In the greater glider this ratio was 2.7. This is higher than that found in eutherian folivores such as the three-toed sloth (1.8; Nagy and Montgomery 1980) and the howler monkey (2.0; Nagy and Milton 1979) but similar to values in the koala (Nagy and Martin 1985). In contrast, small arboreal omnivores such as *Gymnobelideus leadbeateri* (Smith *et al.* 1982) and *Petaurus breviceps* (Nagy and Suckling 1985) have field metabolic rates up to 5.8 times their SMR.

Food and Nutrient Consumption

The only previous estimates of the energy and food intakes of free-living greater gliders are those of Marples (1973). His estimate of gross energy intake of 450 kJ d⁻¹ is only about 40% of our values, and after allowing for losses of energy in the urine and the faeces, is only marginally above the standard metabolic rate. Marples' (1973) estimate was based on changes in the mass and energy content of stomach digesta at different times of the day and night. The lower value found by Marples (1973) might be explained if digesta were leaving

the stomach more rapidly during feeding than when the animals are at rest. This is likely to be the case. Additionally, energy-rich compounds such as essential oils may have been lost from the stomach digesta by either rapid absorption (Foley *et al.* 1987) or when the material was oven-dried prior to analysis. This would result in the food intake being underestimated.

Dietary nitrogen intake by greater gliders at Wongi would be insufficient to satisfy the maintenance nitrogen requirement of animals eating *E. radiata* foliage in captivity (Foley and Hume 1987). These latter animals required leaf of between 1.6 and 1.7% nitrogen to remain in positive nitrogen balance. However, at Wongi, the tree with the highest nitrogen level that we measured was *E. exserta* at 1.4% nitrogen and the 'average diet' (Table 3) was only about 1.0% nitrogen. Since animals at Wongi maintained body mass we assumed that they ate sufficient nitrogen. This discrepancy lends support to the suggestion of Foley and Hume (1987) that the nitrogen requirements of eucalypt-feeders can be strongly affected by other dietary and metabolic processes such as the need to detoxify ingested allelochemicals. Although laboratory and field nitrogen requirements are usually thought to be similar (excluding late lactation), care should be taken in extrapolating from laboratory to field in the case of animals feeding on diets high in allelochemicals. Similarly, the importance of urinary energy losses in determining metabolisable energy intake in eucalypt feeders suggests that a method of measuring this factor in the field would be valuable. One possibility may be to collect urine samples when animals are captured and convert these to daily outputs on the basis of their creatinine content. Validation experiments would be required to assess the variability of creatinine excretion on different diets.

Although the largest part of the water intake of greater gliders came from preformed water in the leaves and metabolic water, a significant proportion must have been ingested as free water. Licking of rainwater and dew from the surfaces of leaves is a common behaviour seen in captive animals and the frequent rain and dew during the study was probably the source of the free water intake. In captivity, greater gliders must be provided with sources of drinking water and Henry (1985) has observed free-living animals drinking from tree hollows. Although there was little if any thermal load on the animals during the period of our study, greater gliders rely heavily on evaporative cooling at moderate (30°C) and high ambient temperatures (Rubsamen *et al.* 1984) and summer temperatures at our study area may reach 40°C. Although young leaves produced in spring and summer will contain more water than the old leaves available in winter, sources of free water are likely to be of greater importance to these animals in the hotter months of the year.

Field Energy Budget

The field metabolic rates (Table 3), together with the data on energetics of captive greater gliders presented by Rubsamen *et al.* (1984) and Foley (1987) allow a preliminary energy budget to be proposed (Table 4). At 6°C (the mean minimum temperature at night during the study), the metabolic rate of resting, non-fasted greater gliders is 342 kJ kg⁻¹ d⁻¹ (Rubsamen *et al.* 1984). At the thermoneutral point of 20°C, metabolic rate of the same animals in the same conditions was 243 kJ kg⁻¹ d⁻¹. The average period of activity of greater gliders at Wongi was 8 ± 1.2 h (Kehl, unpublished), and since the tree hollows that they used as daytime shelters were well insulated (W. J. Foley, unpublished), we calculate that the animals would have expended about 33 kJ kg⁻¹ d⁻¹ above thermoneutral zone metabolism for thermoregulation each day during our study.

Differences between the energy expended by resting and fasted greater gliders at the thermoneutral point [i.e. standard metabolic rate 205 kJ kg⁻¹ d⁻¹; Foley (1987)] and those resting but fully fed (243 kJ kg⁻¹ d⁻¹; Rubsamen *et al.* 1984) largely reflects the energy expended in digestive processes such as gut motility and fermentation. This represents some 38 kJ kg⁻¹ d⁻¹. Similarly, the difference in energy expenditure between resting, fully-fed animals and those actively feeding (361 kJ kg⁻¹ d⁻¹; Foley 1984) is a measure of the energy required for prehension, mastication and grooming and posture. This amounted to 118 kJ kg⁻¹ d⁻¹.

Finally, travel costs have been estimated from data (Kehl, unpublished) on the proportion of time that gliders spent moving and the types of movements made. These data

indicate that there was considerable variation in movement patterns both among individuals of the same sex and between males and females. Male greater gliders spent 22% of their time outside the den moving and visited 22 trees (range 8–37) whereas females spent only 11% of their time moving and visited 14 trees (range 7–19) per night. In both cases, the majority of these movements were movements within, rather than between trees. We estimate that the minimum vertical movement per tree was about 10 metres. Therefore assuming that climbing requires 24 kJ per kg body mass per vertical kilometre (Robbins 1983), male greater gliders expended about 6 kJ kg⁻¹ d⁻¹ and female greater gliders about 3 kJ kg⁻¹ d⁻¹. Movement in the horizontal plane probably involves even less energy and we estimate that total travel costs are only of the order of 5–10 kJ kg⁻¹ d⁻¹.

This leaves a balance of about 117 kJ. A small component of this is likely to be the result of variation in individual animal activity patterns. However, since total travel costs are only estimated to account for a small proportion of total energy expenditure, differences in activity among individual animals will have a minimal effect on this residual.

Similarly, variation in the total amount of time greater gliders were outside the den each night may account for some small part of this residual. Undoubtedly, part reflects errors in extrapolating from laboratory measurements to the field. Also free-living animals must expend energy for activities such as the maintenance of social organisation and communication which are suppressed during laboratory investigations.

Arboreal marsupials exist in only a small proportion of the eucalypt forests of eastern Australia (Braithwaite *et al.* 1983). At present, this patchy distribution is thought to be a reflection of nutritional 'quality' although at present we do not know how to measure the quality of leaves for folivores such as the greater glider. Further studies of the factors affecting the nutrient requirements of arboreal folivores need to be combined with measures of energy and water turnover of animals in different habitats to evaluate this hypothesis.

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