

## Chapter 10

**ENERGY AND WATER METABOLISM IN FREE LIVING GREATER GLIDERS****10.1 Introduction**

Free living animals must expend energy at greater rates than captive animals to meet the additional costs of thermoregulation, reproduction and activity. Energy intakes of captive Greater Gliders fed on *E. radiata* foliage in this study were only marginally above maintenance requirements (Chapter 8). This was suggested to be related to the low metabolizability of *E. radiata* gross energy. Since *E. radiata* appears to be one of the principal food items of this species, at least in parts of N.S.W. and Victoria (Section 1.5.4), this raises the question of how Greater Gliders maintain energy balance in the wild. It would seem that ME intakes would have to be substantially higher to meet the energy demands of free existence.

Thermoregulation, particularly at low ambient temperatures, may require significant energy expenditure since the high surface area to body mass ratio of the Greater Glider may lead to heat loss (Iversen, 1972). On the other hand, fur insulation and postural changes may compensate for heat loss from the large surface area (Rübsamen *et al.*, 1984).

Some arboreal folivores (e.g. Howler Monkeys, Nagy and Milton (1979a), Sloths, Nagy and Montgomery (1980) and Koalas, Nagy and Martin (pers. comm.) have been shown to have "field metabolic rates" only about two to two-and-a-half times their basal metabolism; this has been interpreted to indicate a need for energy conservation. However, these species are all at the upper end of the range of body masses for arboreal folivores; smaller animals such as the Greater Glider might be expected to have higher mass specific energy requirements.

This chapter describes measurements of the water turnover and CO<sub>2</sub> production rates of free-living Greater Gliders in a mixed eucalypt forest

in south-eastern Queensland. This population has been under intensive study for some years by Mr. J. Kehl (Forestry Department: Queensland) and much is known of the diet and pattern of activity and habitat use. This has enabled assumptions to be made about likely energy requirements for activity and thermoregulation so that field metabolic rates, feeding rates and a daily energy budget could be derived from the water turnover data.

## 10.2 Materials and Methods

### 10.2.1 The 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 type was a mixed eucalypt forest known colloquially as "Wallum". It forms part of the Colton Land System described by Coaldrake (1961). Structurally, the vegetation is an open, grassy forest with a excess of overmature trees ranging from 14 to 24m tall at a density of 90 to 150 stems per ha. The soil is a dense clay loam which is waterlogged in summer. The annual rainfall is 1200mm with a pronounced summer peak. Mean summer maximum temperature is 29.5°C and mean winter minimum temperature is 10.1°C.

### 10.2.2 Water turnover

Eight Greater Gliders (six males, two females) were caught at night by cutting the branch on which they were sitting with a rifle shot (Kehl and Borsboom, 1984). Animals were weighed, sexed and fitted with a small (*ca* 7-10 g) reflective collar and 150 MHz radio transmitter (A.V.M. Instruments, Illinois) and a reflective tail tag. An initial blood sample (*ca* 2 ml) was taken for measurement of isotope background levels by cutting and aspirating a vein on the outer edge of the gliding membrane. The animals were then injected intraperitoneally with about 0.5 ml H<sub>2</sub>O containing 3.7 MBq [<sup>3</sup>H] and 50 atom % [<sup>18</sup>O] per ml. The precise injection volume was determined by later weighing an equivalent volume of distilled water. After allowing four hours for isotope equilibration with the body

water pool, a second blood sample (ca 2 ml) was taken and the animal then released in the tree from which it was captured. Blood samples were stored in heparin coated vials at 4°C.

The den trees of these animals were radiolocated each day but none of the labelled animals was disturbed at night. Five days and again ten days after administration of isotopes all animals were recaptured and blood samples were collected as before.

### 10.2.3 Diet

The diet of six individual Greater Gliders was determined by dusk-to-dawn observations in blocks of forest adjacent to the study area. Samples of leaves consumed by the Greater Gliders were then collected by shooting down the branches. This, together with observations from previous years (J. Kehl unpub.), allowed an estimate to be made of the diet of Greater Gliders in the study area. Faeces were collected from captured animals whenever possible.

### 10.2.4 Analytical

[<sup>3</sup>H] content of water distilled from blood samples was determined at the University of California, Los Angeles by liquid scintillation counting (Nagy, 1983). [<sup>18</sup>O] content was determined by isotope-ratio mass-spectrometry by Dr. I. Kaplan (University of California, Los Angeles).

Dry matter, energy and nitrogen content of the diet was determined as described previously (Section 2.4). CO<sub>2</sub> productions and water fluxes were computed from the equations of Lifson and McClintock (1966) as modified by Nagy (1983).

TABLE 10.1: Diet and diet composition of Greater Gliders at Wongi, July 1982

Species	Time spent feeding (%)	Intake/100 g dry matter intake			Gross energy (kJ)
		H <sub>2</sub> O (g)	N (g)		
<i>E. umbra</i>	70	72.6	0.64		1600
<i>E. intermedia</i>	10	11.1	0.12		220
<i>E. erserta</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

TABLE 10.2: Details of body weight, water input and output rate and CO<sub>2</sub> production rate of Greater Gliders at Wongi in winter

Animal	Measurement period	Mean body weight (kg)	Body weight change (%/day)	H <sub>2</sub> O input (ml.kg <sup>-1</sup> .d <sup>-1</sup> )	H <sub>2</sub> O output (ml.kg <sup>-1</sup> .d <sup>-1</sup> )	CO <sub>2</sub> production rate (ml.g <sup>-1</sup> .h <sup>-1</sup> )
Males						
1	A	0.903	+0.12	91.0	90.1	0.997
	B	0.913	+0.33	90.0	87.8	1.061
	AB	0.910	+0.22	90.5	88.9	1.030
2	A	1.038	+0.31	79.3	77.3	0.922
	B	1.043	-0.10	83.3	83.9	1.098
	AB	1.035	+0.10	81.4	80.7	1.013
3	A	1.085	-1.29	96.7	107.0	*
	B	1.070	+0.76	82.1	76.4	*
	AB	1.105	-0.27	89.3	91.4	0.928
4	A	1.023	-0.30	106.0	108.0	*
	B	1.008	-0.30	75.8	78.0	*
	AB	1.015	-0.30	90.7	92.8	1.143

5	A	1.100	+0.62	82.5	77.7	*
	B	1.098	-0.84	85.4	91.9	*
	AB	1.078	-0.04	83.9	84.3	1.257
6	A	1.128	-0.45	99.9	103.5	*
	B	1.098	-0.64	86.2	91.1	*
	AB	1.110	-0.55	93.0	97.3	1.310
Non-lactating female	A	0.860	-0.48	88.1	91.7	*
	B	0.835	-0.71	76.6	81.8	*
	AB	0.845	-0.60	82.4	86.8	1.204
Lactating female	A	1.028	-0.51	93.1	96.5	1.280
	B	1.010	-0.20	83.1	84.5	*
	AB	1.023	-0.35	88.0	90.4	*
MEAN (males)		1.042 ± 0.017	-0.15 ± 0.12	88.2 ± 1.8	89.3 ± 2.3	1.076 ± 0.041
MEAN (all)		1.015 ± 0.018	-0.23 ± 0.09	87.4 ± 1.5	89.2 ± 1.8	1.104 ± 0.039

\* Data not yet available

## 10.3 Results

### 10.3.1 Temperature and rainfall

Maximum daytime temperatures ranged from 18–26°C (Mean = 22.8°C) and minimum night temperatures ranged from 1–14°C (Mean = 6.0°C). Temperatures measured inside a nest hollow used by one of the labelled animals were 3–4°C cooler than the outside daytime maximum and 2–3°C warmer than the outside nighttime minimum.

Light rain fell intermittently on six of the 14 nights of the study, but even on dry nights there was dew on the leaves by 2100 h.

### 10.3.2 Diet

The diet was found to be comprised primarily of the mature foliage of *E. umbra* with minor amounts of four other eucalypts (Table 10.1) and one non-eucalypt species. Immature foliage was present in the study area only on certain *E. intermedia* trees and was not seen to be eaten. Although three labelled animals were caught in flowering *Melaleuca* trees, Greater Gliders have not been observed feeding on *Melaleuca* flowers in the study area (J. Kehl pers. comm.). The moisture, nitrogen and gross energy contents of the dietary items are given in Table 10.1.

### 10.3.3 Body mass and sex of captured animals

The mean body mass of animals captured during the study (Table 10.2) were lower than those of other adult Greater Gliders captured at Wongi State Forest. However, all animals were within the range of typical adult mass (Kehl and Borsboom, 1984). Most animals lost minor amounts of mass during the study (Mean = -0.23%/day). The sex ratio of captured animals (3:1) was higher than that observed on the study area during the longer term study of Greater Glider social organization (Kehl and Borsboom, 1984). Only two female animals were captured, one of which was lactating, and so little can be said of sex differences in water turnover and metabolic rates.

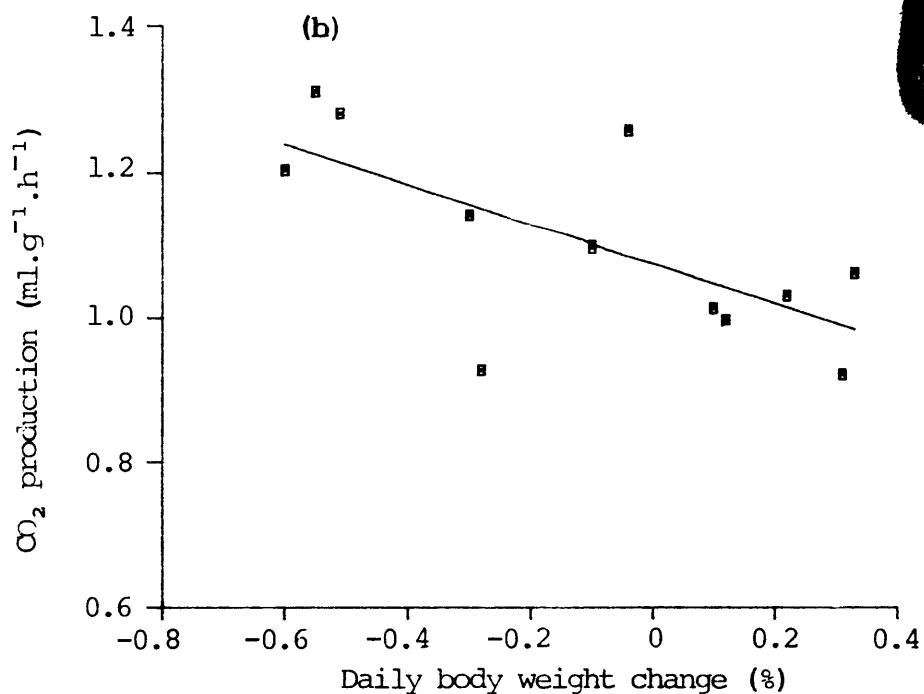
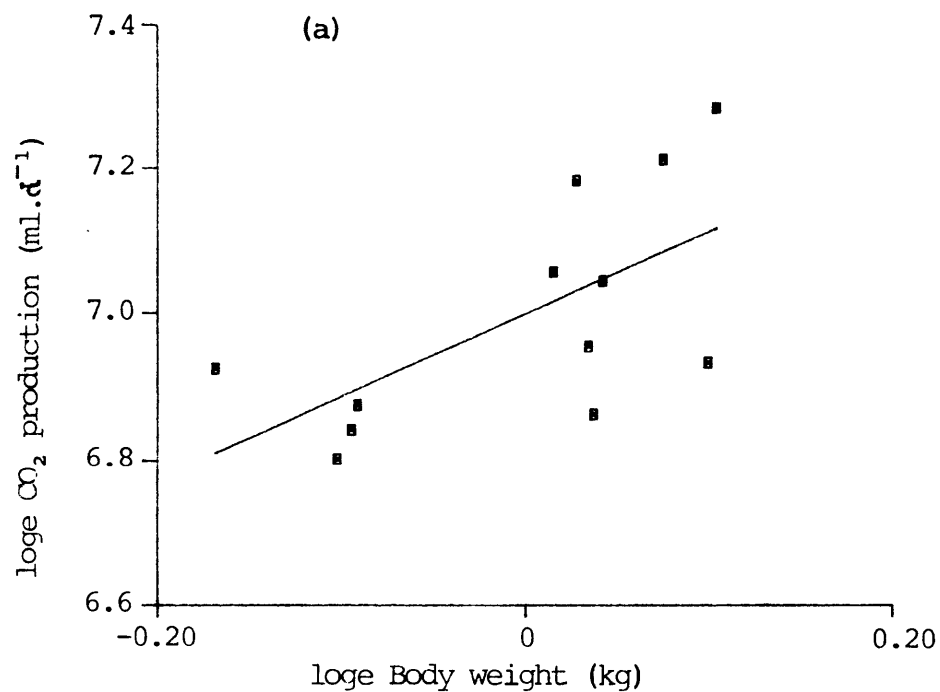


FIGURE 10.1: Relationship between field  $CO_2$  production rate in Greater Gliders and -  
 (a) body weight; and  
 (b) percentage daily body weight change.

Regression equations:

(a)  $y = 7.000 + 1.123x$ ,  $r = 0.589$  ( $P < 0.05$ ),  $RSD = 0.347$   
 (b)  $y = 1.074 - 0.275x$ ,  $r = 0.644$  ( $P < 0.05$ ),  $RSD = 0.103$



TABLE 10.3: Details of metabolic rate, feeding rate and water balance in Greater Gliders at Wongi in winter.

Animal	Measurement period	Metabolic rate (kJ.kg <sup>-1</sup> )	Feeding rate (g.kg <sup>-1</sup> .d <sup>-1</sup> )	H <sub>2</sub> O (from) feed (ml.kg <sup>-1</sup> .d <sup>-1</sup> )	H <sub>2</sub> O (metabolic) (ml.kg <sup>-1</sup> .d <sup>-1</sup> )	H <sub>2</sub> O (balance) (ml.kg <sup>-1</sup> .d <sup>-1</sup> )
Males						
1	A	507	45.9	48.3	16.2	26.5
	B	540	48.9	51.4	17.3	21.3
	AB	524	47.4	49.9	16.8	23.8
2	A	469	42.5	44.7	15.0	19.6
	B	559	50.6	53.2	17.9	12.2
	AB	514	46.5	48.9	16.5	16.0
3	A	*	*	*	*	*
	B	*	*	*	*	*
	AB	472	42.7	44.9	15.1	29.3
4	A	*	*	*	*	*
	B	*	*	*	*	*
	AB	581	52.6	55.3	18.6	16.8

5	A	*	*	*	*	*	*	*
	B	*	*	*	*	*	*	*
	AB	639	57.8	60.8	20.5	2.6		
6	A	*	*	*	*	*	*	*
	B	*	*	*	*	*	*	*
	AB	667	60.4	63.5	21.3	8.2		
Non-lactating female 7	A	*	*	*	*	*	*	*
	B	*	*	*	*	*	*	*
	AB	613	55.5	58.4	19.6	4.4		
Lactating female 8	A	650	58.8	61.9	20.8	10.4		
	B	*	*	*	*	*	*	*
	AB	*	*	*	*	*	*	*
MEAN (males)	547 ± 20.8	49.5 ± 1.9	52.1 ± 2.0	17.5 ± 0.7	17.6 ± 2.6			
MEAN (all)	561 ± 20.0	50.8 ± 1.8	53.4 ± 1.9	18.0 ± 0.6	15.9 ± 2.5			

\* Data not yet available

#### 10.3.4 Water Influx and efflux rates

Details of the water influx and efflux rates are given in Table 10.2. All animals were in approximate water balance and the water flux rates of both the lactating and non-lactating females overlapped those of the male animals. There was no significant relationship between water influx rate and body mass change.

#### 10.3.5 CO<sub>2</sub> production rates

Problems with the analysis of [<sup>18</sup>O] at very low levels at the University of California (e.g., loss of some samples in the gas handling system) has meant that the results are as yet incomplete. However, at least one value has been obtained for each captured animal.

Table 10.2 shows the available CO<sub>2</sub> production data. CO<sub>2</sub> production rates of both lactating and non-lactating females overlapped those of the male animals. There was no relationship between CO<sub>2</sub> production rate and water influx rate. However, CO<sub>2</sub> production rate was related to daily body mass change (Figure 10.1b) ( $P < 0.05$ ). There was a significant ( $P < 0.05$ ) relationship between log CO<sub>2</sub> production and log body mass (Figure 10.1a). However, the body mass exponent (1.123) was not significantly different from unity and so calculated metabolic rates were scaled to kg<sup>-1</sup> only.

#### 10.3.6 Metabolic rates, feeding rates and water balance

Metabolic rates were calculated assuming an RQ of 1.00 (carbohydrate oxidation) and computed using the equation of Brouwer (1965). The mean metabolic rate of Greater Gliders at Wongi in winter was 547 kJ·kg<sup>-1</sup>·d<sup>-1</sup> (males) or 561 kJ·kg<sup>-1</sup>·d<sup>-1</sup> (males + all females). Levels of acid insoluble ash were too low (< 0.01% dry matter) to allow confident estimates of energy digestibility to be made using this indicator method (Van Keulen and Young, 1977). Other commonly used internal markers such as lignin and manganese are positively digested by Greater Gliders (Chapter 8, W.J. Foley unpub.). Energy intakes were therefore calculated using data from Greater Gliders fed *E. radiata* foliage (Chapter 4) (apparent

digestibility of energy = 57%) but urinary energy losses were assumed to be only 15% of digestible energy intake: see Discussion). Feeding rates (Table 10.3) were calculated from the energy intake and the energy content of the diet (Table 10.1). These calculations assume that the animals were at energy equilibrium during the measurement period. The mean intake of dry matter was estimated to be  $50.8 \text{ g}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$  or for males alone,  $49.5 \text{ g}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$  ( $\approx 102 \text{ g}$  wet matter). This would have resulted in an intake of about  $0.48 \text{ g N}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$ .

Water from the leaves provided the major source of water intake (61%). Water formed from the oxidation of foodstuffs contributed some 21%. This left about  $16 \text{ ml}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$  which probably resulted from the ingestion of dew and rainwater on leaf surfaces.

## 10.4 Discussion

### 10.4.1 Validity of the doubly labelled water method

In recent years the doubly labelled water method has gained acceptance as a valid method for estimating  $\text{CO}_2$  production rates in free living animals. Results of validation studies using the high level technique in mammals (Nagy, 1980) have shown the results to be accurate within  $\pm 10\%$ . However, in some desert tenebrioid beetles, the isotope technique overestimated  $\text{CO}_2$  production by up to 30% (Cooper, 1983). Only one validation study has been reported using the low level technique applied here. Schoeller and van Santen (1982) showed that  $\text{CO}_2$  production estimated using low doses of doubly labelled water ( $\text{D}_2 \text{ } ^{18}\text{O}$ ) in humans was within  $1 \pm 6\%$  of measured  $\text{CO}_2$  production. Although a validation study was carried out with Greater Gliders as part of the present work, the results are not yet available. Nonetheless, the fact that the  $\text{CO}_2$  production, feeding rates and water fluxes of the field animals are close to expected values gives confidence that the results are a reasonable representation of the field situation.

TABLE 10.4: *Effect of variation in assumed faecal and urinary energy loss on calculated gross energy intake*

Urinary energy loss (% DE)	Faecal energy loss (% GE)		
	55	50	45
5	1280	1152	1047
10	1351	1216	1105
15	1430	1287	1170
20	1519	1368	1243
			40
			960
			1013
			1073
			1140

#### 10.4.2 Validity of assumptions

Calculation of metabolic rates and feeding rates required several assumptions. All experiments with Greater Gliders fed *E. radiata* foliage *ad libitum* (Chapter 8) have resulted in RQs = 1.00. Similarly the RQ of Greater Gliders restricted to 85% *ad libitum* was also close to 1.00. Several doubly labelled water studies have used inappropriate RQs in the conversion of measured CO<sub>2</sub> productions to heat productions. For example Smith *et al.* (1982) used an RQ of 0.8 for both field metabolic rate measurements and measurements on fasted Leadbeaters Possums. The relationship between daily body mass change and CO<sub>2</sub> production (Figure 10.1b) could indicate that high CO<sub>2</sub> productions occurred at the expense of body energy reserves. However, the range of body mass changes was very narrow and these may simply reflect differences in gut or bladder fill. Until the above relationship can be re-examined over a wider range of body masses it is probably reasonable to assume that animals were close to energy equilibrium in this study.

Since it was not possible to determine the digestibility of the energy of the field diet by reference to an internal marker, the digestibility of *E. radiata* gross energy was taken as an approximation. This value (57%) is within the range of values found for Koalas (Cork, 1981) and Ringtail Possums (Chilcott and Hume, 1984a) fed eucalypt diets. However, urinary energy losses by Greater Gliders feeding on *E. radiata* foliage comprised about 45% of their digestible energy intake. Much of this was attributed to the detoxification products of ingested terpenes in the urine (Chapter 8). *E. radiata* contains 9-13% (DM) essential oils, but the field diet would have contained less than one-fifth this level (minimum = *E. umbra* 1.0% DM; maximum = *M. quinquenervia* 3.0%) (Baker and Smith, 1920). It is reasonable to assume that the urinary excretion of essential oils and detoxification products and hence energy would have been proportionally lower on the field diet. The estimate of urinary energy losses (15% (DE)) of Greater Gliders on this diet is based on the range of data from Koalas, Ringtail Possums and Brushtail Possums. The effect of variations in this value and the estimate of the digestibility of energy on the calculated energy intake are shown in Table 10.4.

#### 10.4.3 Field metabolic rate and energy budget

The only previous estimate of energy and feed intakes of free-living Greater Gliders is that of Marples (1973). His estimate of gross energy intake of 450 kJ is only about 40% of the estimates made here. After allowing for likely faecal and urinary energy losses it is only marginally above standard metabolic rate (Chapter 8). Marples' (1973) calculations were based on the mass and energy content of the stomach digesta at different times of the day and night. The discrepancy between the two estimates might be explained if digesta were moving out of the stomach more rapidly during the feeding period than during the day. This is likely to be the case. Alternatively, if high energy compounds such as essential oils were lost during the oven drying of the digesta, then the calculated energy intake would be an underestimate.

The ratio of field metabolic rate to standard metabolic rate in the Greater Glider was 2.7. This is higher than that found in Howler Monkeys (2.0) (Nagy and Milton, 1979a) and Three-toed Sloths (1.3) (Nagy and Montgomery, 1980) but similar to that in Koalas (2.7) (Nagy and Martin, pers. comm.), the only other arboreal folivores for which data are available. Small arboreal and semi-arboreal omnivores such as Leadbeater's Possum (Smith *et al.* 1982), the Sugar Glider (G. Suckling and K. Nagy unpub. in Smith, 1980) and *Antechinus stuartii* (Nagy *et al.*, 1973) have field metabolic rates up to 5.8 times their SMR. This is at the upper end of the range of values for small rodents summarized by King (1975) and tends to illustrate the relatively low energy expenditures of arboreal folivores. To some extent, the size of the differences between animals such as *Gymnobelideus* and *Petauroides* reflects differences in their proportions of actively metabolizing tissues, with up to 15% of the body mass of *Petauroides* being gut contents (W.J. Foley unpublished; Smith, 1980). In contrast, gut contents of *Gymnobelideus* are only 3-4% of body mass (Smith, 1980). However, even this effect does not account for all the differences and it seems likely that real variations in total energy expenditure exist between these two groups.

TABLE 10.5: *Estimated field energy budget for male Greater Gliders at Wongi in winter*

	Energy flux $\text{kJ}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$	Percentage of input	Percentage of metabolism
INPUT:			
Food	1130		
OUTPUT:			
Faeces	485	43	
Urine	97	9	
Metabolism	547	48	
Basal	205		37
Heat increment and heat fermentation	28		5
Thermoregulation	47		8
Activity	140		26
Locomotion	3		1
Residual	124		23



The field metabolic energy expenditure must provide for the energy requirements of basal metabolism, thermoregulation, locomotion and activity. From the data presented in Chapter 8 and those of Rùbsamen *et al.* (1984) it is possible to make some reasonable estimates of the proportions of energy allocated to these categories. The estimated field energy budget is given in Table 10.5.

At 6°C (the mean minimum night-time temperature during the study) the metabolic rate of resting, non-fasted Greater Gliders is 342 kJ·kg<sup>-1</sup>·d<sup>-1</sup> (Rùbsamen *et al.* 1984) and during the study Greater Gliders were outside their den hollows for about 8 h per night. Insulation by the tree hollows should have been adequate (Section 10.3.1), so that there was no heat load imposed on resting animals during the day. The Greater Glider has a thermoneutral point at 20°C (Rùbsamen *et al.* 1984). Hence, while the animals were active at night, they would have expended some 47 kJ for thermoregulation.

The above discussion assumes that metabolic heat (i.e. the heat increment of the food and heat formed during activity) cannot substitute for necessary thermoregulatory heat at low ambient temperatures. While some authors (e.g., Robbins, 1983) in fact consider that the heat increment of the diet probably does substitute for thermoregulatory costs, this effect is probably only transitory. On the other hand, it is generally agreed that there is no substitution of heat generated during activity for thermoregulatory heat (Hart and Jansky, 1976, Gates and Hudson, 1978, Yousef *et al.*, 1973).

Comparison of the data in Chapter 8 on the energy expenditure of fasted, resting Greater Gliders at thermoneutrality (the standard metabolic rate) with those of Rùbsamen *et al.* (1984) (resting at thermoneutrality but non-fasting) allows calculation of the heat increment of the food and the heat of fermentation. This is essentially the energy expended in the digestive process (e.g. for gut motility and heat produced by activity of hindgut micro-organisms) and also reflects the energetic inefficiency of the reactions by which absorbed nutrients are metabolized (McDonald *et al.* 1973). This amounts to 28 kJ. However, this will be an underestimate,

since the measurements in Chapter 8 were not made on completely post-absorptive animals.

The difference between Rübsamen *et al.*'s (1984) estimates of metabolic rate in resting animals and those in Chapter 8 which were actively feeding allows some estimate of the energy required for prehension, mastication, grooming and posture. This involves about 140 kJ but may also be an underestimate of the energy cost of feeding in the field since the captive animals did not have to search for leaves.

Movement in a three-dimensional habitat may involve significant energy demands (Smith *et al.* 1982). This may be especially so for gliding animals since they must climb vertically to recover the height lost during gliding. The energy cost of vertical movement appears to be independent of body mass and angle of ascent, at least within the range of 0-37° (Robbins, 1983), but depends on the mechanical efficiency of the muscles (Taylor *et al.*, 1972). In an animal as adapted to life in trees as the Greater Glider, this efficiency would be expected to be high. Data from a wide range of arboreal and terrestrial mammals (all eutherians and most larger than 12 kg) suggest a mean cost of 24 kJ/kg body mass/vertical kilometre (ARC, 1980, Robbins, 1983). There are no published data available on the distances travelled in the vertical and horizontal by Greater Gliders, but personal observations at Wongi suggest vertical movements are of the order of 50 m per night. This would involve an energy expenditure of only 1-2 kJ/day. The energy cost of movement in the horizontal plane is independent of velocity at low speeds (Taylor *et al.*, 1970) and probably requires even less energy. Therefore, total locomotion costs are only of the order of 3 kJ/animal/day. This is only a very small component of the total field metabolic rate but is comparable to Nagy and Milton's (1979a) estimate of travel cost in Howler Monkeys ( $8 \text{ kJ}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$ ). In contrast, locomotion costs may be one of the major reasons for the high energy cost of activity in Leadbeater's Possum (Smith *et al.*, 1982).

This leaves a balance of about 124 kJ. To some extent this residual energy reflects errors in all the above energy costs - particularly in the extrapolation of results for captive animals fed *E.*

*radiata* foliage to the field. For example, the heat increment of the field diet may be greater than for *E. radiata*. Similarly, energy required for mastication may be greater for the field diet. Also, windchill effects may have lowered the effective ambient temperatures or fur insulation may not have been as effective as in the animals used by RübSamen *et al.* (1984). Finally, maintenance of social organization and communication (primarily olfactory, Henry, 1984) are likely to be significant factors that are suppressed during laboratory investigations and which may contribute to total energy expenditure in the field.

Animals were able to obtain the majority of their water requirements from food and oxidation water. Although dew licking has not been specifically observed in the wild, it is a common behaviour in captive animals (personal observation). Dew either licked from the surface of leaves or ingested during feeding can probably explain the balance of the water intake. Nevertheless, Greater Gliders have been observed visiting tree hollows containing free water in eucalypt forests in Victoria (S. Henry, pers. comm.).

RübSamen *et al.* (1984) concluded that Greater Gliders relied extensively on evaporative cooling at high ambient temperatures. The maximum daytime temperatures, tempered by the insulative nature of the den hollow, resulted in little, if any, thermal load. However, summer maximum temperatures in the study area can be in excess of 40°C and the extra water required for evaporative cooling may comprise a significant additional water requirement. The mean water influx rate (87 ml·kg<sup>-1</sup>) is lower than the standard water turnover rate (103 ml·kg<sup>-1</sup>·day<sup>-1</sup>) predicted for an animal of this body mass (Nicol, 1978) which in turn is similar to that recorded in captive animals (W.J. Foley unpub).

These results have several important implications for the interpretation of the results from the captive studies. First, the dietary nitrogen intake of the Greater Gliders at Wongi in winter was less than half that of the captive animals fed *E. radiata* foliage (Chapter 5). Greater Gliders feeding on *E. radiata* leaf would need about 1.6-1.7% dietary N to remain in positive nitrogen balance, yet at Wongi, the tree

with the highest nitrogen leaf (*E. exserta*) was only 1.42% and the average diet only 0.93% N. Clearly, Greater Gliders must be able to maintain nitrogen balance on a diet of lower N content than that of *E. radiata*.

Second, since Greater Gliders feeding on *E. radiata* in the laboratory were only in slight positive energy balance (Chapter 8), animals feeding to a large extent on this species in the wild may have difficulties meeting the energy demands for activity and thermoregulation. Alternatives open to these animals include feeding on species of higher metabolizable energy content or else increasing the rate of intake of digestible nutrients at the possible expense of energy gains from fermentation. This may also result in an increased intake of allelochemicals. Comparative data are required from habitats where *E. radiata* forms a large proportion of the diet before these questions can be addressed.

### 10.5 Summary

The metabolic rate of free-living Greater Gliders (FMR) was found to be  $561\text{kJ}\cdot\text{kgW}^{-1}\cdot\text{d}^{-1}$  or 2.7 times the SMR. FMR is a similar multiple of SMR in Koalas, Three-toed Sloths and Howler Monkeys but up to six times SMR in small marsupial omnivores. Feeding rates were calculated to be  $51\text{g DM}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$ . Preformed water in the leaves was the major source of water intake (61%); free water as dew was estimated to provide 18% of total intake. The major energy expenditure was for basal metabolism and heat increment followed by activity and thermoregulation, but 23% of FMR could not be explained.

## Chapter 11

**GENERAL DISCUSSION**

This work has shown that both the Greater Glider and the Brushtail Possum can maintain nitrogen and energy equilibrium solely on a diet of mature *Eucalyptus* foliage and water *ad libitum*. Both species thus seem to be exceptions to the general relationship between body size and diet quality (e.g. Janis, 1976, Parra, 1978, Van Soest, 1982). Many studies have suggested that smaller animals, because of their higher mass-specific energy requirements, will be restricted to eating highly digestible foods because of the gut filling effects of a large bulk of slowly digesting fibre. Similarly, both species have coped with the high levels of plant secondary compounds without some of the adverse effects that might be predicted from studies on other species (e.g. Dollahite *et al.*, 1962, Nagy *et al.*, 1964).

Although mature leaf diets alone were sufficient to maintain captive animals, it seems unlikely that free-living animals of either species could survive on these diets. For example, the intake of metabolizable energy by captive Greater Gliders was only  $350\text{kJ}\cdot\text{kgW}^{0.75}\cdot\text{d}^{-1}$  (Chapter 8) whereas free-living animals required some  $560\text{kJ}\cdot\text{kg}^{-1}\cdot\text{d}^{-1}$  at a time when there were relatively few demands for thermoregulatory expenditure (Chapter 10). Field metabolic rate (FMR) has not been determined in Brushtail Possums but it is likely to be a similar multiple of SMR as found for Greater Gliders and Koalas (i.e. 2.7; Chapter 10). If this is true, then free living Brushtail Possums would require  $480\text{kJ}\cdot\text{kgW}^{0.75}\cdot\text{d}^{-1}$ , whereas their ME intake in the present study was only  $260\text{kJ}\cdot\text{kgW}^{0.75}\cdot\text{d}^{-1}$ . While FMR's of this magnitude are low compared with values found for arboreal omnivores, it is clear that both species would have to increase their ME intakes significantly in the wild. On the other hand, nitrogen requirements determined in the laboratory should closely reflect those in the field. However, free-living Greater Gliders at Wongi appeared to maintain themselves on diets of a much lower nitrogen content

than that found in *E. radiata* (Chapter 10). This may have been due to differences in the availability of the leaf nitrogen or to more efficient nitrogen retention.

The present study has identified several factors which affect the intake of dry matter and metabolizable energy and the retention of nitrogen in the two species of folivore. These can be divided into physical factors and factors related to the composition of the diet.

(a) **Physical Factors**

The data in Tables 3.2a,b showed that mastication in the Brushtail Possum resulted in more coarse and less fine particles than in the Greater Glider. This is consistent with observed differences in dental morphology with phalangerids employing more a coarse grinding action and less of the fine cutting action found in the Greater Glider and Ringtail Possum (Gipps, 1980). Creation of a larger pool of fine particles would reduce the gut-filling effect of a given amount of fibre and should increase the potential digestibility of the diet.

The large capacity of the hindgut of both species can be seen as a further advantage in dealing with a fibrous diet. Parra (1978) has derived relationships between the wet mass of digesta in the fermentation region of both hindgut and foregut fermenting herbivores and body mass. The contents of the caecum and proximal colon of the Brushtail Possum are 100% of Parra's (1978) expected values for foregut and hindgut fermenters combined and 121% of the value expected for hindgut fermenters alone. The contents of the caecum of the Greater Glider are 139% of expected values for all animals but 166% for hindgut fermenters. Although both species have a greater gut capacity than other hindgut fermenters of similar body mass, the larger hindgut capacity of the Greater Glider may partly explain the higher intakes of dry matter and metabolizable energy by this species.

A major difference between the Greater Glider and Brushtail Possum was that the Brushtails lacked an effective mechanism for selectively

retaining fine particles in the hindgut. This conclusion was reached on the basis of the uniformity of particle size classes in different parts of the gut, the similarity of the  $^{51}\text{Cr}$ -EDTA and  $^{103}\text{Ru}$ -P MRTs, and the lack of net solute secretion into the proximal colon (Rübsamen *et al.*, 1983). Greater Gliders, Koalas, and Ringtail Possums have all been shown to possess hindgut separation mechanisms. Separation mechanisms are thought to allow the hindgut to be cleared of fibre more rapidly and so allow intake to be maintained at a relatively high level. This may have been one reason for the higher dry matter intakes of foliage by Greater Gliders, Ringtail Possums and Koalas compared with Brushtail Possums.

Separation mechanisms have also been suggested to aid in nitrogen conservation by retaining a portion of the bacterial fraction that would otherwise be lost in the faeces (Sperber, 1968). In this study, the excretion of NDFN was a markedly higher proportion of dry matter intake in the Brushtail Possums than in other marsupial folivores. Some of this effect may be attributable to dietary differences between different studies but the lack of a hindgut separation mechanism may also be responsible. The high faecal nitrogen loss as NDFN was primarily responsible for the high maintenance nitrogen requirement of the Brushtail Possum in this, compared with other studies (Wellard and Hume, 1981a).

#### (b) Dietary Factors

Both *E. radiata* and *E. melliodora* leaves contained a high proportion of crude lipid and a low proportion of ash compared with many other tree foliages (Chapter 4). Both these features would tend to increase the digestible energy content of eucalypt leaves compared to tree foliage consumed by other arboreal folivores. On the other hand, most eucalypts, including *E. radiata* and *E. melliodora*, contain a high proportion of lignified fibre. It was suggested that the high content of lignin was one of the main reasons for the low digestibility of the fibre fraction of the two foliages. The high degree of lignification was also reflected in low rates of fermentation (Chapter 9) and scanning electron micrographs (Chapter 4) suggested that few bacteria attached to or degraded these lignified tissues.

Although several other studies have suggested that essential oils could deleteriously affect microbial activity, this did not appear to be the case in the present study (Chapter 7). The essential oils of both eucalypt species were almost completely absorbed prior to the hindgut and it is unlikely that significant interactions between oils and microbes occurred in either species. However, the urinary excretion of essential oils and their conjugated detoxification products was suggested as the principal reason for the low metabolizability of the energy of *E. radiata* by Greater Gliders. Greater Gliders lost 43% of their digestible energy in the urine compared with only 15-20% of DE in Brushtail Possums, Ringtail Possums and Koalas. The loss of nitrogen in the urine of the Greater Glider as  $\text{NH}_4$  would also have contributed to high urinary energy losses.  $\text{NH}_4$  may have been excreted to balance the urinary loss of acidic, conjugated detoxification products.

The loss of energy in the urine was the principal factor limiting ME intake in Greater Gliders. Similarly, the need to compensate for urinary N losses was the main reason for the high maintenance nitrogen requirement of the Greater Glider compared with most other marsupial herbivores.

While some tannins have been shown to complex dietary proteins (McLeod, 1974), their effect on nitrogen retention, in the Brushtail Possum at least, was minimal in the present study. However, deactivating the tannins of *E. melliodora* with PEG 4000 resulted in increased intakes of dry matter, and most importantly, ME. This appeared to be partly due to higher rates of microbial activity as reflected in a higher NDF digestibility. Thus the low digestibility of the fibre fraction of *E. melliodora* was attributable to its high degree of lignification and the inhibitory effects of tannins on microbial enzymes. This, together with the Brushtail Possum's apparent inability to rapidly excrete large particles, restricted dry matter intake and was the the principal factor limiting ME intake.

Two options appear to be open to free-living animals to increase their ME intakes in the wild. They must either feed on items of a higher



ME content while maintaining their intake of nitrogen, or else increase their intakes of readily digestible nutrients by increasing the rate of turnover of digesta in the hindgut. The mean retention time of solute and particulate digesta in both species was long compared with the retention of fibrous diets in other herbivores (Chapter 3). Since the maximum extent of fibre digestibility was probably closely approached, increasing the rate of digesta passage appears to be the most realistic strategy for both species to adopt. However, such a strategy may not be possible because of;

i) the importance of hindgut absorption and secretion processes in electrolyte and water conservation (Rübsamen *et al.*, 1983).

ii) the increased intake of allelochemicals accompanying the increased intake of dry matter. The energy cost of detoxification may well be greater than the energy gain from easily digestible nutrients above a particular intake threshold.

iii) the need to "detann" tannin-protein complexes. Lomdahl (1983) has shown that hindgut micro-organisms in the Ringtail Possum can degrade tannin-cytoplasm complexes but nothing is known of the kinetics of this process. However, on thermodynamic grounds, it is likely to occur only very slowly.

Clearly, a major problem with the interpretation of the patterns discussed above is a lack of detailed knowledge of the diets selected by these and other arboreal marsupials. For example, while *E. radiata* is an important dietary item of Greater Gliders in several areas, it is not known whether this species is ever eaten exclusively. Similarly, no observations have been made of the extent that *E. andrewsii* is eaten by Ringtail Possums. Data are needed on the amounts of foliage and other dietary items ingested by marsupial arboreal folivores, as well as their content of primary nutrients and allelochemicals. A promising start in this area has been made by Cork and Pahl (1984), who showed that wild Ringtail Possums

chose a mixed diet of young leaves (including non-eucalypts) that maximized their intake of nitrogen and minimized the intake of cell walls. In the present study, the high nitrogen requirement of the Greater Glider appeared to be linked to the high allelochemical content of *E. radiata*, and nitrogen equilibrium in this species can probably be maintained on species of lower nitrogen content so long as allelochemical content is also lower. Future comparative studies should concentrate on finding common diets, and the possibility of developing non-eucalypt diets for these folivores should not be ignored.

The separation mechanism in the hindgut were suggested as an important feature for increasing the effective gut capacity and allowing a higher intake of dry matter in the Greater Glider compared with the Brushtail Possum. Although the present study showed that there was little separation between the fine and coarse particulate digesta phases in the Brushtails, further studies are required to evaluate the extent of retrograde transport in this species. The recent demonstration of mucous layers in the hindgut of rats and lemmings that have a high affinity for bacteria (Sperber *et al.*, 1983) is an important advance in the understanding of the utilization of fibrous diets by small herbivores. The possibility of similar mechanisms occurring in small arboreal mammals should be investigated in future studies.

Several aspects of the utilization of leaf allelochemicals are also worthy of further study. In particular, data are required on the nitrogen and energy costs for detoxification, and in particular the requirement for  $\text{NH}_4^+$  for maintenance of acid-base balance. The Ringtail Possum may be more suitable for the study of this problem than the Greater Glider. In the studies of Chilcott and Hume (1984b), the Ringtail also excreted a negligible proportion of its urinary nitrogen as urea, and its diet can be more easily manipulated than that of the Greater Glider. Supplementation with PEG was a useful way of studying some of the effects of tannins on digestion in the Brushtail Possum. Although Greater Gliders would not accept PEG in their drinking water, spraying of a PEG solution onto the leaves could be tried in future studies. More information is also

required on the kinetics of PEG binding with tannins as well as on the biochemical characteristics of eucalypt tannins and proteins.

The gap between dietary studies and studies of digestive physiology and nutrition of marsupial arboreal folivores has already been highlighted. Surprisingly, the situation with eutherian arboreal folivores is the opposite, with nutritional studies lagging behind those of diet choice. Comparative studies of the digestive physiology of folivorous eutherians (e.g. *Hylobates* and *Presbytis*) would allow examination of the relative advantages and disadvantages of foregut and hindgut fermentation in the utilization of foliage diets. This work has important implications for the conservation of threatened species and for an understanding of the evolution of the human diet and should receive high priority from funding agencies in the future.

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APPENDIX 1a: Percentage composition of steam volatile essential oil from *E. radiata* and Greater Glider faeces (Exp2)

Peak number (Fig.7.1a)	Identification	<i>E. radiata</i> (%)	Greater Glider faeces (%)
1	$\alpha$ -pinene	4.86	1.11
1a	---	-	0.78
2	$\beta$ -pinene	0.30	0.32
3	Unknown	0.43	0.19
4	Myrcene	0.90	1.80
5	$\alpha$ -phellandrene	9.33	3.74
6	$\alpha$ -terpinene	4.43	1.88
7	Limonene	0.62	0.43
8	1,8 cineole	4.30	1.86
9	$\gamma$ -terpinene	7.46	2.27
10	p-cymene	10.53	2.42
11	Terpinolene	2.15	0.87
12	C <sub>10</sub> H <sub>18</sub> O	0.27	0.19
12a	C <sub>10</sub> H <sub>18</sub> O	-	0.29
13	C <sub>10</sub> H <sub>18</sub> O	0.43	0.20
14	C <sub>10</sub> H <sub>18</sub> O	0.44	0.29
15	Trans-p-menth-2en-1-ol	4.47	4.78
15a	---	-	0.87
15b	---	-	0.74
16	Terpinen-4-ol	19.78	3.39
17	Cis-p-menth-2en-1-ol	3.34	2.65
17a	---	-	0.73
17b	---	-	0.66
18	Cis-piperitol	1.37	1.06
19	$\alpha$ -terpineol	2.14	0.90
20	Piperitone	0.69	0.54
21	Trans-piperitol	2.58	2.86
22	Unknown	1.02	0.33
23	4-phenyl butanone	1.51	0.18
23a	---	-	21.32

/continued

Appendix 1a: (continued)

Peak number (Fig.7.1a)	Identification	<i>E. radiata</i> (%)	Greater Glider faeces (%)
23b	---	-	2.87
24	Unknown	1.06	0.67
25	Viridiflorol	0.43	0.40
25a	---	-	0.32
26	$\gamma$ -eudesmol	1.19	1.00
26a	---	-	0.98
26b	---	-	1.42
27	$\alpha$ -eudesmol	1.08	0.92
28	$\beta$ -eudesmol	1.57	1.32

APPENDIX 1b: Percentage composition of steam volatile essential oil from *E. melliadora* and from Brushtail Possum faeces

Peak number (Fig.7.1b)	Identification	<i>E. melliadora</i> (%)	Brushtail Possum faeces (%)
1	Unknown	0.6	(a)
2	Iso-valeric aldehyde	2.0	2.48
3	$\alpha$ -pinene	7.5	7.64
4	Unknown	0.8	0.98
5	Limonene	4.9	3.14
6	1,8 cineole	63.1	3.42
7	$\gamma$ -terpinene	0.3	0.54
8	p-cymene	2.2	1.54
9	Terpinolene	0.3	0.24
10	Terpinen-4-ol	0.8	4.73
11	Unknown	0.8	1.33
11a	---	-	1.00
11b	---	-	2.00
12	Unknown	0.7	0.54
13	$\alpha$ -terpineol	1.7	1.05
14	Unknown	0.7	0.87
15	Unknown	0.4	1.35
16	Unknown	0.3	-
16a	---	-	14.42
16b	---	-	2.03
16c	---	-	20.5
17	Unknown	0.9	1.55
18	Unknown	0.6	1.34
19	Unknown	1.8	1.57
19a	---	-	1.95
20	Unknown	0.8	1.40

(a) Coinjected with solvent

## APPENDIX 2

### STRUCTURE AND IDENTITY OF FAECAL UNKNOWN

Examination of the infra-red spectrum of the faeces oil from the Greater Glider showed a strong peak suggesting the presence of an ester in large amounts. The electron impact (EI) mass spectrum did not show a molecular ion but suggested that the compound was aliphatic and non-terpenoid. The chemical ionization (CI) mass spectrum indicated that the compound had a molecular weight of 286 and high resolution measurements on this peak indicated a composition of  $C_{16}H_{30}O_4$ .

The assignment of the major component as an ester was confirmed by hydrolysis. The oil was saponified and the alkaline solution extracted with pentane. The aqueous solution was acidified and extracted with methylene chloride and methylated. GLC of the pentane extract revealed that the major (ester) peak had been removed but all other peaks remained. However, the trace did not show the presence of the expected alcohol resulting from the hydrolysis. GLC-MS of the methylene chloride extract gave a peak of MW 148 which was assigned as an octane-diol due to similarities with published spectra of octane-diols. Presumably the compound was too polar to be extracted by pentane hence remained with the acid fraction.

The ester then appeared to be a diester of an octane-diol in which case, the esterifying acid could be either butyric or isobutyric acid (assuming symmetrical substitution). A small peak was apparent in the chromatogram of the methylated acid fraction which could be tentatively assigned as methyl butyrate.

While butyrates of terpene alcohols are known as essential oil constituents, (E.V Lassak, pers. comm.) the appearance of the unknown peak in and posterior to the caecum suggested that it was not a component of the original oil that had been concentrated by selective absorption of other

components. Similarly, the relative lack of isobutyric acid compared with butyric acid in the hindgut of both species suggests that the esterifying acid is most likely butyric acid.

The structure of the octane-diol is as yet uncertain. However, synthetic esters were prepared from 2-ethyl hexan-1,3 diol and both butyric and isobutyric acid. While the mass spectra of these two compounds showed certain similarities with the unknown compound, they were not identical. Furthermore, the retention time of these two esters was considerably longer than the unknown but this could be explained by postulating a branched structure for the octane-diol.

APPENDIX 1a: Percentage composition of steam volatile essential oil from *E. radiata* and Greater Glider faeces (Exp2)

Peak number (Fig.7.1a)	Identification	<i>E. radiata</i> (%)	Greater Glider faeces (%)
1	$\alpha$ -pinene	4.86	1.11
1a	---	-	0.78
2	$\beta$ -pinene	0.30	0.32
3	Unknown	0.43	0.19
4	Myrcene	0.90	1.80
5	$\alpha$ -phellandrene	9.33	3.74
6	$\alpha$ -terpinene	4.43	1.88
7	Limonene	0.62	0.43
8	1,8 cineole	4.30	1.86
9	$\gamma$ -terpinene	7.46	2.27
10	p-cymene	10.53	2.42
11	Terpinolene	2.15	0.87
12	C <sub>10</sub> H <sub>18</sub> O	0.27	0.19
12a	C <sub>10</sub> H <sub>18</sub> O	-	0.29
13	C <sub>10</sub> H <sub>18</sub> O	0.43	0.20
14	C <sub>10</sub> H <sub>18</sub> O	0.44	0.29
15	Trans-p-menth-2en-1ol	4.47	4.78
15a	---	-	0.87
15b	---	-	0.74
16	Terpinen-4-ol	19.78	3.39
17	Cis-p-menth-2en-1-ol	3.34	2.65
17a	---	-	0.73
17b	---	-	0.66
18	Cis-piperitol	1.37	1.06
19	$\alpha$ -terpineol	2.14	0.90
20	Piperitone	0.69	0.54
21	Trans-piperitol	2.58	2.86
22	Unknown	1.02	0.33
23	4-phenyl butanone	1.51	0.18
23a	---	-	21.32

/continued



## Appendix 1a: (continued)

Peak number (Fig.7.1a)	Identification	<i>E.</i> <i>radiata</i> (%)	Greater Glider faeces (%)
23b	---	-	2.87
24	Unknown	1.06	0.67
25	Viridiflorol	0.43	0.40
25a	---	-	0.32
26	$\gamma$ -eudesmol	1.19	1.00
26a	---	-	0.98
26b	---	-	1.42
27	$\alpha$ -eudesmol	1.08	0.92
28	$\beta$ -eudesmol	1.57	1.32

APPENDIX 1b: *Percentage composition of steam volatile essential oil from E. melliadora and from Brushtail Possum faeces*

Peak number (Fig.7.1b)	Identification	<i>E. melliadora</i> (%)	Brushtail Possum faeces (%)
1	Unknown	0.6	(a)
2	Iso-valeric aldehyde	2.0	2.48
3	$\alpha$ -pinene	7.5	7.64
4	Unknown	0.8	0.98
5	Limonene	4.9	3.14
6	1,8 cineole	63.1	3.42
7	$\gamma$ -terpinene	0.3	0.54
8	p-cymene	2.2	1.54
9	Terpinolene	0.3	0.24
10	Terpinen-4-ol	0.8	4.73
11	Unknown	0.8	1.33
11a	---	-	1.00
11b	---	-	2.00
12	Unknown	0.7	0.54
13	$\alpha$ -terpineol	1.7	1.05
14	Unknown	0.7	0.87
15	Unknown	0.4	1.35
16	Unknown	0.3	-
16a	---	-	14.42
16b	---	-	2.03
16c	---	-	20.5
17	Unknown	0.9	1.55
18	Unknown	0.6	1.34
19	Unknown	1.8	1.57
19a	---	-	1.95
20	Unknown	0.8	1.40

(a) Coinjected with solvent