THE UTILIZATION OF EUCALYPTUS FOLIAGE BY THE GREATER GLIDER

(Petauroides volans) AND THE BRUSHTAIL POSSUM (Trichosurus vulpecula).

A thesis submitted for the degree of Doctor of Philosophy in the University of New England.

by

WILLIAM JOHN FOLEY

B. Nat. Res. Hons II(i)

The Department of Biochemistry and Nutrition, The University of New England, Armidale, N.S.W., Australia

August, 1984.

PREFACE

The studies presented in this thesis were completed by the author while a postgraduate student in the Department of Biochemistry and Nutrition at the University of New England, Armidale, N.S.W., Australia. Assistance given by other persons is indicated in the text or in the list of acknowledgements. All references cited are included in a bibliography. The work is otherwise original.

* * *

I certify that the substance of this thesis has not already been submitted for any degree and is not being currently submitted for any other degree. I certify that any help received in preparing this thesis and all sources used, have been acknowledged in the thesis.

AUGUST, 1984

W. J. FOLEY.

SUMMARY

The utilization of *Eucalyptus* foliage as a food source by Greater Gliders (*Petauroides volans*) and Brushtail Possums (*Trichosurus vulpecula*) was studied in captive animals fed diets of *E. radiata* and *E. melliodora* respectively.

The rate of passage of solute (⁵⁴Cr-EDTA) and particulate (¹⁰³Ru-Phenanthroline) digesta markers was slow in both species. The mean retention time (MRT) of the two markers was 50h and 46h in the Greater Gliders and 51h and 46h in the Brushtail Possums. The lack of separation between these two markers was consistent with the lack of selective retention of fine particles in the hindgut of the Brushtail Possum. However, fine particles occurred in greater quantities in caecal digesta of the Greater Glider (48% DM) than in the stomach (30% DM) or faeces (16% DM). The rate of passage of an alternative particle marker (⁵¹Cr-mordanted large particles (<1.0mm>0.5mm)) in the Greater Gliders, was less than half that of ¹⁰³Ru-P. From this it was concluded that ¹⁰³Ru-P excretion reflected the excretion of fine digesta particles which were selectively retained in the caecum along with solute digesta.

The foliage fed to both species was relatively low in nitrogen compared with many other plant species, and although the NDF content was moderate, this fibre was highly lignified (lignin:NDF \simeq 0.4-0.5). There was little seasonal variation in foliage composition. The digestibility of the fibre fraction of the leaves, although low, was similar to or higher than that found in a range of herbivores fed browse or foliage diets. Observations made of digesta fragments from the gut of both species with a scanning electron microscope showed that mesophyll and the less lignified parts of the vascular bundles were digested first. The epidermis and the more highly lignified tissues such as vessel elements proved most resistant to digestion. Bacteria were the only micro-organisms observed in the hindgut of either species, and many of these attached to plant particles by means of extracellular materials. Both species maintained positive nitrogen balance on the foliage diets but maintenance nitrogen requirements were higher than those of other arboreal marsupials fed eucalypt diets. Greater Gliders required 0.56 g $\cdot kgW^{-0.75} \cdot d^{-1}$ of truly digestible nitrogen while Brushtail Possums required 0.42 g $N \cdot kgW^{-0.75} \cdot d^{-1}$. The major nitrogen loss in the Brushtails was faecal nitrogen and in particular NDFN. This was attributed to relatively low feed intakes, a low digestibility of fibre and to the lack of an effective mechanism for retaining fine particles such as bacteria in the caecum. In contrast, the high maintenance nitrogen requirement of the Greater Glider was due to the loss of more than 50% of the truly digestible nitrogen intake in the urine, principally as NH4. It was proposed that NH4 was excreted to balance the urinary excretion of acidic detoxification products.

Supplementation of Brushtail Possums with polyethylene glycol (PEG) resulted in higher intakes of dry matter $(37 - 48 \text{ g} \cdot \text{kgW}^{-0.75} \cdot \text{d}^{-1})$ metabolizable energy (ME) $(0.27 - 0.45 \text{ MJ} \cdot \text{kgW}^{-0.75} \cdot \text{d}^{-1})$ and truly digestible nitrogen $(0.44 - 0.64 \text{ g} \text{ N} \cdot \text{kgW}^{-0.75} \cdot \text{d}^{-1})$ and higher digestibilities of neutral detergent fibre (27 - 48%). The overall dry matter digestibility of the diet was unchanged. These effects were attributed to the removal of the inhibitory effects of leaf tannins on microbial enzymes by PEG.

Although *E. radiata* contained significantly higher levels of essential oils than did *E. melliodora*, these were virtually completely absorbed in both species. Most of this oil was absorbed cranial to the hindgut and there seemed little possibility of significant interaction with the hindgut micro-organisms. Loss of terpenes during mastication occurred in Greater Gliders but was an insignificant route of loss compared to absorption from the stomach and small intestine.

The major factor limiting metabolizable energy intake in the Greater Glider was the high loss of energy in the urine. This was attributed to the excretion of essential oils and phenolic compounds, their detoxification products and nitrogen as NH4. The maintenance energy requirement of the Greater Glider was estimated to be 0.35 MJ·kgW^{-0.75}·d^{-1.} The lower intakes and digestibilities of *E. melliodora* dry matter in the

Brushtail Possum were the major reasons for the lower intake of digestible energy compared with the Greater Glider, but lower uninary energy losses meant that ME intake as a proportion of GE intake was similar in the two species.

Measurement of the concentration of short chain fatty acids (SCFA) throughout the gut confirmed that the caecum of the Greater Glider and the caecum and proximal colon of the Brushtail Possum were the principal sites of microbial activity. The rate of SCFA production *in vitro* was 33 mmol $\cdot kgW^{-0.75} \cdot d^{-1}$ in the Greater Glider and 40 mmol $\cdot kgW^{-0.75} \cdot d^{-1}$ in the Greater Glider and 40 mmol $\cdot kgW^{-0.75} \cdot d^{-1}$ in the Brushtail Possum. These rates were slow compared with most other herbivores and this was attributed to the high degree of lignification of the diets. Acetate was the principal SCFA produced in both species followed by propionate in the case of the Greater Glider and by butyrate in the case of the Brushtail Possum. SCFA production contributed 8% of the digestible energy intake (DEI) of the Greater Glider but 16% of the DEI of the Brushtail Possum.

The energy required for free existence of Greater Gliders was measured (using $H^3 H^{1.6}$ O) in mixed eucalypt forest in south-eastern Queensland. The field metabolic rate for males was 547 kJ·kgW^{-1.dt-1}. The major energy expenditure was for basal metabolism and heat increment (43%) followed by activity (26%) and thermoregulation (9%). Feed intake was estimated to be about 50g of dry matter per day. Intake of water was 87 ml·kg^{-1.dt-1} of which 61% came from preformed water in the leaves and 20% as oxidation water, with 16ml from sources such as dew or rainwater on leaves.

Efficient mastication and a relatively large hindgut, together with the selective retention of fine particles in the case of the Greater Glider, were important adaptations for utilizing *Eucalyptus* foliage diets. However, it seemed unlikely that either marsupial species could survive solely on these single species diets in the wild unless they were able to substantially increase their intake of easily digestible nutrients.

ACKNOWLEDGMENTS

I thank my supervisor, Associate Professor I.D. Hume for initially stimulating my interest in marsupial nutrition and for his guidance and advice in all stages of this study.

Greater Gliders were captured with the enthusiastic assistance of a large number of forestry workers but in particular I thank Messrs J. Brandis, J. Brandt, M. Inman, S. Sinclair, and D. Williams of the N.S.W. Forestry Commission and Mr C. Schubert of Allen Taylor Pty. Ltd. Mr and Mrs M. Ross of Ebor kindly allowed me to cut leaves from trees on their properties.

I am pleased to acknowledge the active collaboration of Dr E. Lassak (N.S.W. Department of Agriculture) and Dr J. Brophy, (University of New South Wales) in the studies described in Chapter 7 and Mr J. Kehl (Queensland Forestry Department) and Associate Professor K. Nagy (University of California, Los Angeles) in the studies described in Chapter 10.

Technical assistance was provided at various times by Mrs R. Busby, Mrs L. Jenkins, Mr J. Kent, Mr J. Lea and Ms A. Parker. Staff of the Faculty of Rural Science workshop and animal house, in particular Messrs H. Deiderick, M.E. Hope and D. Sharp. I extend my grateful thanks for the enthusiastic support of all these people. I would also like to thank the staff of the Electron Microscope Unit (Mr. M. Speak and Mr. P. Garlick) for their advice.

I am indebted to Dr S. Cork (CSIRO Wildlife and Rangelands Research), Mr M. Chilcott (University of New England), Dr D. Dellow, (DSIR Applied Biochemistry, New Zealand), Dr R. Jenness (University of Minnesota), Mr D. Tucker, (University of New England), Dr and Mrs K. Rübsamen, (Universitat Hohenheim, Federal Republic of Germany) and Dr R. White, (University of Alaska) for useful discussions and assistance when required. Dr V. Bofinger provided statistical advice whenever necessary.

I also thank all the other technical and academic staff and postgraduate students of the Department of Biochemistry and Nutrition for their help and for providing such a pleasant working environment. In particular, I thank the departmental secretaries, Mrs J. Hansford and Mrs B. Harrison for their typing skills.

I thank Ms A. Hennell for her continuing support and encouragement throughout the study. I am also grateful to my parents for their support throughout my time at university. The work was funded by a University of New England Postgraduate Research Scholarship and the Department of Social Security. TABLE OF CONTENTS

PREFACE

SUMMARY

ACKNOWLEDGEMENTS					
LIST OF TA	BLES				
LIST OF FIG	LIST OF FIGURES				
INTRODUCTIO	N	1			
CHAPTER 1	LITERATURE REVIEW	4			
1.1	Eucalyptus - Evolution and Life History 1.1.1 Distribution and leafing patterns 1.1.2 Evolution of Eucalyptus 1.1.3 Herbivory and Eucalyptus 1.1.4 Evolution of gliding mammals and Eucalyptus allelochemicals	4 4 5 6 7			
1.2	Problems Faced by Arboreal Folivores 1.2.1 Characteristics of arboreal folivores 1.2.2 The problem of body size 1.2.3 Tree foliage as a food resource 1.2.4 Food choice by arboreal folivores	9 9 11 12 13			
1.3	Adaptations of Arboreal Folivores 1.3.1 Metabolic rate 1.3.2 Rate of passage of digesta 1.3.3 Fermentation 1.3.4 Detoxification 1.3.5 Fermentation strategies and plant allelochemicals	15 15 17 18 21 22			
1.4	Eucalyptus as a Food Resource 1.4.1 Eucalyptus primary nutrients 1.4.2 Allelochemical profile 1.4.2.1 Essential oils 1.4.2.2 Polyphenolics and tannins 1.4.2.3 Cyanide 1.4.2.4 Miscellaneous 1.4.2.5 Conclusion 1.4.3 Digestibility of eucalypt foliage	25 26 26 28 31 32 33			
1.5	The Greater Glider and Brushtail Possum as Arboreal Folivores	34			

	<pre>1.5.1 Distribution and life history 1.5.2 Degree of arboreality and folivory 1.5.3 Structure of the digestive tract 1.5.4 Diet 1.5.5 Energetics 1.5.6 Response to primary nutrients</pre>	34 36 37 39 39 39 39 40 41 41 42 42
1 (1.5.7.2 Other	43
1.5	Recapitulation	44
CHAPTER 2	GENERAL MATERIALS AND METHODS	45
2.1	Animals	45
2.2	Animal Husbandry 2.2.1 Holding enclosures 2.2.2 Maintenance feeding 2.2.3 Collection of foliage 2.2.4 Disease and management	45 45 45 46 47
2.3	Experimental Conditions 2.3.1 Rooms and cages 2.3.2 Input/output measurements	47 47 48
2.4	Analytical 2.4.1 Dry matter 2.4.2 Ash and acid-insoluble ash 2.4.3 Gross energy 2.4.4 Nitrogen compounds 2.4.5 Crude lipid 2.4.6 Total non-structural carbohydrate 2.4.7 Dietary fibre 2.4.8 Phenolic compounds 2.4.9 Essential oils	49 49 50 50 50 51 52 52 52 52
2.5	Statistical	54
CHAPTER 3	THE RATE AND PATTERN OF DIGESTA FLOW THROUGH THE GUT OF THE GREATER GLIDER AND BRUSHTAIL POSSUM	55
3.1	Introduction	55
	PART A	
3.2	Materials and Methods 3.2.1 Design	56 56

ix

	3.2.2 Markers 3.2.3 Collection of faeces and urine 3.2.4 Analysis of markers 3.2.5 Statistical 3.2.6 Distribution of digesta particle sizes	57 57 58 59
3.3	Results 3.3.1 Marker behaviour 3.3.2 Marker excretion and retention times 3.3.3 Particle size distribution	59 59 59 60
3.4	Discussion	61
	PART B	
3.5	Materials and Methods 3.5.1 Preparation of particles 3.5.2 Preparation of mordants 3.5.3 Administration of markers 3.5.4 Analysis	65 65 66 66 66
3.6	Results 3.6.1 Marker behaviour 3.6.2 Excretion of markers	67 67 67
3.7	Discussion	68
3.8	Mechanisms and Advantages of Selective Digesta Retention	70
3.9	Summary	73
CHAPTER 4	DIGESTION OF EUCALYPTUS FOLIAGE BY THE GREATER GLIDER AND BRUSHTAIL POSSUM	74
4.1	Introduction	74
	PART A COMPOSITION OF THE DIET	
4.2	Materials and Methods	75
4.3	Results	76
4.4	Discussion	77
	PART B DIGESTION OF FOLIAGE CONSTITUENTS	

4.5 Materials and Methods

х

4	.6 Results 4.6.1 Dry matter and cell contents 4.6.2 Fibre digestibility	80 80 81
4	.7 Discussion 4.7.1 Dietary bias 4.7.2 Intake and digestibility of dry matter	82 82
	and cell contents 4.7.3 Fibre digestibility 4.7.4 Lignin digestibility	83 84 87
	PART C MICROSCOPIC EVALUATION OF FOLIAGE DIGESTION	
4	.8 Materials and Methods	89
4	.9 Results 4.9.1 Plant ultrastructure in intact and	89
	degraded tissues 4.9.2 Micro-organisms involved with degraded	89
	plant tissues	90
4	.10 Discussion	91
4	.11 Digestion of Eucalypt Foliage by Arboreal Marsupials	94
4	.12 Summary	97
CHAPTER	5 NITROGEN AND UREA METABOLISM IN THE GREATER GLIDER AND BRUSHTAIL POSSUM	98
5	.1 Introduction	98
5	 2 Materials and Methods 5.2.1 Nitrogen intake and excretion 5.2.2 Urea metabolism 5.2.3 Composition of urinary nitrogen 5.2.4 Alteration of Greater Glider urinary urea:ammonia ratio 	99 99 100 101 101
5	 .3 Results 5.3.1 Nitrogen intake and excretion 5.3.2 Non-dietary faecal nitrogen and the true digestibility of dietary nitrogen 5.3.3 Maintenance nitrogen requirement 5.3.4 Urea metabolism 5.3.5 Composition of urinary nitrogen 5.3.6 Greater Glider urinary nitrogen excretion 	101 103 103 104 104 105
5	.4 Discussion	105
5	.5 Summary	113

xi

CHAPTER 6	THE EFFECT OF TANNINS ON DIGESTION IN THE BRUSHTAIL POSSUM	114
6.1	Introduction	114
6.2	Materials and Methods 6.2.1 Leaf phenolics 6.2.2 PEG supplementation 6.2.3 Statistical	115 115 115 116
6.3	Results 6.3.1 Relationships between leaf phenolics and leaf intakes 6.3.2 Brushtail Possums: PEG supplementation	117 117 117
6.4	Discussion	119
6.5	Summary	125
CHAPTER 7	ESSENTIAL OIL METABOLISM	
7.1	Introduction	127
7.2	Materials and Methods 7.2.1 Experiment 1 7.2.2 Experiment 2 7.2.3 Experiment 3 7.2.4 Experiment 4	128 128 128 128 128 129
7.3	Results 7.3.1 Experiment 1 7.3.2 Experiment 2 7.3.3 Experiment 3 7.3.4 Experiment 4	129 129 130 131 131
7.4	Discussion	131
7.5	Summary	137
CHAPTER 8	ENERGY METABOLISM AND BALANCE IN THE GREATER GLIDER AND BRUSHTAIL POSSUM	139
8.1	Introduction	139
8.2	Materials and Methods 8.2.1 Energy intake and excretion 8.2.2 Heat production 8.2.2.1 Respirometers 8.2.2.2 Analysis 8.2.3 Fasting heat production 8.2.4 Energy retention 8.2.5 Methane production	140 140 140 140 140 141 141 141

xii

	8.2.6 Plant respiration	142
8.3	Results 8.3.1 Fasting heat production of Greater Gliders 8.3.2 Energy intake and excretion 8.3.3 Energy retention in Greater Gliders 8.3.4 Methane production 8.3.5 Plant respiration	143 143 143 144 144 144
3.4	Discussion 8.4.1 Fasting heat production 8.4.2 Energy intake and excretion 8.4.3 Energy retention in Greater Gliders 8.4.4 Maintenance energy requirement	145 145 147 150 153
8.5	Summary	15 4
CHAPTER 9	MICROBIAL DIGESTION IN THE GREATER GLIDER AND BRUSHTAIL POSSUM	155
9.1	Introduction	155
9.2	Materials and Methods	156
9.3	Results 9.3.1 Concentration of SCFA at different sites in the gut 9.3.2 SCFA production rates	157 157 157
9.4	Discussion	159
9.5	Summary	165
CHAPTER 10	ENERGY AND WATER METABOLISM IN FREE-LIVING GREATER GLIDERS	166
10.3	1 Introduction	166
10.2	2 Materials and Methods 10.2.1 The study area 10.2.2 Water turnover 10.2.3 Diet 10.2.4 Analytical	167 167 167 168 168
10.3	3 Results 10.3.1 Temperature and rainfall 10.3.2 Diet 10.3.3 Body weights and sex of captured animals 10.3.4 Water influx and efflux rates 10.3.5 CO ₂ production rates 10.3.6 Metabolic rates, feeding rates and water balance	169 169 169 169 170 170 170

xiii

10.4 Discussion 10.4.1 Validity of the doubly-labelled water method 10.4.2 Validity of assumptions 10.4.3 Field metabolic rate and energy budget 10.5 Summary	171 171 172 173 177
CHAPTER 11 GENERAL DISCUSSION	178
REFERENCES	185

APPENDICES

LIST OF TABLES

		Facing
1.1	Composition of plant parts available to arboreal mammals.	12
3.1a	Measures of the retention of single oral doses of ⁵¹ Cr-EDTA and ¹⁰³ Ru-P estimated by faecal collection in Greater Gliders.	59
3.1b	Measures of the retention of single oral doses of ⁵¹ Cr-EDTA and ¹⁰³ Ru-P estimated by faecal collection in Brushtail Possums.	59
3.2a	Proportions of digesta from various gut segments of Greater Gliders retained on sieves of different sizes.	60
3.2b	Proportions of digesta from various gut segments of Brushtail Possums retained on sieves of different sizes.	60
3.3	Rate of passage of digesta markers in herbivores.	62
3.4	Summary of digesta passage studies in Brushtail Possums.	63
3.5	Measures of the retention of single oral doses of a $^{51}{\rm Cr-mordant}$ of <i>E. radiata</i> cell walls (> 0.5mm \leqslant 1.0mm) and $^{103}{\rm Ru-P}$ estimated by faecal collection in Greater Gliders.	67
4. 1A	Composition of <i>E. radiata</i> foliage eaten by Greater Gliders during different experiments.	76
4.1b	Composition of <i>E. melliodora</i> foliage eaten by Brushtail Possums during different experiments.	76
4.2	Variation in foliage constituents within a single <i>E. radiata</i> and a single <i>E. melliodora</i> tree.	76
4.3a	Effect of sequential extractions and sodium sulphite on the determination of cell wall constituents of <i>E. radiata</i> and Greater Glider faeces.	77
4.3b	Effect of sequential extractions and sodium sulphite on the determination of cell wall constituents of <i>E. melliodora</i> and Brushtail Possum faeces.	77
4.4	Composition of the mature foliage of diets offered to or selected by some arboreal folivores.	79
4.5	Body weight and body weight change of Greater Gliders and Brushtail Possums during feeding experiments.	79
4.6a	Intake, excretion and apparent digestibility of dry matter by Greater Gliders.	80

xv

4.6b	Intake, excretion and apparent digestibility of dry matter by Brushtail Possums.	80
4.7a	Intake, excretion and apparent digestibility of cell contents by Greater Gliders.	80
4.7b	Intake, excretion and apparent digestibility of cell contents by Brushtail Possums.	80
4.8a	Intake, excretion and apparent digestibility of cell wall constituents of <i>E. radiata</i> foliage by Greater Gliders.	81
4.8b	Intake, excretion and apparent digestibility of cell wall constituents of <i>E. melliodora</i> foliage by Brushtail Possums.	82
4.9	Intake and digestibility of dry matter and digestibility of cell walls in marsupials fed eucalypt foliage diets.	83
4.10	Digestibility of the dry matter and fibre of foliage or browse diets by some herbivores.	85
5.1a	Intake, excretion, retention and apparent digestibility of nitrogen in Greater Gliders.	101
5.1b	Intake, excretion, retention and apparent digestibility of nitrogen in Brushtail Possums.	101
5.2a	Non-dietary faecal nitrogen (NDFN) excretion and the true digestibility of dietary nitrogen in Greater Gliders.	103
5.2b	Non-dietary faecal nitrogen (NDFN) excretion and the true digestibility of dietary nitrogen in Brushtail Possums.	103
5.3	Summary of techniques used to estimate NDFN excretion in the Greater Glider and the Brushtail Possum.	103
5.4	Kinetics of [14C] urea in (a) Greater Gliders and (b) Brushtail Possums derived using a single injection of [14C] urea.	104
5.5	Composition of urinary nitrogen.	105
5.6	Maintenance nitrogen requirements of several marsupial and eutherian herbivores.	105
5.7	Partitioning of nitrogen excretion in several species of herbivorous marsupials at similar levels of truly digestible nitrogen intake.	105
5.8	Non-dietary faecal nitrogen excretion in several eutherian and marsupial herbivores.	107
5.9	Parameters of urea kinetics in several marsupial and eutherian mammals fed low protein diets.	108

xvi

6.1	Content of total phenolics and leucoanthocyanidins and the astringency of methanolic extracts of <i>E. radiata</i> and <i>E. melliodora</i> foliage.	117
6.2	Intake, excretion and apparent digestibility of dry matter by Brushtail Possums supplemented with PEG.	117
6.3	Intake, excretion and apparent digestibility of cell contents by Brushtail Possums supplemented with PEG.	117
6.4	Intake, excretion and apparent digestibility of cell wall constituents by Brushtail Possums supplemented with PEG.	117
6.5	Intake, excretion and apparent digestibility of nitrogen in Brushtail Possums supplemented with PEG.	117
6.6	Intake and excretion of energy by Brushtail Possums supplemented with PEG.	117
6.7	Effect of PEG4000 on the determination of cell wall constituents of Brushtail Possum faeces.	117
6.8	Means of all feeding experiments with Brushtail Possums supplemented with or lacking PEG.	118
7.1	Yield of essential oil from the foliage and from different parts of the gut of the Greater Glider and Brushtail Possum.	129
7.2a	Major components of the steam volatile oil from <i>E. radiata</i> and the concentration in different parts of the gut of the Greater Glider.	130
7.2b	Major components of the steam volatile oil from <i>E. melliodora</i> and the concentration in different parts of the gut of the Brushtail Possum.	130
8.1	Body weight, heat production and respiratory quotients of fasted, resting, Greater Gliders.	143
8.2a	Intake and excretion of energy by Greater Gliders.	143
8.2b	Intake and excretion of energy by Brushtail Possums.	143
8.3	Energy intake, heat production and energy retention in Greater Gliders fed various levels of <i>E. radiata</i> foliage.	144
8.4	Standard metabolic rate in some arboreal mammals.	146
8.5	Digestible, metabolizable and net energy coefficients in several eutherian and marsupial herbivores.	148
8.6	Methane production in several non-domesticated herbivores.	149

	٠		
V117	1		-
ΛV	т	т	Т

9.1a	Concentration and molar proportions of SCFA in digesta from different sites in the gut of the Greater Glider.	157
9.1b	Concentration and molar proportions of SCFA in digesta from different sites in the gut of the Brushtail Possum.	157
9.2a	<i>In vitro</i> production rates of SCFA in the caecum of two Greater Gliders at each of three times of day.	158
9.2b	<i>In vitro</i> production rates of SCFA in the caecum and proximal colon of the Brushtail Possum.	158
9.3a	Weight of caecal digesta and the contribution of caecal SCFA to energy intake of Greater Gliders.	158
9.3b	Weight of digesta in the caecum and proximal colon and the contribution of digesta produced therein to energy intake in the Brushtail Possum.	158
9.4	Short chain fatty acid production in several eutherian and marsupial herbivores.	160
10.1	Diet and diet composition of Greater Gliders at Wongi, July 1982.	169
10.2	Details of body weight, water input and output rate and $\rm CO_2$ production rate of Greater Gliders at Wongi in winter.	169
10.3	Details of metabolic rate, feeding rate and water balance of Greater Gliders at Wongi in winter.	170
10.4	Effect of variation in assumed faecal and urinary energy loss on calculated gross energy intake.	172
10.5	Estimated field energy budget for male Greater Gliders at Wongi in winter.	174

LIST OF FIGURES

1.1	The alimentary tract of (A) the Greater Glider and (B) the Brushtail Possum.	36
2.1	Metabolism cage and collection apparatus used in feeding experiments.	48
3 .1 a	Change in faecal concentration of ^{\$1} Cr and ¹⁰³ Ru with time in one Greater Glider following an oral dose of ⁵¹ Cr-EDTA and ¹⁰³ Ru-P.	59
3.1b	Change in faecal concentration of ⁵¹ Cr and ¹⁰³ Ru with time in one Brushtail Possum following an oral dose of ⁵¹ Cr-EDTA and ¹⁰³ Ru-P.	59
3.2	Relationships between body weight of Greater Gliders and (a) ⁵¹ Cr and (b) ¹⁰³ Ru mean retention time.	60
3.3	(a) Cumulative faecal excretion and (b) change in faecal excretion of ⁵¹ Cr and ¹⁰³ Ru with time in one Greater Glider following an oral dose of ⁵¹ Cr-mordanted cell walls and ¹⁰³ Ru-P.	67
3.4	Change in faecal concentration of ⁵¹ Cr with time in one Greater Glider following an oral dose of ⁵¹ Cr-mordanted cell walls (≤ 1.0mm ≥ 0.5mm).	67
4.1	U-V spectra of acetyl bromide-soluble lignin from (A) <i>E. radiata,</i> (B) Greater Glider faeces, (C) <i>E. melliodora</i> and (D) Brushtail Possum faeces.	78
4.2	Relationship between concentration of cell contents in the diet and apparent digestibility of cell contents by Greater Gliders.	81
4.3	Scanning electron micrographs of intact eucalypt leaf and sections from stomach contents.	89
4.4	Scanning electron micrographs of eucalypt fragments from the hindgut of the Greater Glider and the Brushtail Possum.	90
4.5	Scanning electron micrographs of eucalypt fragments from the faeces of the Greater Glider and the Brushtail Possum.	90
5.1	Relationship between nitrogen intake by Greater Gliders and (a) faecal nitrogen excretion and (b) urinary nitrogen excretion.	102

xix

5.2	Relationship between nitrogen intake by Brushtail Possums and (a) faecal nitrogen excretion and (b) urinary nitrogen excretion.	102
5.3	Relationship between nitrogen intake and faecal nitrogen excretion in (a) Greater Gliders and (b) Brushtail Possums.	103
5.4	Relationship between dietary nitrogen intake and apparently digestible nitrogen in (a) Greater Gliders and (b) Brushtail Possums.	103
5.5	Relationship between nitrogen balance in Greater Gliders and (a) dietary nitrogen intake and (b) truly digestible nitrogen intake.	104
5.6	Relationships between nitrogen balance in Brushtail Possums and (a) dietary nitrogen intake and (b) truly digestible nitrogen intake.	104
5.7	Relationship between intake of digestible energy and nitrogen balance in (a) Greater Glider and (b) Brushtail Possums.	104
5.8	Effect of changing the diet of Greater Gliders from <i>E. radiata</i> to <i>Angophora floribunda</i> on the proportion of urinary nitrogen excreted as urea or NH4.	105
6.1	The effect of adding graded levels of eucalypt tannin on the optical density (578nm) of a solution of ovine blood in Tris-HCl buffer.	117
7.1a	GLC traces of steam volatile essential oils from (a) <i>E. radiata</i> foliage and (b) Greater Glider faeces.	130
7.1b	GLC traces of steam volatile essential oils from (a) <i>E. melliodora</i> foliage and (b) Brushtail Possum faeces.	130
7.2	Qualitative GLC trace of cyclohexane-soluble fraction from respired air of Greater Gliders eating <i>E. radiata</i> foliage.	131
8.1	Diagrammatic representation of a closed circuit respirometer used for measurement of heat production of Greater Gliders.	140
8.2	Relationship between log. body weight and log. fasting heat production in Greater Gliders.	143
8.3	Relationship between gross energy intake and faecal energy excretion in (a) Greater Gliders and (b) Brushtail Possums.	144
8.4	Relationship between metabolizable energy intake and energy retention in Greater Gliders.	144
8.5	Relationship between fresh weight <i>E. radiata</i> leaf and volume of CO_2 produced in respirometers.	144

9.1	The change in concentration with time of acetic, propionic and butyric acid during the <i>in vitro</i> incubation of caecal content of (a) one Greater Glider and (b) one Brushtail Possum.	157
10.1	Relationships between field CO ₂ production rate in Greater Gliders and (a) body weight and (b) percentage daily body weight change.	170