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THE FEEDING ECOLOGY OF THREE SPECIES OF NORTH QUEENSLAND UPLAND RAINFOREST RINGTAIL POSSUMS, *HEMIBELIDEUS LEMUROIDES*, *PSEUDOCHEIRUS HERBERTENSIS* AND *PSEUDOCHEIRUS ARCHERI* (MARSUPIALIA: PETAURIDAE)

Thesis submitted by

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in June 1990

for the degree of Doctor of Philosophy in

the Department of Zoology at

James Cook University of North Queensland.

DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

Nicole J. Goudberg

June 1990

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Frontispiece: Climbing to catch possums in their dens. (Steve Williams photo).

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ABSTRACT

The feeding behaviour of three species of upland rainforest ringtail possums (*Hemibelideus lemuroides*, *Pseudocheirus herbertensis* and *P. archeri*) was studied in the field for 30 months in 1982, 1983 and 1985. They were found to be selective folivores, choosing diverse diets that changed with the phenology of favoured food species. Mature leaves constituted the bulk of the diet of *P. archeri* and *H. lemuroides*, while *P. herbertensis* ate more young leaves. Tree species and seasonal food items (young leaves, fruits, flowers) were not exploited in the same proportion in which they occurred. Rather, condensed tannin and fibre content determined whether they were included in the diet. Protein was not an important correlate to species feeding preferences although *P. herbertensis* selected a higher protein diet than the other species. *H. lemuroides* selected for a low fibre diet, and *P. archeri* selected for high fibre.

Both *P. herbertensis* and *P. archeri* preferred to feed on continuously leafing tree species. The diets of all three species became more specialized during the more difficult dry season, and became increasingly opportunistic during the wet season when there was more suitable food available. Foods were partitioned almost completely at the species and item levels. No interference competition for food between or within the three possum species was ever observed.

The field energy requirements of *P. herbertensis* and *H. lemuroides* were determined by the doubly labelled water method during September-October 1985 (spring). Although both rainforest species have a similar food intake, *H. lemuroides* uses more energy for free existence than *P. herbertensis*, and obtains extra energy from a significantly higher quality diet than *P. herbertensis*. Behavioural adaptations reduce the energy needs of all three species.

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CHAPTER 1 GENERAL INTRODUCTION

This thesis investigates the feeding ecology of three species of ringtail possums (family Petauridae) living in sympatry in upland rainforest in north Queensland. The diet of each species was determined by observation (Chapter 5), the phenologies of their food plants recorded (Chapter 4), the nutrient contents of their foods analysed (Chapter 6) and the animals' field metabolic rates calculated (Chapter 7). I aimed to provide some base-line information on three little known species of tropical marsupial while examining how these very similar species partition their food resources and adapt to a difficult, low energy diet.

Animals which include large amounts of non-woody plant material in their diets are referred to as herbivores. Their diets include leaves and soft stems, but not fruits, flowers or plant exudates. The more restrictive term "folivore" is used to describe those herbivores which feed mainly on leaves. While many animals practise herbivory, only 4% of mammals are tree dwelling (arboreal) herbivores and less than 1% are classified as arboreal folivores (Eisenberg 1978). To discover why there are so few mammalian arboreal folivores, it is necessary to be aware of the problems facing animals living on a leafy diet.

1.1 Foraging strategies

Since the papers by Emlen (1966) and MacArthur and Pianka (1966), many attempts have been made to predict the strategies animals use to meet their nutritional requirements. The resultant models form part of the field of foraging strategy theory. It is postulated that natural selection operates to increase the fitness of an animal by maximizing the capture rate of nutrients (Pyke et al. 1977;Schoener 1971). Many models measure the food value of prey items in terms of energy. They assume that if an animal obtains adequate energy, it also obtains a balanced supply of nutrients (Emlen 1966; Lindroth 1979; Pyke et al. 1977; Werner & Hall 1974). They also assume that different foods can be substituted for each other if they have an equal energy content, varying only in yield per prey item and search and handling costs. Food items can thus be ranked by the ratio of food value (in weight or caloric content) to the cost of procurement and the optimal diet predicted.

These classical models have generally been successful in predicting the optimal diets of secondary consumers, but not of primary consumers (Lindroth 1979). Unlike carnivores, whose prey species probably contain a constant and balanced set of nutrients, herbivores are faced with an array of possible foods containing variable and unpredictable amounts of allelochemicals (plant toxins) and a generally low, variable and incomplete supply of nutrients. Plant items are not "substitutable" (*sensu* Rapport 1980). As plant nutrients are usually low and do not provide a balanced intake, it has been proposed that a complement of foods must be eaten to optimize the nutrient mix (Clark 1982; Pulliam 1975; Rapport 1980; Westoby 1974, 1978).

The simpler energy based foraging strategies predict that animals will have no "partial preferences", that is, either food will be totally included or excluded from the diet (Pyke et al. 1977). However, herbivores do show partial preferences. They do not take all items of a particular food they may encounter (Westoby 1978). Sampling has also been found to be common amongst generalist herbivores (Clark 1982; Milton 1979). As a leafy food supply changes seasonally or faster, herbivores need to monitor the nutritional and allelochemical quality of both familiar and novel foods. Sampling behaviour is probably also valuable for inducing detoxification systems for unfamiliar secondary compounds (Clark 1982; Freeland & Janzen 1974; Lindroth 1979).

One of the consequences of feeding on herbage is the high intake of relatively indigestible fibre (Maynard & Loosli 1969). As this necessitates a protracted period of digestion, Westoby (1974) proposed that digestion time rather than search time was the limiting factor for herbivores. He suggested that food quality was more important than abundance in determining a herbivore's optimal diet.

Plant defence compounds have also been implicated in determining food choice by herbivores (Freeland & Janzen 1974). Allelochemicals can have adverse effects in even tiny quantities and may act synergistically with other previously tolerated compounds. Thus the value of a food item is not independant of other food items taken during the same period (Westoby 1978).

These observations have led to some predictions about the foraging strategies of generalist herbivores. These are summarized:

1. Herbivores should include a variety of foods in their diets.
2. Herbivores should specialize on nutritionally complete and/or complementary foods in times of their high abundance.
3. Food quality is more important than availability.
4. Nutritionally valuable food is retained in the diet over a wide range of availability.
5. Herbivores should show partial preferences.
6. Herbivores should cautiously sample novel food items.

1.2 Leaves as a food source

Until recently, herbivores were considered to be surrounded by large amounts of continuously available food. However it has been recognised that plants, far from passively waiting for predators (herbivores) to attack, are very well defended (Freeland & Janzen 1974; Levin 1971). Plants have evolved a number of defences which reduce the amount and quality of food available to folivores. Commonly several defences are used simultaneously to deter herbivores (Rhoades &Cates 1976).

1.2.1 Structural Compounds

The cell walls in plant tissues consist of cellulose and lignin. Structural carbohydrates such as cellulose, potentially a very important energy source for herbivores, are impervious to enzymatic digestion by mammals. Only those species with a complex gut flora of cellulolytic bacteria are able to utilize some of this energy (Van Soest 1977).

The cellulose fraction of plant fibre can be degraded by gut microbes but is digested more slowly than the cell contents. Lignin cannot be degraded in this way, and is regarded as an anti-nutrient as it reduces a plant's digestibility and can retard the digestion of other constituents (Hungate 1966; Van Soest 1977). Typically plant tissues contain 30-60% dry weight of fibre (Milton 1979). Herbivores therefore have to have behavioural and/or digestive adaptations to deal with plant fibre.

1.2.2 Secondary compounds

The secondary compounds in plants, once dismissed as metabolic waste products, have been implicated as plant defence chemicals or allelochemicals (Freeland & Janzen 1974; Janzen 1978; Oates et al. 1977, 1980; Rhoades & Cates 1976). Allelochemicals have been suggested to affect herbiores in two ways: as specific toxins or by reducing the digestibility and nutrient content of plant tissues (Freeland & Janzen 1974; Rhoades & Cates 1976). More recently it has been found that, although tannins do inhibit feeding and growth of many, particularly vertebrate species (eg. Cooper at al 1988; review by Mole & Waterman 1987a), their role as anti-digestive agents is in doubt (Bernays et al 1989).

Toxins

Biological toxins affect the animal's bodily functions, even at low dosages. They can act as nerve toxins (alkaloids, pyrethrins, rotenoids), affect muscle function (cardiac glycosides, saponins) and interfere with kidney and liver function (alkaloids, oxalates)(Rhoades & Cates 1976). Toxins can also act as a drain on essential nutrients such as glucose, amino acids or sulphate groups which are essential in detoxification pathways (Freeland & Janzen 1974; Moir 1968).

Biological toxins are effective in very small quantities against generalist herbivores, but are easily detoxified by specialists. This has led to apostatic selection for divergent species of toxins to which generalists are enzymatically naive (Rhoades & Cates 1976). As toxins are effective in small quantities, are cheap to produce and do not tie up valuable resources, they are often found in ephemeral plants and tissues (Rhoades & Cates 1976).

Digestibility reducing compounds

The polymeric tannin group is the best known of the so called "digestibility reducing compounds" (DRC). *In vitro* tannins complex with natural polymers such as dietary proteins, digestive enzymes and polysaccharides (Feeny 1970; Mole & Waterman 1989b; Rhoades & Cates 1976; Waterman et al 1980). However, recent work suggests that it is unlikely that digestive enzymes *in vivo* are exposed to significant amounts of dietary tannin. Blytt et al (1988) found that the digestive enzymes in

1.2.3 Nutrient content

Leaves are a poor food source due to their low nutritive levels (Westoby 1974). While they are often rich in protein, especially when young, leaves are poor in non-structural carbohydrates and lipids. They also often lack certain essential amino acids and trace elements (Hladik & Hladik 1972; Freeland & Janzen 1974; Hladik 1977a, 1977b). Therefore, to obtain a balanced nutrient intake, folivores must select from many food items.

1.2.4 Variability

The chemical makeup of plants varies greatly both within and between different species and seasonally within individuals (Dement & Mooney 1974; Feeny 1970; Levin 1976; Macauley & Fox 1977). For example, mature oak leaves have higher tannin and lower protein levels than immature oak leaves (*Quercus robur*, Feeny 1970), whereas the reverse is true for creosote bush (*Larrea* spp., Rhoades & Cates 1976). Birdsfoot trefoil is polymorphic for cyanogenic glycosides (Jones in Rosenthal 1986) while the leaves of the chaparral shrub, *Heteromeles arbutifolia*, vary in the tannin and toxin content with time of year (Dement & Mooney 1974). Chemical variability between and within plant species is very common.

1.2.5 Ephemerality

Escape in time

Many tropical tree species show some degree of intraspecific synchronization in their leafing, fruiting and flowering phenologies (Frankie et al. 1974a). Trees usually have very discrete periods of seasonal production in a year, but may skip several years between successive crops (Milton 1979; J.Tracey, pers. comm). As this occurs on both the individual and specific levels, animals cannot depend upon obtaining a constant supply of new leaves, fruits or flowers from specific trees. This acts to reduce specialization by herbivores on ephemeral food resources (Feeny 1976; Rhoades & Cates 1976).

Synchrony of crop production may protect trees against predation by swamping the herbivore populations with food. It has been suggested that one defence strategy used by some tree species is to produce new leaves while the herbivore populations are low, then to mature them before the animals have a chance to increase (McKey 1975; Rockwood 1974). When leaves mature they generally contain more fibre and allelochemicals (Feeny 1970) reducing their food value to herbivores. Therefore, by the time the herbivore populations have increased, they have outstripped their food supply and the populations crash. Synchrony in phenology can thus act to restrict the herbivore carrying capacity of a forest.

Some studies indicate that plant species react to leaf damage within 24 hours by increasing the concentrations of proteinase inhibitors (allelochemicals) in their leaves (Ryan & Green 1974). Other studies suggest an airborne chemical may warn nearby trees of herbivore damage and induce them to increase their allelochemical defences (Rhoades 1983). Thus young leaves of some species may only be optimally edible for a day, escaping their predators in time.

Escape in Space

Tropical forests are typically made up of a high diversity of plant species, none of which is dominant (Richards 1952). The cost of specializing on one or several plant species in such a forest may be prohibitive for a small herbivorous mammal, as the area of supply would be large. The more ephemeral and widely dispersed the plant, the longer the search and the higher the specialist mortality. Thus it has been suggested that it might be possible for plants to protect themselves against specialist herbivores by being randomly distributed in the forest (Feeny 1976; Rhoades & Cates 1976). Coley (1983b) found this not to be the case in lowland rainforest, where ephemeral pioneer plants suffered higher levels of herbivory than apparent species growing in the same light gaps. Thus escape in space may not be possible for ephemeral plants with highly mobile predators (eg. some insects).

1.3 Digestion

The problems of small size

Most studies of mammals suggest that large species are more able to utilize plant fibre than smaller species (Hungate et al. 1959; Janis 1976; Jarman 1974; Parra 1978). This is because large animals have a larger gut volume to body weight ratio, a relatively low mass- specific metabolic rate and lower nutritional requirements per unit weight (Clutton Brock & Harvey 1977; Hume & Warner 1980; Van Soest 1982).

The relatively higher energy requirement by smaller animals means that they must either increase their nutrient intake or increase the rate of fermentation and subsequent energy release. As the fermentation rate is fixed, the animals are forced to increase their intake. However, as intake increases, so too does the rate of passage. As fibre digestion is time dependant, this in time leads to a lower fibre digestibility (Clutton Brock & Harvey 1977). Some animals, for example the horse, have traded greater intake of soluble nutrients for lower fibre digestibility, however, there is a limit past which food is not worth eating. This point is quickly reached in smaller herbivores as their relative gut capacity decreases with decreasing body weight.

Digestive morphology

Arboreal herbivores have, like terrestrial herbivores, evolved both foregut and hindgut fermentation systems. Although the foregut strategy has traditionally been regarded as superior due to more complete fibre digestion, the differences between the two are small (Janis 1976; Parra 1978). In the ungulates these two strategies appear to represent adaptations to different fibre levels in the diet rather than alternative solutions (Jarman 1974; Janis 1976). The biochemistry and bacterial flora possessed by both fore and hind gut digesters are basically the same, as is the fermentation process (Janis 1976).

As fermentation occurs anterior to the small intestine, foregut fermenters are able to digest and absorb microbial protein flushed from the fermentation chamber (Janis 1976). This enables the animal to survive on a diet low or lacking in essential amino acids. However, due to the large amounts of waste products formed by foregut fermenters (eg. methane, heat), their slow rate of passage and the relative inefficiency of metabolizing volatile fatty acids on a low energy diet (Black 1971; Hume & Warner 1980; Parra 1978), few foregut fermenters have been able to exploit arboreal folivory. That there are some arboreal foregut fermenters (eg: *Colobus* spp.; Oates 1977) indcate that the problems are not insurmountable.

By practising coprophagy and increasing the absorptive surface area of the proximal colon and/or the caecum, many hindgut fermenters reduce the loss of microbial nitrogen. Urea recycling has also been demonstrated in some members of this group (Cork 1981; Hume 1982). Although hindgut fermenters digest cellulose with only 70% the efficiency of ruminants, the rapid rate of passage allows a larger amount of forage to be processed (Clutton Brock & Harvey 1977). Therefore hindgut fermentation is a more viable option for small (<20kg) herbivores, such as arboreal folivores, which feed extensively on fibrous diets and so require a fast rate of throughput to achieve adequate nutrition (Parra 1978).

The more complete digestion of structural carbohyrates by ruminants is primarily due to the reticulo-omasal constriction. This retains food particles until they are small enough to pass through the orifice. While this ensures efficient fibre digestion, it does limit flexibility. The animal cannot voluntarily increase its food intake or rate of passage, regardless of decreasing food quality (Hume & Warner 1980; Janis 1976). The complex stomachs of the nonruminant foregut digesters do not have this constriction. Therefore the macropods and presumably the arboreal foregut digesters (eg. *Colobus* spp.), are able to vary the food intake and passage rates dependant on food quality (Langer et al. 1980).

Hume and Warner (1980) divide the hindgut digesters into two groups, the colonic and the caecal fermenters. The latter retain the liquid and fine particulate phase of digesta, allowing the coarse particulate phase to pass rapidly through the system. This is a particularly useful strategy for animals on a high fibre diet. They can increase their intake without the penalties associated with a lot of retained bulk. This strategy is often associated with caecotrophy (ie. reingesting faeces). It is probably widespread amongst the smaller herbivores and is practised by rabbits and lemmings (Hume & Warner 1980; Pickard & Stevens 1972; Sperber 1968).

The colonic fermenters, such as the horse, retain the particulate digesta while increasing the passage rate of the liquid phase. This allows an increase in soluble nutrients as well as a significant fibre digestibility (Janis 1976). Due to the large amount of slower moving fibre, this digestive strategy is less available to smaller animals with their concomitant smaller gut capacities.

species would:

(i) have a diverse diet that changed in composition with season;

(ii) exploit preferred items intensively when they were available, while continually sampling potential food sources;

(iii) become specialized on species that provided a longterm source of more nutritious food items.

To test these expectations I collected data to determine the following:

(i) the number of plant species eaten,

(ii) the relative proportion of those species in the diet,

(iii) the proportion of leaf and non-leaf items in the diet,

(iv) the maturity of the preferred leaf items,

(v) the extent of dietary overlap between the three species,

(vi) the extent of dietary specialization, and

(vii) the extent of habitat partitioning.

CHAPTER 2 THE STUDY ANIMALS

2.1 Taxonomic relationships

All possum and glider species, once grouped together into a single family Phalangeridae in the order Marsupialia (Simpson 1945), form a diverse, primarily herbivorous subgroup of the recently established marsupial order Diprotodonta, along with the koala (Family Phascolarctidae), wombats (Family Vombatidae), kangaroo rats (Potoroidae), and kangaroos and wallabies (Macropodidae) (Strahan 1983). The possums and gliders are grouped into a total of four families (Phalangeridae, Petauridae, Burramyidae and Tarsipedidae) (McKay 1988a, 1988b, 1988c and 1988d; Strahan 1983). Smith (1984) recommended that the ringtail possums (*Pseudocheirus*), lemuroid ringtail (*Hemibelideus*), and greater glider (*Petauroides*) be grouped together as a distinct family, Pseudocheiridae, on the basis of relative brain volume, diet and gastro-intestinal morphology, cranial and dental morphology, and serology, blood proteins and blood albumens. However, the generally accepted classification is to place *Pseudocheirus* (including *Pseudocheirops*), *Hemibelideus* and *Petauroides* with *Dactylopsila*, *Gymnobelideus* and *Petaurus* in the family Petauridae (Strahan 1983; McKay 1988b), order Diprotodonta, subclass Metatheria or Marsupialia (Strahan 1983). This is the classification followed here.

The three upland rainforest inhabiting ringtail possums studied in this project, *Hemibelideus lemuroides* (Collett, 1884), *Pseudocheirus archeri* (Collett, 1884), and *P. herbertensis herbertensis* (Collett, 1884), belong to the family Petauridae (McKay 1988b; Strahan 1983) (Fig 2.1). The lemuroid ringtail, *H. lemuroides*, now raised to full generic status (Baverstock 1984; McKay 1988b; McQuade 1984; Smith 1984) is closely related to the greater glider, *Petauroides volans* (McQuade 1984). The green ringtail (*P. archeri*), is serologically more closely related to *H. lemuroides* than to the common ringtail *P. peregrinus* (Baverstock 1984). McKay (1988b) now calls *Pseudocheirus archeri* (Collett, 1884) *Pseudocheirops archeri* (Collett, 1884). While the two subspecies of *P. herbertensis (P. h. herbertensis* and *P. h. cinereus*) are closer to *P. peregrinus* than to *P. volans*, they show greater serological differences between one another than do *Hemibelideus* and *Petauroides* (Baverstock 1984).

2.2 Distribution

All three species occur on the Atherton Tablelands west of Cairns, north Queensland, where they are sympatric in the southern wetter areas. Of the three, *H. lemuroides* has the most restricted range and habitat requirements. It is found only in dense rainforest above 480m (Atherton Tablelands) or 900m (Mt Carbine) in the wettest regions between the Herbert River and Kuranda (Winter 1978, 1984). There are two disjunct populations of *H. lemuroides*. The smaller occupies some 22,400 hectares at Mt.Carbine, and is separated from the main population block on the Atherton Tablelands (275,900ha) by the Black Mountain Corridor. This low altitude barrier has been in place for over 10,000 years, resulting in a much higher proportion of all-white individuals in the Mt. Carbine isolate (Winter 1984).

A study by Pahl (1979) indicated that of the three endemic rainforest species, *H. lemuroides* was the most disturbed by logging practices and rainforest fragmentation. Of the 11 rainforest patches he examined (size range: 2.5-74.5ha) only the four largest patches contained *H. lemuroides*. The population densities in the patches were considerably lower than in nearby continuous forest.

The green ringtail *P. archeri*, is the most widely distributed of the three species. It is found in forest down to 300m (Winter 1978). This lower altitude range allows this species to maintain a continuous population across the Black Mountain Corridor disjunction covering some 368,410ha between the Atherton Uplands and the Mt. Carbine Tableland (Winter 1984). The distribution of the species extends south to the Mt. Spec block (north of Townsville) which is separated from the main range of the species by the deeply incised Herbert River Valley. In total the range of *P. archeri* covers some 368,410 hectares (Winter 1984). Its ability to cross cleared pasture-land between rainforest patches (Russell 1980) and its dietary and denning habits enables *P. archeri* to maintain populations in small isolated patches. Pahl (1979) found that nine of his 11 study patches supported populations of green ringtails.

The Herbert River ringtail (*P. herbertensis*) is found in two isolates, the Mt. Lee population (36,050ha) to the west of Ingham, and the main Atherton Tableland population (294,340ha) separated by the Herbert River gorge (Winter 1984). This species occurs in forest down to an altitude of 350 metres, and like *H. lemuroides* is also adversely affected by logging disturbances. Pahl (1979) found that for this possum population, density was related to the size of the rainforest patch. It occurred in only six of his 11 patches and then only in low numbers.

The subspecies, *P. h. cinereus*, occurs further north of the range of *P. h. herbertensis* and is not considered in this thesis.

When the three species are ranked according to habitat usage, abundance and altitudinal range, *H. lemuroides* is the most restricted followed by *P. herbertensis* and *P. archeri* (Winter 1984). Winter (1978) believes *H. lemuroides* is not presently endangered due to the large tracts of rainforest still present in its prime habitat, its high population numbers and its apparent ability to survive in larger selectively logged forests, albeit in small numbers. Similar reasoning can probably be applied to *P. herbertensis*, which relies less on climax forest trees than does *H. lemuroides* (Chapter 5) and has a larger geographic and altitudinal range. *P. archeri* is the most adaptable of the three species and appears to be the least threatened.

2.3 Background natural history

This outline, compiled both from the literature and my field notes, is intended to provide an introduction to the study animals. Unless indicated by a citation, the observations are my own.

2.3.1 H. lemuroides

H. lemuroides is a gregarious possum, occurring most frequently in male/female pairs and sometimes with young to one year old. It weighs between 810 - 1270g (mean = 966g, Winter 1983c).

It is strictly nocturnal, denning in tree hollows during the day, emerging just after dusk. Most dens are at least 10m from the ground in canopy tree species. A family of two or three animals usually share the same den, but I have occasionally observed members of marked pairs to sleep apart. Several different dens may be used by a family of lemuroid ringtails, although most groups only use one den. Where secondary dens are used, other possum species are also known to make use of them occasionally. Movement through the trees is along arboreal runways which are used often by all possum species in the area. Scentmarking of these runways is frequently observed. The same arboreal runways are used night after night.

H. lemuroides often jumps between trees, leaping gaps of up to 3m with the fore and hind legs spread apart and a small membrane extended between them. Robert Grant (in Troughton 1965) commented on this '..rudimentary membrane, [which is] indicated by a ridge of fur about an inch long on each flank..'. When alarmed, animals extend this membrane by raising their forearms in a threat gesture. The tail, which is evenly fluffy for its length, is reminiscent of that of its close relative *P. volans* and is used as a rudder during leaping.

I observed mating (three times) all in May, although Breeden and Breeden (1970) report that young are born throughout the year. In May, courting males are frequently seen to chase other animals and fighting is more prevalent than at other times. I was not able to determine the sex of the animals being chased. Pouch young start to emerge and ride on their mother's backs in late October and early November. The subadult from the previous year usually leaves its parents in September or early October. Although the pouch contains two nipples, only one young per year has ever been observed (Breeden & Breeden 1970; pers. obs.).

This species has not been successfully kept in captivity despite attempts by Queensland National Parks and Wildlife Service (QNPWS) at Townsville (A. Haffenden, pers. comm.). Little is known about its life history as no long-term capture, mark and recapture study of this species has ever been attempted.

2.3.2 P. herbertensis

The Herbert River ringtail is a solitary nocturnal species. It is often seen in understorey trees and colonizing species such as Sarsparilla (*Alphitonia petriei*) or in the canopy of the Silver Quandong (*Elaeocarpus ruminatus*). Its average weight is 1070g (range 700-1450g, Winter 1983a). The only prior field study was a short ecological project in the Longlands Gap State Forest by Seawright (1981). He found that males and females had overlapping homeranges of between 0.5-1.0ha. During May courtship behaviour was evident. One or more males would follow a female for up to 48 days before (presumably) mating took place. The male(s) then disappeared leaving the female to raise one or two young. I have observed a female carrying three young on her back, although *P. herbertensis* has only two functional nipples. *P. herbertensis* has been successfully kept in captivity by the QNPWS in Townsville. Wild caught individuals bred successfully, but captive bred animals did not (Haffenden 1984). Breeding occurred from April to December with the peak in May/June, when 74% of all births were recorded (Haffenden 1984). One captive female produced two litters per year over two years.

The eyes of the young open at 105 days. Young vacate the pouch permanently at 115-120 days at a weight of between 115 to 120 grams. Weaning occurs at 150-160 days after an on-back phase of two weeks (Haffenden 1984; Seawright 1981). Young can survive and forage for themselves when only 10 days out of the pouch (M.J. Smith 1980) emerging and retiring to the den independantly of the female. Independance occurs when the young weigh about 300g (Seawright 1981; Winter 1982).

P. herbertensis moves cautiously and is rarely observed to jump even short distances. It dens singly in mistletoe clumps (Russell 1980), in tree hollows and amongst epiphytic ferns. On three occasions I observed this species using dreys made of thin branches. I watched a subadult animal build a drey by weaving thin branches of *Neolitsea dealbata* amongst a dense vine thicket. It carried the branches in its curled tail, in the manner of the common ringtail. Two of the dreys used by this species were cup-shaped, while the third was domed on top with a side entrance. All were less than two metres above the ground. Troughton (1965) mentions a subspecies, *P. h. colletti*, described by Waite in 1899, which was collected from a swampy area which has since been covered by the waters of Lake Tinaroo. Upon collection, it was noted that this subspecies built dreys similar to those of *P. peregrinus*, unlike the more typical species of the higher forests which never build dreys. Seawright (1981) did not find evidence of dreys during his study, which probably indicates that they are an unusual occurrance.

This species is very suseptible to stress at certain times of the year, dying in the field (Seawright 1981) and in captivity of stress-related diseases. Most deaths occur during the June to August period (Speare et al. 1984). During the present study two *P. herbertensis* were found dead, hanging by their tails in canopy trees, one during July 1982 and the other in August 1983. Due to their position in the canopy neither was recoverable for autopsy.

Predation by Rufous Owls, *Ninox rufa*, appears to be the other main source of loss of adult *P. herbertensis* as I observed once in July 1983. The owl was first seen shortly after it had taken a known female (weight = 1200g) which had been feeding in the canopy of a 20m high *A. petriei*. The owl ate the body in three hours, leaving only the gut, the skull, the paws and the tail. Another four piles of similar remains were found in the course of the study (one in September 1983, three in October 1986). Three were remains of P. herbertensis and one of *H. lemuroides*.

2.3.3 P. archeri

P. archeri is a thickly furred possum (average weight 1190g, range 1075 - 1350g, Winter 1983b) with a thick, bushy tail tapering to a naked finger-like tip. It is not as strictly nocturnal as the other two species, and occasionally moves about and feeds during the day (Russell 1980; *pers. obs.*). Winter (1984) suggests this may be a function of its habit of sleeping on tree limbs or amongst vines during the day, rather than in a den where it is less liable to be disturbed.

This species is notable for its greenish-yellow fur colouration, which is unusual in mammalian species (Troughton 1965). This colour perfectly matches the foliage of its major food trees, *Ficus* spp., in which it often sleeps during the day. This cryptic colouration, together with its habit of sitting curled and unmoving for several hours at a time suggests a predator avoidance strategy similar to that of the prosimian, *Perodicticus potto*, in Madagascar (Hladik 1979).

Due to husbandry problems (Haffenden, *pers. comm.*) and its cryptic and secretive habits, little is known of the life history or reproductive behaviour of this species. A single young is born mainly in the winter or late spring, although some February/March births have been reported (M.J. Smith 1980). Animals are solitary, the female raising the young alone. Whenever pairs of *P. archeri* are seen, it is almost certainly a mother and offspring pair (Winter *et al.* 1984). The young stays with the mother for at least 10 months.

2.4 Previous studies

There have been few detailed, long-term studies of arboreal folivores from the Australian wet tropics. Table 2.1 gives a summary of studies to date.

The diets of the ringtail possums endemic to northern rainforests are known from three main sources. Proctor-Gray (1984) published 141 feeding observations she collected for *P. archeri* in Curtain Fig Tree State Forest near Yungaburra (17° 17'S, 145° 4'E). Seawright (1981) included a list of 101 feeding observations of *P. herbertensis* from Longlands Gap State Forest, my study site near Herberton (17° 23'S, 145° 23'E). Winter *et al.*

(in prep.) collated feeding data from Seawright (1981), Goudberg (unpubl.) and incidental observations made by Atherton and himself in the course of northern fauna surveys. Food items known to be eaten by rainforest ringtail possums is given in Table 2.2.

Table 2.1

Studies of arboreal folivores from the wet tropics of Australia.

Topic	Pa	Hl	Hrr	Tvj	Dl	Pho	Phm	Source
Breeding, growth			x					Haffenden 84
Diseases	x	x	x			x	x	Speare et al 84
Social group size	x	x	x					Winter & Atherton 84
Biogeography	x	x	x	x		x		Winter 84
Dietary ecology	x			x	x			Proctor-Gray 84
Ecology			x					Seawright 81
Ecology	x	x	x	x				Russell 80
Dietary ecology	x	x	x					Winter et al (in prep).
Conservation ecology	x	x	x					Pahl 79

Hl = *H. lemuroides* Pa = *P. archeri* Hrr = *P. herbertensis* Tvj = *Trichosaurus vulpecula johnstoni*
Dl = *Dendrolagus lumholtzii* Pho = *Phalanger orientalis* Phm = *P. maculatus*

Table 2.2

Diet of *P. herbertensis* and *P. archeri* as indicated by studies to date.

Species	Food Species	Proportion (%)	Source
P. archeri	*Ficus* spp.	10.6	Proctor-Gray 84
	Dendrocnide photinophyla	17.7	
	Aleurites moluccana	26.6	
	Argyrodendron spp	9.9	
	Elaeagnus triflora	12.1	
	others	23.5	
	Ficus spp	NP	Russell 80
	Dendrocnide photinophyla	NP	
P. herbertensis	*Acmena resa*	11.0	Seawright 81
	Alphitonia petriei	45.0	
	Proteaceae	9.0	
	Elaeocarpaceae	8.0	
	flowers	NP	Russell 80
	Amylotheca spp.	NP	
	Schinus terebinthifolia #	NP	

# Introduced species
NP = Proportions not indicated.

Figure 2.1

TOP:	*H. lemuroides*
BOTTOM:	*P. herbertensis*
OVER PAGE:	*P. archeri*

CHAPTER 3 THE STUDY SITE

3.1 Location

My study site, covering approximately 9 hectares, is located in upland rainforest in Longlands Gap State Forest (State Forest 194), sixteen kilometres south-east of Herberton (17^0 23'S 145^0 23'E) in the southern Atherton Tablelands of North Queensland (Fig. 3.1). This forest is part of a larger block of some 15,320 hectares running along the Hugh Nelson Range. Extensive clearing for grazing land has occurred around the State Forest boundaries, resulting in the forest becoming a large island.

The study site is centred around a ridgetop snigging track on acidic basaltic soil at an altitude of about 1100 metres. The floristics change markedly at the eastern end of the ridge where the soil is rhyolitic. For this reason the study site included only forest on soil of basaltic origin.

3.2 Forest type

This rainforest is classified as Type 5a by Tracey (1982), ie. Complex Notophyll Vine Forest in cloudy wet highlands (Tracey & Webb 1975). The canopy, reduced by selective logging of the larger trees, is uneven. It reaches to 25m with occasional emergent strangler figs (*Ficus* spp.) and *Acmena resa* to 30m.

Selective logging occurred here in the 1950's and again, more intensively in 1972/3 (Winter 1984), leaving smaller diameter trees and encouraging early succession species. A network of logging tracks is still clearly evident.

Over the period of the study I made a survey of trees measuring at least 20cm diameter-at-breast-height (DBH) in 57 quadrats each measuring 20m X 25m. This showed that there was an average of 84.6 trees per hectare in the study area. These included 126 tree species of 20cm DBH or more, (95% were identified). The most common tree species are listed in Table 3.1. There are also numerous species of vines and shrubs. Although the density of the latter was not calculated, the most common shrubs included *Aglaia ferruginea*, *Ochrosia powerei* and *Macarangia inoamena*. Vines included *Cissus* species, *Ripogonum papuanum* and *Smilax australis*.

3.3 Temperature and rainfall

The town of Herberton, 16 km to the north-west, is the closest weather station to the study site. Herberton is usually warmer and drier than Longlands Gap (pers. obs.), with a yearly rainfall of 1132mm (Australian Bureau of Meteorology, 1977). Tracey (1982) included the Longlands Gap area within the 1500-2000mm rainfall isohyet. Although the Herberton records under-represent the rainfall at my study site, they have been used to indicate the rainfall pattern (Fig 3.2). Likewise, temperature records for Herberton, although generally more extreme than the the study area (average range 9.5 - 29.3 C), indicate seasonal patterns (Fig 3.2). In the forest, the vegetation has an important buffering effect, damping temperature fluctuations (A. Hladik 1978). The extremes of temperature recorded at Herberton are unlikely to occur on the forest floor at Longland's Gap.

Most rainfall in the area is recorded between November and April during the summer wet season. Falls in excess of 200mm a month are often recorded, and temperatures may climb to 30^0C. The winter months from May through October are usually cool and dry. Night-time temperatures fall below 15^0C with occasional frosts, and monthly rainfall is usually below 50mm.

When compared with longterm rainfall records for the area, the rainfall pattern recorded at Herberton during 1982 and 1983 was unusual.

Nineteen eighty two was a drier than average year with unusually heavy rains in August (80mm compared with an average of 17mm) and a much drier November (18mm compared with an average of 73mm). The first six months of 1983 were atypical. January and February were amongst the driest on record, receiving only 30% of expected rainfall. By contrast, four times the average rainfall was recorded in May (183mm compared with 42mm). This brought the rainfall received during 1983 to about 75% of the average. Rainfall in 1985 closely corresponded to the average.

Table 3.1

The 20 most common tree species in the study site. All trees equal to or greater than 20cm DBH in 57 quadrats totalling 2.85ha in area were identified. Only these trees were used in this ranking. Smaller species and individuals were excluded. Species after Hyland (1982).

SPECIES OF TREES*	NO. OF INDIVIDUALS >20cm DBH	NO. PER HECTARE
Flindersia brayleyana	139	48.8
Darlingia ferruginea	89	31.2
Euodia sp. nov. 305	53	18.6
Endiandra sp. code 62	41	14.4
Castanospora alphandii	39	13.7
Stenocarpus sinuatus	35	12.3
Alphitonia petriei	30	10.5
Litsea leefeana	29	10.2
Neolitsea dealbata	28	9.8
Flindersia bourjotiana	26	9.1
Elaeocarpus ruminatus	25	8.8
Acronychia crassipetala	23	8.1
Halfordia scleroxyla	22	7.7
Acmena resa	21	7.4
Synima cordieri	20	7.0
Casearia sp.	19	6.7
Cardwellia sublimis	16	5.6
Helicia lamingtoniana	16	5.6
Syzygium cormiflora	15	5.3
Sloanea langii	14	4.9

Figure 3.1

Location of study site in Longlands Gap State Forest, north Queensland, Australia.

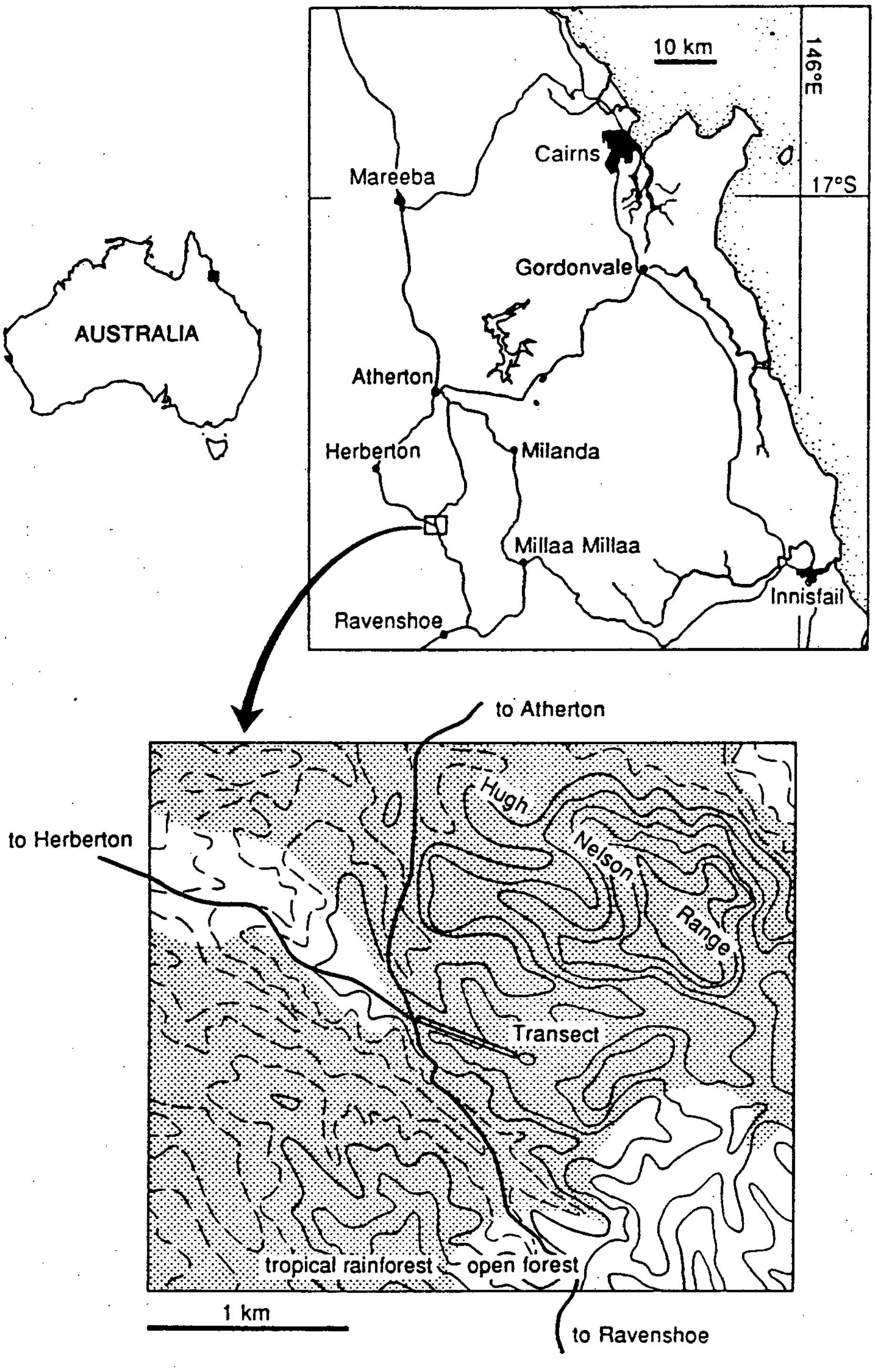
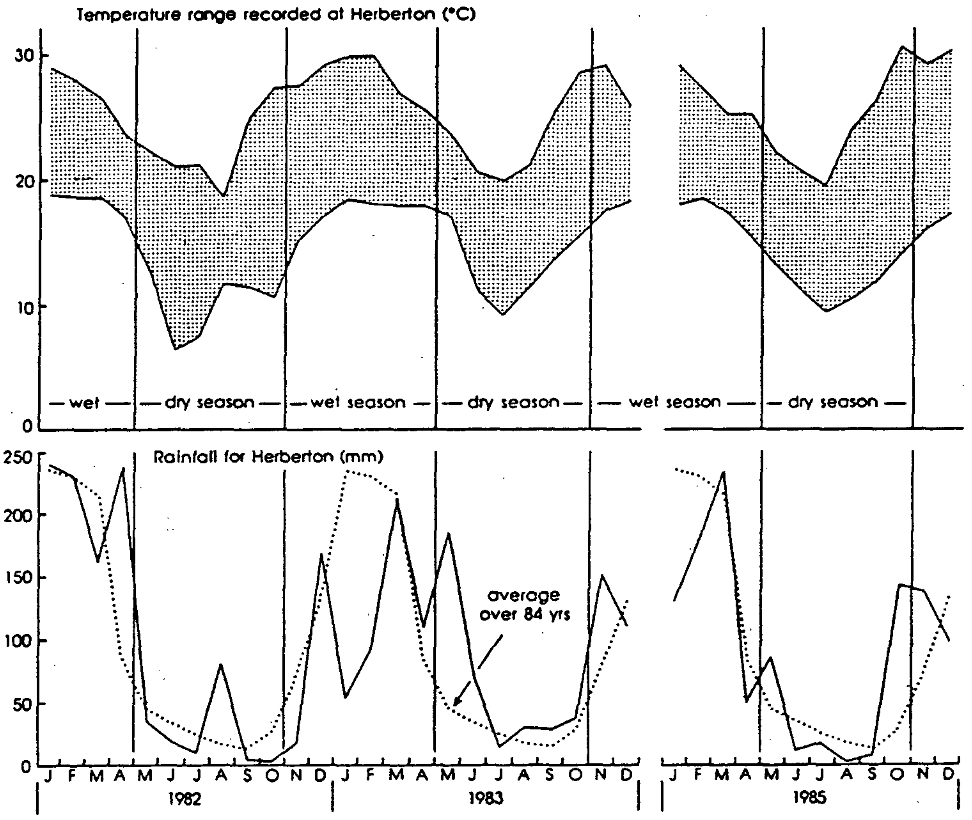

10 km
146°E
17°S
Cairns
Mareeba
Gordonvale
AUSTRALIA
Atherton
Herberton
Milanda
Millaa Millaa
Innisfail
Ravenshoe
to Atherton
to Herberton
Hugh
Nelson
Range
Transect
tropical rainforest
open forest
1 km
to Ravenshoe

Figure 3.2

Temperature and rainfall records for Herberton, the nearest weather station to the study site. Dotted line shows average rainfall over 84 years.


Temperature range recorded at Herberton (°C)
30
20
10
0
— wet —
— dry season —
— wet season —
— dry season —
— wet season —
— dry season —
Rainfall for Herberton (mm)
250
200
150
100
50
0
average over 84 yrs
J F M A M J J A S O N D J F M A M J J A S O N D
1982
1983
J F M A M J J A S O N D
1985

CHAPTER 4 PHENOLOGY

4.1 Introduction

It has been demonstrated that many herbivores, (but not all, Cork 1981; Cork & Pahl 1984) feed preferentially on young foliage (Milton 1979). This tends to be lower in structural carbohydrates and phenolic compounds (eg. tannins & lignins) and higher in primary nutrients than mature leaves (Feeny 1970; Rhoades & Cates 1976).

As a result, it has been suggested that some plant species time leaf production to counter predation on young foliage (Feeny 1970, 1976; Rhoades & Cates 1976). Feeny (1970) found that the larvae of winter moth (*Operophtera brumata*) experienced increased mortality when bud-burst on oak trees and larval hatching were out of synchrony. Other invertebrate studies have shown similar results eg. Hanover (1975).

4.1.1 Leafing phenology

The strategy of relatively unpredictable leafing is most effective against specialist predators (ie: those which eat only a limited number of plant species or items to the exclusion of everything else) which have few alternative resources; it is less effective against generalists which feed on many plant species.

The tendancy of many species of rainforest trees to produce new leaves at the same time of the year has been noted by several workers (Frankie et al. 1974a; A. Hladik 1978; Leigh & Smythe 1978; Milton 1980; Opler 1978; Richards 1952). Synchronous budburst has been suggested as a strategy to reduce predation on young leaves and buds, as predators are swamped by food resources for a short period after which there is little new foliage available on which to feed (Struhsaker 1975, 1978). Synchronous leafing is particularly effective against specialist predators and keeps their numbers low (Leigh & Smythe 1978; Montgomery & Sunquist 1978).

A slightly different strategy is to time new plant growth to coincide with periods of low herbivore population density. By the time the herbivore population has built up to exploit this food source, the leaves are mature enough to be unsuitable for food, the young starve and the herbivore population numbers drop back to a low level (Feeny 1976). This strategy is more applicable to invertebrate herbivores because of their short life cycles.

Individuals of some plant species leaf asynchronously throughout the year making the search costs for a specialist predator very high (Rhoades & Cates 1976). Asynchronous leafing is particularly effective when plants are randomly spaced and some distance apart. The high costs of specializing on unpredictable and ephemeral resources mean that they tend to be preyed upon by generalist rather than specialist herbivores. The latter tend to feed on predictable, "apparent" resources such as mature leaves (Feeny 1970).

4.1.2 Flowering Phenology

Not all rainforest plants flower on an annual basis (Janzen 1970; Medway 1972), although rainforests as a whole often exhibit a marked seasonal cycle of flowering (Janzen 1967; McClure 1966; Medway 1972; Rees 1964a). Unlike dry tropical forests (less than 1000mm of annual rainfall) which flower predominantly during the wet season, most, but not all (Frankie et al. 1974a) wet tropical forests (annual rainfall > 1000mm), display flowering peaks during the dry season (Njoku 1963).

Although photoperiodic and climatic factors have been shown to influence flowering periodicity (Lawton & Akpan 1968; Rees 1964a, 1964b), biotic factors are also implicated. Janzen (1969, 1970) suggests that variability in flowering periodicity may be a strategy to deter seed/fruit predators. Herrera (1982) points out, however, that time of flowering often has little bearing on time of fruit maturation; rather he ties fruit maturation to seasonal dispersal opportunities. Competition for pollen vectors may also influence flowering periodicity. The lack of any substantial overlap in flowering periods by congenerics in some tropical forests may minimise competition for pollinating agents (Frankie et al. 1974a, 1974b).

4.1.3 Fruiting Phenology

Predation on leaves, which are needed for photosynthetic energy production, has adverse consequences for the plant. In contrast, fruit predation by vertebrates is often a vital means of seed dispersal in rainforest plants (Herrera 1982; Hladik 1979; Janzen 1978; Milton 1979, 1980; Milton et al. 1982). Consequently, ripe fruit tends to have a relatively low allelochemical load and high soluble carbohydrate content, providing birds and mammals with a valuable energy source. The seed exocarp is resistant to digestion and seeds are passed out of the gut intact usually at some distance from the parent plant (Janzen 1978).

Fruits tend to be dispersed more readily if they provide frugivores with essential nutrients (Janzen 1978), especially when the animals are under nutritional stress. The lipid and soluble carbohydrate content in the fruit of some species changes seasonally, possibly to attract seed dispersers (Herrera 1982). Those species with low nutrient fruit tend not to be competing for dispersers because they are either fruiting outside the major fruiting peaks (Snow 1965), or are closely associated with obligate frugivores (eg. Howler monkeys and *Ficus* spp., Milton et al. 1982).

Fruiting phenology in most temperate climates is seasonally timed to coincide with mild weather (Herrera 1982). In tropical forests suitable weather is often available for most of the year. Consequently, although there are fruiting peaks which coincide with climatic fluctuations (Frankie et al.1974a; Milton 1980; Milton et al. 1982), some plant species fruit throughout the year (Glander 1981; McClure 1966; Milton et al. 1982; Smythe 1970).

4.2 Methods

Beginning in 1982, I tagged and mapped all trees used by possums for any activity. In June 1983, Dr. J.W. Winter tagged and mapped every tree measuring at least 20cm DBH (diameter at breast height) within 20m of the ridge-top spotlighting track. All marked trees were later identified in the field or in the laboratory from foliage samples obtained with a slingshot or shotgun. Mr T. Irvine and Mr J. Tracey of CSIRO, Atherton identified all plant specimens collected as part of this study. They also identified many of the trees tagged previously by Winter and by Seawright (1981). In all, more than 3,000 individual trees have been mapped and identified.

I recorded the phenology of 280 individually tagged plants representing 55 species (49 tree spp., two vines, three shrubs and one species of mistletoe) at four weekly intervals from June to December 1982, January to December 1983 (excluding May) and January to December 1985. The species included in the sample comprised the more common trees and shrubs in the forest and those plants commonly used for food by the three ringtail species. The unseasonably wet weather in May 1983 and the constant low cloud cover prevented my usual observation of canopy tree species and so only the phenologies of subcanopy species were recorded that month.

At least five individuals of most plant species were consistantly observed for the 30-month period. Some species were so uncommon that fewer than five individuals could be located (eg: *Ficus leptoclada*, the vine *Cissus hypoglauca*). In these cases all known individuals were monitored. Additional observations on fewer individuals of each species were made between June and December 1982. However, as five individuals is considered a minimum when extrapolating to the phenology of a population (Frankie et al. 1974a), these observations were not included when calculating phenology scores (see below).

I checked each tree using binoculars and scored the following:

LEAVES a) no new growth evident b) leaf buds forming c) growing leaves less than fully expanded d) fully expanded new leaves, significantly lighter in colour than mature leaves e) mature leaves and new leaves more than four weeks old.

FLOWERS a) no flowers b) flower buds present c) flower buds present and some flowers open d) all flowers open e) most flowers fallen.

FRUIT a) no fruit b) immature fruit c) mature fruit d) seeds dehisced or fruit fallen.

Within each category the observation was ranked as follows:

1) *very few* - less than 10 structures visible

2) *few* - up to 25% of the likely maximum number of structures

3) *some* - 25% to 50% of the likely maximum

4) *many* - greater than 50% of the likely maximum.

On some overstorey trees, small buds, inconspicuous flowers or occasional small amounts of fruit may have been missed. However, full scale leaf flush, flowering and fruiting were easily seen for each species.

Monthly phenological scores for leafing were calculated by adding the leafing scores of each individual and dividing by the number of individuals scored.

As I could not readily distinguish clearly-defined layers in the forest as have been described by some rainforest workers (eg. Richards 1952; Webb 1959), I arbitrarily divided the forest into understorey (<15m) and overstorey (>15m) layers. Overstorey included emergent (>25m), canopy (15-20m) and subcanopy (15-20m) species. Tree species below subcanopy height and those in the shrub layer were included in the understorey.

I have defined flowering activity to include the presence of flower buds and/or flowers. Such a definition differs from that found in some botanical publications (eg. Frankie et al.1974a). As both flowers and buds are used by possums as food sources, I prefer to acknowledge all flowering stages rather than limit it to open blooms. To allow these data to be compared with others I have also indicated *peak flowering* periods when at least 50% of individuals of a species are producing large amounts of flowers.

4.3 Results

The forest consisted almost entirely of evergreen species including all 55 species studied. Only two uncommon species were deciduous at Longlands Gap, *Melia azedarach* var. *australasica* and *Brachychiton acerifolius*. Mature leaves were therefore present in the forest in all months.

While new leaves were produced on all the monitored plant species during the study, some species did not reproduce during the 30 month study period. These species include *Archidendrani vaillantii*, *Flindersia pimentaliana*, *F. brayleana*, *Elaeocarpus largiflorens*, *Euodia* sp. nov. 305, *Macarangia inamoena* and *Acronychia acidula*. A summary of the trees included in this study, together with their rankings based on leafing, flowering and fruiting phenology, is presented in Appendix A.

4.3.1 Leafing

Seasonality

Population leafing patterns

Tree species were divided into seasonal and unseasonal leafers, the former producing leaf flushes in either the wet or the dry and the latter leafing in both seasons. The unseasonal species were subdivided into discontinuous and continuous leafing categories based on leafing periodicity (Fig. 4.1). Some species (eg. *Sloanea langii*) produced discrete flushes of new growth with little or no leafing between, while others (eg. *Rhodomyrtis trineura*) produced small numbers of new leaves continuously. When all species are considered together there are young leaves present in the forest in all months of the year.

The majority of overstorey species leaf unseasonally (16/24; Fig. 4.1) and discontinuously (10/16; eg. *Flindersia brayleyana*, *F. bourjotiana*), while the understorey species tend to leaf seasonally (17/31) or in a continuous trickle. Overall, the periods of major leaf flush are not spread evenly through the year but are concentrated in the wet season (Fig. 4.3). While most of the species which leaf in the wet season are found in the understorey (12/16; Fig. 4.1), there is a positive correlation between average monthly rainfall and both understorey and overstorey leafing in 1985, but not in 1983 (Table 4.1).

Not all species leafed synchronously within the population. There were two types of asynchronous leafing evident: that between under and overstorey trees of the same species, and that within a population of mature trees of the same species.

The first type of asynchronous leafing was most noticeable in *Acmena resa* and *Syzygium luehmanni*. Saplings produced small amounts of new leaves almost continuously while individuals in the overstorey produced synchronous flushes. The asynchrony observed in populations of mature trees involved mainly understorey species (*Lomatia fracsinofolia*, *Brackenridgea nitida*, *Helicia lamingtoniana*, *Sloanea langii*). Individuals of these species flushed at different times of the year, being out of synchrony from between one (*Helicia*, *Sloanea*) and six months (*Lomatia*, *Brackenridgea*).

Individual leafing patterns

Although there were strong correlations between rainfall and leaf flush for pooled phenology species, they were not evident at the individual species level. Of the 18 major food species tested only *Endiandra sankeyana* (Spearman Rank Correlation, $r = 0.724$, $p < 0.05$) and *Cissus hypoglauca* ($r = -0.657$, $p < 0.05$) showed a significant correlation between phenology and rainfall in 1985. There were no significant individual relationships between pooled phenology scores and rainfall during 1983.

Leaf-fall

Although the forest at Longlands Gap is evergreen, four tree species lost noticeably more leaves than others in the dry season: *Eleaocarpus ruminatus*, *Polyosma rhytophloia*, *Syzygium leuhmannii*, *Acmena resa*. In these cases, leaf-fall coincided with the maturation of the fruit crop. *E. ruminatus* did not leaf significantly until about eight weeks later, once flowering had occurred.

Leafing phenology of major food species

The leafing phenologies of the major or "core" food plants of each possum species (section 5.3.1) are presented in Table 4.2. Four of the 17 core species leafed continuously, but most produced new foliage in the wet season. *Hemibelideus lemuroides* is the only species which did not have access to young foliage from core food species in each month (ie. lacking in August and September).

4.3.2 Flowering phenology

Of the 55 species of plants observed during the 30-month study period 91% (50 species) were observed to flower. These have been divided into three groups: seasonal flowering and extended flowering species and those whose flowering periodicities are unknown. The seasonal flowering species bloom in either the wet or the dry season but not both; extended flowering species bloom in both seasons. Extended flowering may occur over consecutive seasons or be disjunct. Fig. 4.2 summarizes the flowering periodicity at the study site.

There are two major peaks of flowering activity evident when all species are pooled, a wet season peak (January, February) and a late dry season peak (September, October; Fig. 4.4). Although the dry season maximum was later in 1985 than in the previous two years the pattern of floral activity is similar. During the periods of the study July 1982 - December 1983, January-July 1985, there was more understorey flowering activity in the wet season, whereas the overstorey species were more active in the late dry season. Peak flowering reflected this pattern when summed over each season.

When the over and understorey species are divided into seasonal and extended flowerers it is apparent that these two flowering types were maximally active at different times of the year.

Overstorey flowering

The peak in seasonally flowering species activity in the overstorey coincides with the dry season peak in total flowering activity (Fig. 4.5). Extended flowering species were more active in the mid to late wet season.

Understorey flowering

The understorey plant species also showed differences in the timing of maximal flowering activity between seasonally and extended flowering groups (Fig. 4.6). Seasonally flowering understorey species were more active at the beginning and end of the year but showed no set patterns. October 1982 was notable as 11/13 understorey species with buds or flowers belonged to the seasonal group. Generally most flowering activity in the understorey was due to seasonally flowering species.

There were several peaks in extended flowering activity, the most noticeable being January/February 1985. Generally, as in the overstorey, extended flowering species were more active in the wet season.

4.3.3 Fruiting Phenology

While open flowers are usually short lived in rainforest, many species bear mature fruits for long periods. There is a notable difference in duration of fruiting between under and overstorey species (Table 4.3). The latter generally bearing ripe fruit for a longer period than the former.

If all fruit in the forest (regardless of stage of maturity) is plotted, three annual peaks appear (Fig. 4.7). These correspond with the mid wet (around March) and early and late dry seasons (June and September/October respectively). Ripe fruit in the understorey is the main contributor to the wet and late dry season peaks but not to the early dry season peak. This peak is due to the large amounts of immature fruit in both the storeys. These three peaks occurred 1-2 months later in 1985 but conformed to a similar pattern. Generally at any one time there were more species bearing ripe fruit in the overstorey than the understorey (Fig. 4.7).

Seasonal versus unseasonal fruiting

Fruits are optimally edible when ripe. For this reason I have categorised trees as seasonal or unseasonal fruiters based on when their fruits ripen. Unseasonally fruiting species bear ripe fruit in either consecutive or disjunct wet and dry seasons; seasonal fruiters in either the wet or the dry season (Fig. 4.8).

Understorey fruiting

Out of 32 understorey species, only *Litsea leefeana*, *Solanum veride* and *Polyscias murrayi* bore ripe fruit at disjunct periods in both seasons. All other species observed fruiting in the understorey qualified as seasonal fruiters.

Overstorey fruiting

The majority of overstorey trees are unseasonal fruiters bearing ripe fruit in both wet and dry seasons, although not necessarily in the same year (Fig 4.7). This unseasonal group fruits mainly in the dry season. The peaks of seasonal species ripe fruit production are irregular, the major peaks appearing in August to October 1983 and January/February 1985. Of the seasonal fruiting species, 63% of overstorey trees and 52% of understorey trees observed during the study fruited in the wet season.

4.4 Discussion

4.4.1 Leafing

Leafing phenology of core food species

Given the differences in leafing periodicity of their major food species, the two *Pseudocheirus* species have a greater opportunity to specialize than *Hemibelideus lemuroides*. They may also have access to a higher quality diet than the latter, as young foliage generally is more nutritious and less toxic than mature foliage (Chapter 6).

Abiotic effects on leafing

Although there is a correlation between rainfall and leaf growth when data for all species are pooled this does not hold for individual species. Trees frequently developed to the budburst stage at the end of the dry season before significant rain had fallen. Although a general correlation has been found between rainfall and leafing in some tropical forests (Frankie et al. 1974a; Hopkins 1970), rainfall is not a primary causal factor. Instead photoperiod has been nominated as the most likely factor controlling apical dormancy (Hopkins 1970; Njoku 1964). Lawton and Akpan (1968) have implicated night-length rather than day-length as the controlling stimulus.

The one month asynchrony in the peak of leaf flush between under and overstorey trees at the end of both 1983 and 1985 suggests that factors other than daylength and rainfall affect leafing. However, no edaphic or microclimate data were collected so the cause of leafing asynchrony is unknown.

Biotic factors

While the majority of understorey plants leafed seasonally, most overstorey species leafed unseasonally. Although the overstorey species appeared out of phase with rainfall patterns, they maintained synchrony within species. This type of unpredictable but synchronised leafing strategy may have evolved in response to predator pressure as Struhsaker (1975) suggests; the folivorous possums at Longlands Gap feed in the overstorey.

The two types of asynchronous leafing patterns evident in some species may have evolved in response to predator pressure, the differences arising due to relative apparency (*sensu* Rhoades & Cates 1976). Saplings are more likely to escape in space than the more conspicuous canopy individuals, thus selection may favour ephemeral foliage rather than the synchronized flush of the larger trees. This strategy reduces the plants' apparency and decreases the likelihood of a specialist predator discovering a single leafing plant in a highly heterogenous environment.

Another possible response to predation pressure is that of continuous leafing. It was observed in approximately 25% of the plants studied (eg. *Alphitonia petriei, Ficus* spp.). These species produced a trickle of new leaves every month. Continuous leafing may be most effective if individual plants are spaced some distance apart. Although *Alphitonia*, a light gap pioneer species, practises this continuous leafing strategy, it suffers large amounts of insect and possum damage. Coley (1983a) found that light gap species were more susceptible to discovery and predation than shade tolerant species. Therefore continuous leafing in this instance most likely reflects *Alphitonia's* pioneering status rather than a predator avoidance strategy. *Ficus watkinsoniana* and *F. pleurocarpa* are late succession species however, and escape with very little leaf damage (Goudberg, unpubl. data). Therefore in some instances, continuous leafing may be an effective method of escaping signficant predation.

Leaf fall

The increased leaf-fall when fruit matures on several overstorey tree species may make the fruit more visible to both avian and mammalian seed dispersers. The small fruits of *Syzygium luehmannii, Acmena resa* and *Elaeocarpus ruminatus* attract large numbers of high flying parrots and pigeons. The larger fruits of the understorey species *Polyosma rhytophloia* attract both avian and mammalian dispersers found within the forest. Presumably increased leaf-fall also increases dispersal opportunities in the understorey.

E. ruminatus does not initiate leafing until after the fruit have matured and the following flower spikes have been pollinated. This may indicate that pollination is more successful when leaves do not interfere with location of the inconspicuous flower spikes by pollinators.

4.4.2 Flowering

The majority of flowering occurred in the mid wet season and the end of the dry during both rainy and dry periods. In addition, the 1985 dry season flowering peaked after early rains in October. These observations lend support to the theory advanced by Janzen (1967) and Lawton and Akpan (1968) that a sequence of dry and wet is needed to stimulate flowering.

While there were many species with synchronised mass flowerings over a short interval (less than four weeks), some species flowered over long periods (eg. *Syzygium cormiflora, Solanum veride, Darlingia ferruginea*). These species opened several flowers a day over 3-5 months suggestive of plants that accomodate "trapline" pollinators (Janzen 1971).

Despite the four week interval between phenology observations there is an indication of some separation of flowering intervals between species. This is suggested by the generally even distribution of peak flowering through the year, especially during 1985. Additionally, peak flowering of understorey shrubs occurred between November and February, rather than during the period when most trees were flowering (February to October). A separation of flowering periods between species would minimize competition for pollinators

4.4.3 Fruiting

Not all species reproduced annually during the study period (eg. *Flindersia brayleyana*). It is not uncommon for some Australian rainforest species to produce fruit only every eight to ten years (Mr. J. Tracey and Dr. G. Stocker, *pers. comm.*). Long inter-fruiting intervals have also been noted by workers in other parts of the world (Ashton 1969; Frankie et al. 1974a, 1974b; Janzen 1970; Medway 1972). Janzen (1970) suggests that this strategy of unpredictablilty has evolved to enable flowers and fruit to escape specialist predators. Such unpredictability also makes it unlikely that these species would have the benefit of obligate pollinators or dispersers.

Many overstorey species bear large fruits for extended periods. This strategy ensures a more constant and reliable food supply for avian and mammalian dispersers, which in turn makes it more likely that reliable dispersers will maintain a sedentary population nearby (Snow 1965). The decreasing number of fruit bats (*Pteropus* spp.) and cassowaries (*Casuarius casuarius*), the main dispersers of massive fruits in the area, has serious implications for tree species with this reproductive mode.

Most understorey plants are seasonal fruiters. Although there are peaks of ripe fruit production at the beginning and end of the year, ripe fruit is available in all months. As the fruit producing period of understorey species is usually less than six weeks, continual availability indicates that staggered fruiting occurs in this forest as it does elsewhere (Snow 1965; Herrera 1982).

Snow (1965) studied 18 species of *Miconia* (Melastomaceae), secondary shrubs and trees, in rainforest in Trinidad. Although there was no obvious ecological separation between the species, fruiting occurred progressively through the year with minimum overlap. He attributed this phenomenon to selection for decreased competition for dispersal agents. Mass synchrony between and within species would swamp the dispersers, leading to wastage of reproductive resources. Additionally, staggered fruiting leads to a decrease in seedling competition and more efficient seed dispersal as animals forage in the area year round. It is therefore probable that the lack of obvious fruiting synchrony between and within over and understorey species at Longlands Gap is due to selection favouring asynchrony.

4.5 Summary

Most plants leafed during the wet season, budburst occurring just prior to wet season rains. Although rainfall may influence leafing periodicity, photoperiod has been implicated as a major causal factor. Overstorey species tend to discourage specialist predators using a strategy of unpredictable but synchronised leaf flushing. Many understorey species leaf continuously or asynchronously. Both these strategies rely on the plant's low apparency for escape from predators. Several overstorey species practise continuous leafing while saplings, and discrete flushing once in the overstorey.

The major food species of the possums leafed during the wet season, but for four which leafed continuously. *Hemibelideus lemuroides* was the only species which did not have access to young foliage of its preferred species in every month.

Flowering is predominantly a seasonal activity in both storeys. Overstorey plants are usually more active in the dry season, while there is little pattern to understorey flowering periodicity. Extended flowerers in both storeys are more active in the wet season.

Most understorey species produce ripe fruit seasonally, with no peak in either wet or dry, unlike overstorey species which fruit unseasonally with a peak in the dry season.

Overall, when many plant species are considered together, large numbers of flowers, ripe fruit and young leaves are available to the possums throughout the year. Given this, do possums in fact utilize all the available plant resources, and if not, how and on what basis do they select their food items? These questions are addressed in the following chapters.

Table 4.1

The correlation between leaf flush in understorey and overstorey species and rainfrall that fell in the same month and the previous month as the flush. Spearman rank correlation, significance: * $p < 0.01$, ** $p < 0.005$.

	Rainfall	
	same month	previous month
1983		
Understorey	0.129 n.s	1.473 n.s
Overstorey	0.430 n.s	0.112 n.s
1985		
Understorey	0.882 **	0.893 **
Overstorey	0.718 *	0.853 *

Table 4.2

Periods of major leaf flush of core food species.

Species used by:	Months											
	J	F	M	A	M	J	J	A	S	O	N	D
H. lemuroides												
Flindersia brayleyana		x	x							x	x	
Sloanea langii				x	x	x	x			x	x	
Elaeocarpus ruminatus	x	x									x	x
Endiandra sp. 62	x	x				x				x	x	x
Castanospora alphandii			x								x	
Litsea leefeana		x	x			x				x	x	x
P. archeri												
Endiandra sankeyana	x	x	x								x	x
Ficus watkinsoniana	x	x	x	x	x	x	x	x	x	x	x	x
Cissus hypoglauca			x	x						x	x	
Litsea leefeana		x	x			x				x	x	x
Ficus pleurocarpa	x	x	x	x	x	x	x	x	x	x	x	x
Cryptocarya rigida		x	x									
P. herbertensis												
Alphitonia petriei	x	x	x	x	x	x	x	x	x	x	x	x
Elaeocarpus ruminatus	x	x									x	x
Acmena resa						x			x			
Acronychia crassipetala		x	x								x	x
Syzygium luehmannii						x				x	x	
Polyscias murrayi	x	x	x	x	x	x	x	x	x	x	x	x

Table 4.3

The time during which ripe fruit is available on individual overstorey and understorey trees at Longlands Gap State Forest.

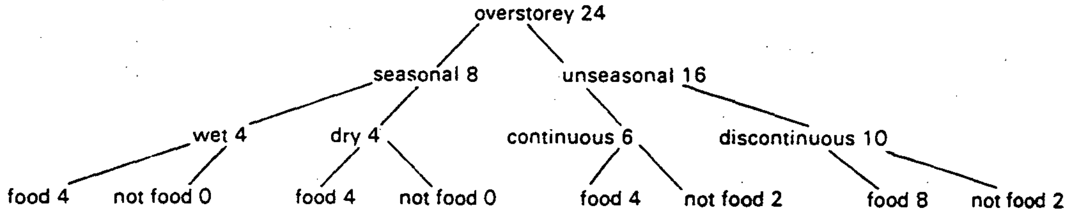
Duration in months	Understorey tree species %	Overstorey tree species %
<1	53.0	16.7
<2	29.4	50.0
<3	17.6	16.7
<4	0.0	8.4
<5	0.0	8.4

Figure 4.1

Phenological grouping of 55 tree species based on their leafing characteristics observed over 30 months. Numbers represent number of species. See text for details.

LEAFING PHENOLOGY

55 species



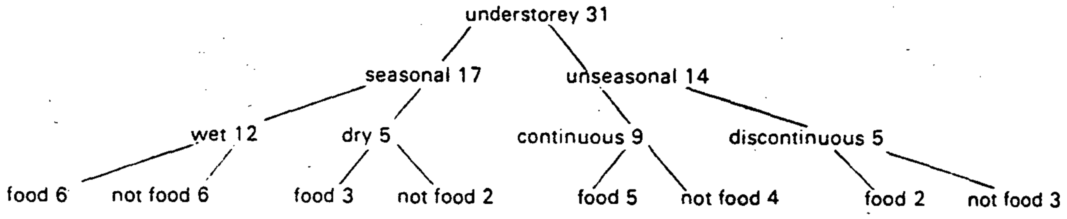
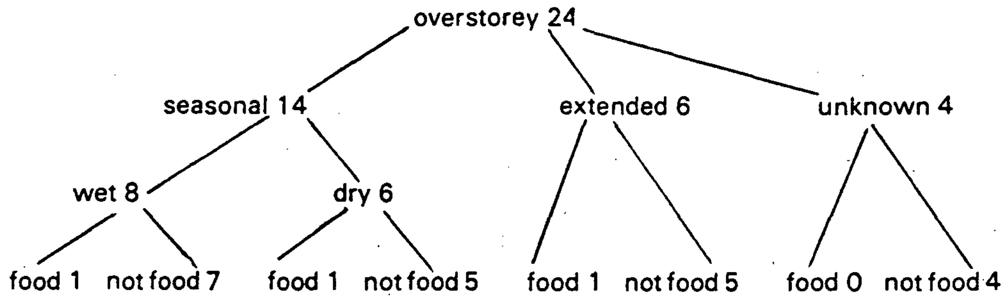


Figure 4.2

Phenological grouping of 55 tree species based on flowering characteristics observed over 30 months.

FLOWERING PHENOLOGY

55 species



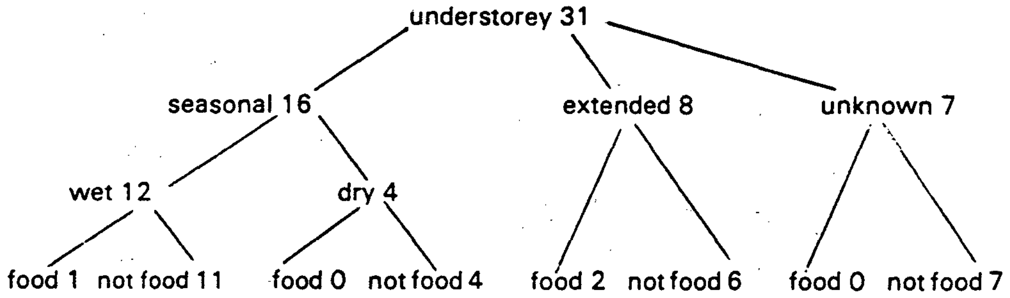


Figure 4.3

Leafing and major flush periods of understorey and overstorey tree species. Broken lines indicate number of species in full leaf flush, while solid lines indicate number of species producing small amounts of new leaves. Vertical lines separate wet season months (November - April) from dry season months (May - October).

Figure 4.4

Flowering phenology of understorey and overstorey species. Broken lines indicate full scale flowering of overstorey (top) and understorey (bottom) species, while solid lines indicate all flowering/budding activity.

Figure 4.5

Extended and seasonally flowering species in the overstorey.

Figure 4.6

Extended and seasonally flowering species in the understorey.

Figure 4.7

Fruiting phenology of understorey and overstorey plant species. Broken lines indicate number of species producing ripe fruit in the overstorey (pale) and understorey (heavy), while solid lines indicate all fruit production, ripe and unripe.

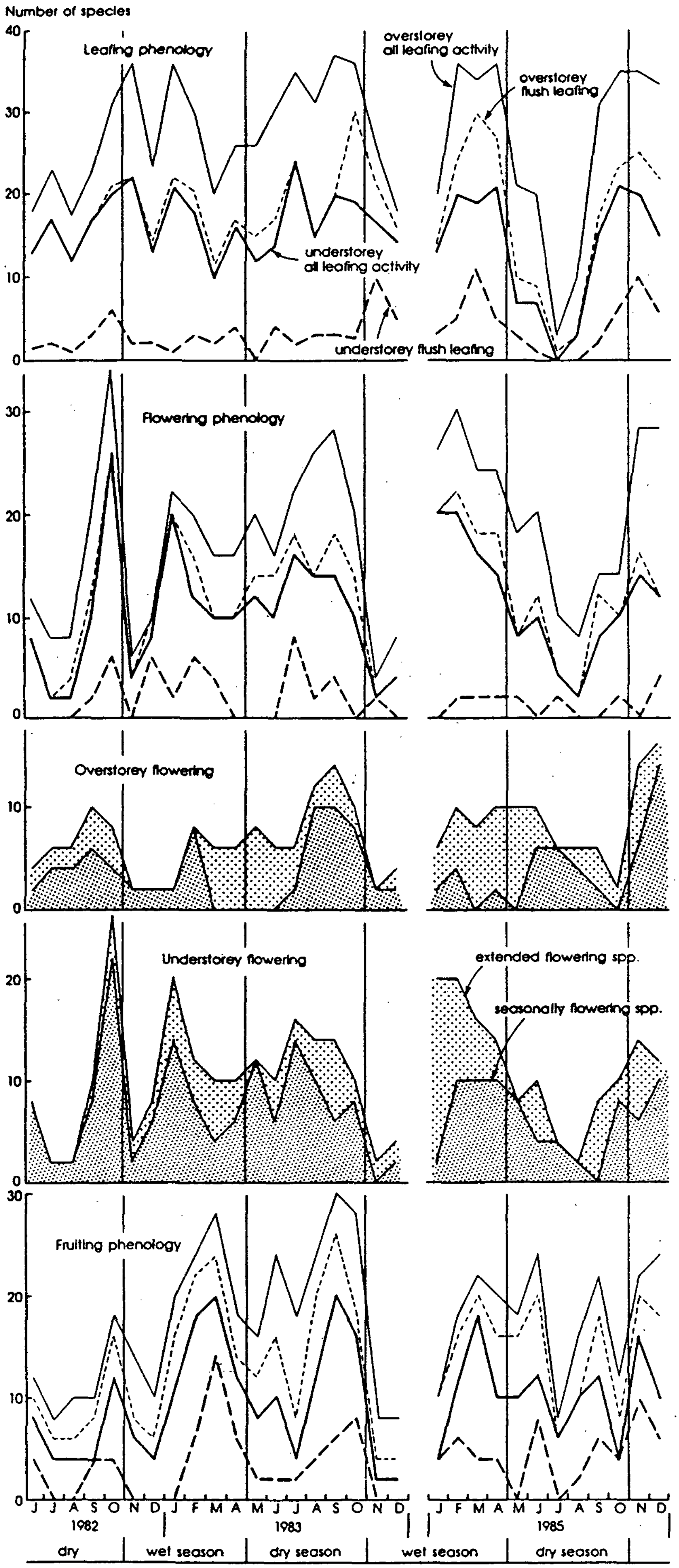
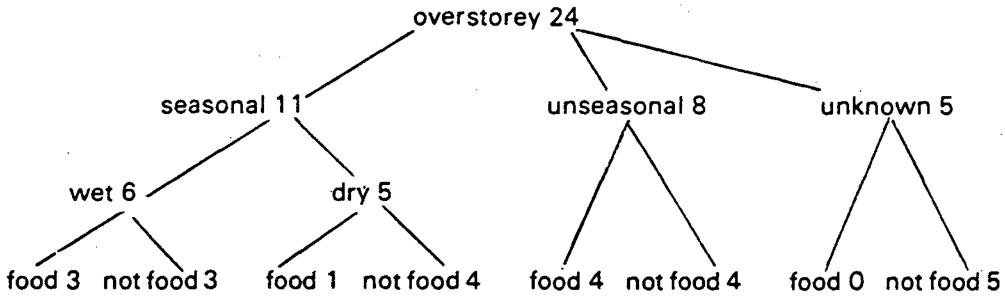
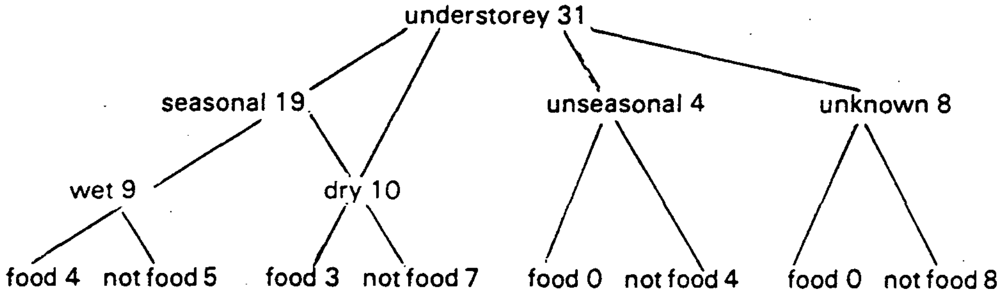

Number of species
40
30
20
10
0
Leafing phenology
overstorey all leafing activity
overstorey flush leafing
understorey all leafing activity
understorey flush leafing
Flowering phenology
Overstorey flowering
Understorey flowering
extended flowering spp.
seasonally flowering spp.
Fruiting phenology
J J A S O N D J F M A M J J A S O N D
J F M A M J J A S O N D
1982
1983
1985
dry
wet season
dry season
wet season
dry season

Figure 4.8

Phenological grouping of 55 plant species based on fruiting characteristics observed over 30 months.

FRUITING PHENOLOGY





CHAPTER 5 DIET AND FOOD SELECTION

5.1 Introduction

Eisenberg (1978) recognises four major groups of mammalian arboreal folivores: marsupials (eg. the koala *Phascolarctos cinereus*, the possum genera *Pseudocheirus* and *Petauroides*); primates (including the Colobidae and some of the Indriidae); rodents (eg. *Arborimus, Capromys*) and sloths (*Bradypus, Choloepus*). Most is known about the first two groups.

5.1.1 The Primate arboreal folivores

Of the 54 primate genera spread across Asia, Africa, Madagascar and South America, 13 are classed as predominantly folivorous (Eisenberg 1978). These include members of the Lemuridae (*Lemur, Hapalemur and Lepilemur*) and Indriidae (*Indri, Avahi, Propithecus*) of Madagascar; the colubid leaf-monkeys of Asia (*Presbytis, Nasalis*) and of Africa (*Colobus*); and the new world folivorous genera, the howler monkeys *Alouatta* and the woolly spider monkey, *Brachychteles*. Few of these species, however, are totally arboreal; most spend varying amounts of time foraging on the ground (Hladik 1978, 1979; Marks et al 1988; Oates et al. 1977; Oates 1977).

It has been shown that the proportion of foliage in the diet of primates increases with body size (Clutton Brock & Harvey 1977). Since the amount of protein required to balance an animal's protein budget scales to the 0.75 power of body weight (Robbins 1983), small animals need to select items higher in protein content. Hladik (1978) contends that leaves are the major protein source available to larger primates as insects cannot be caught in sufficient quantity to maintain positive nitrogen balance. Small prosimians like *Galago demidovii* catch the same bulk of insects as larger species such as *Cebus capucinus* (Charles-Dominique 1971). While insects may satisfy the protein needs of the former, they account for less than 20% of the needs of the latter (Hladik & Hladik 1972). Most primates weighing between two and three kilograms include large amounts of fruit in their diet and supplement their protein needs with insects. As body size increases, leaves replace insects as the protein source (Hladik 1978). For example the Indri (*Indri indri*) the largest of the prosimians (6kg) is also the most folivorous (Pollock 1977). However, there are some exceptions to this general rule. The much smaller prosimians, *Hapalemur* (weighing 1200g) and *Lepilemur* (weighing 600g) are highly specialized folivores (Charles-Dominique & Hladik 1971; Ganzhorn 1988).

Alternatively Clutton Brock and Harvey (1977) suggest that it is physiologically necessary for folivores to have a large body size. This is due to limitations on forage intake, throughput and digestibility when feeding on a fibrous, low nutrient resource such as foliage.

Amongst the folivorous primates there are two major foraging strategies. The first is to feed on low nutrient, readily available and evenly spaced food resources, which demand little energy to locate. The alternative is to range over large areas searching for highly clumped but more nutritious foods. *Lepilemur mustelinus* (Pollock 1977), *Colobus guereza* (Oates 1977) and *Presbytis senex* (Hladik 1978) all practise the lower cost/lower energy-return strategy. *Presbytis entellus* (Hladik 1978), *Indri indri* (Pollock 1977), *Colobus badius* (Clutton Brock 1975), *Alouatta palliata* (Glander 1981; Leighton & Leighton 1982; Milton 1979, 1980), *Macaca fuscata* (Maruhashi 1980) and *Lemur fulvus* (Hladik 1979) practise the higher cost/higher energy-return strategy.

Foraging strategies are closely related to social systems and affect group size, home-range and territoriality (Hladik 1979; Ganzhorn 1988). The sympatric leaf monkeys, *Presbytis senex* and *P. entellus*, illustrate this relationship. *P. senex* feeds on the mature leaves of common low nutrient plants and lives in small groups in small home ranges in which travel is minimised. Its congener lives in groups of up to 30 individuals which travel widely in large home ranges searching for high nutrient fruits and young foliage (Hladik 1978).

Folivores tend to have a diverse diet, but less diverse than that of frugivores (Clutton Brock 1977; Hladik & Hladik 1972; Struhsaker & Oates 1975; Struhsaker 1978). For example, *Presbytis senex* (for which three species of plant constitute 70% of its diet) has a less diverse diet than *P. entellus* (for which ten species constitute 70% of its diet) (Hladik & Hladik 1972; Hladik 1978). The frugivore's more diverse diet probably reflects the highly seasonal nature of its food supply. Additionally, various studies have suggested that dietary diversity in both groups is essential for balanced nutrition and may also help to prevent secondary compound overloads in primates (Clutton Brock 1977; Nagy & Milton 1979; Oates 1977).

Many primates feed selectively on younger foliage in preference to mature leaves (Clutton Brock 1975; Glander 1981; Milton 1979). Often young leaves have more protein and lower levels of secondary compounds than mature leaves (Feeny 1970; Hladik 1979; Rhoades & Cates 1976), but this is not always the case (Cork & Pahl 1984). There also tend to be fewer structural carbohydrates in young foliage. However, some studies have found no relationship between preferred food species and their chemical composition (Glander 1981; Oates et al. 1980).

Sampling behaviour has been noted in howler monkeys (Glander 1981; Milton 1980) and may be a widespread phenomenon amongst the generalist folivorous primates. Sampling may be a consequence of the variability in nutritional and allelochemical status of different aged leaves.

Fruit, a major item in the diet of most larger primates, provides soluble carbohydrates which leaves usually lack. Several species of primates have been shown to travel over greater distances when fruit is available in the forest (Pollock 1977). *P. entellus* offsets some of its high search costs by opportunistically consuming up to 90% fruit in its diet over several days (Hladik & Hladik 1972). Likewise, *Alouatta palliata* returns to a central fig tree to feed on fruit between ranging bouts (Milton 1980).

5.1.2 Marsupial arboreal folivores

The species commonly referred to as marsupial arboreal folivores are the koala (*Phascolarctos cinereus*), the common ringtail possum (*Pseudocheirus peregrinus*), the common brushtail possum (*Trichosaurus vulpecula*), the greater glider (*Petauroides volans*), the grey cuscus (*Phalanger orientalus*) and the spotted cuscus (*Phalanger maculatus*) (Cork 1981; Ride 1970). Other less well known species which also belong in this category are the tree kangaroos (*Dendrolagus lumholtzi* and *D. bennettianus*) and the three rainforest possums which are the subject of this study. Of 65 Australian marsupial genera, only seven are classed as arboreal folivores (Eisenberg 1978). Most of these seven genera feed to some extent on *Eucalyptus* foliage (Cork 1981). I discuss the species for which information is available below.

Trichosurus vulpecula

The common brushtail possum (weight: 1500-4500g; How 1983) is the most widely spread and adaptable of all Australasian possums, living in forests across the continent (Troughton 1965). It exhibits a latitudinal cline in body weight, ranging from 1500g in the north of Australia to 4500g in Tasmania (Kerle 1984a).

Data on dietary preferences of the common brushtail possum from various localities indicate differences in the amount of *Eucalyptus* foliage in their diets. Animals living in the eastern eucalypt forests of Australia include from 66% (Freeland & Winter 1975) to 95% (Suckling, in Kerle 1984a) *Eucalyptus* foliage in their diet, while those in Tasmania, the Northern Territory, and the rainforests of north Queensland eat very little if any eucalypt foliage (Fitzgerald 1984; Goudberg, unpubl. data; Kerle 1984a, 1984b).

Extensive dietary studies of *Trichosurus* in New Zealand, where it is an introduced pest species, reveal that the possum is very selective in its diet, changing food preferences with season and availability (Fitzgerald 1976). It feeds opportunistically. Fruits and flowers make up to 40% of the diet in certain seasons (Fitzgerald 1976; Kerle 1984b; Proctor-Gray 1984). It will also feed on insects when available (Fitzgerald 1978).

Of the large number of foods available to *Trichosurus* in any one habitat, the common brushtail possum feeds on only a few species. In open eucalypt forest, the brushtail was found to eat an average of three species of *Eucalyptus* per night. This was supplemented by ground feeding on herbs and grasses (Freeland & Winter 1975). In the Northern Territory Kerle (1984b) found that faecal pellets consisted of more than 99% *Erythrophleum chlorostachys* leaf fragments. Suckling (in Kerle 1984b) found that leaves of *E. camaldulensis* constituted over 95% of the stomach contents of the brushtails he examined. However, an analysis of faeces obtained from possums trapped at three sites in Tasmania indicated a varied diet of *Eucalyptus* and *Acacia* species, grasses, herbs and various understorey and shrub species (Fitzgerald 1984). Over all its habitats, this species' dietary range is very large indicating a high degree of dietary flexibility.

The ability of *T. vulpecula* to survive on toxic foods such as *Solanum mauritianum, S. seaforthianum* (Proctor-Gray 1984), *Gastrolobium* spp. (King et al. 1978) and *Erythrophleum chlorostachys* (Kerle 1984b) indicates that the toxins in these plants are able to be safely ingested by this species. In addition, the numerical dominance of *T. vulpecula* in *Eucalyptus* forests along the east coast of Australia (Braithewaite et al. 1983) indicates that it can survive in areas of poor nutritional quality better than other possum species.

Pseudocheirus peregrinus

The common ringtail possum (weight 700-1100g; McKay 1983) is the smallest of the marsupial folivores (Hume 1982). It is highly herbivorous (Thompson & Owen 1964) but not as folivorous as the koala or the greater glider (Marsh 1967), as it includes flower buds, seeds and leaf shoots in its diet. Mature leaves constitute over half the food intake in a diet consisting mainly of *Eucalyptus* (Thompson & Owen 1964). Although *P. peregrinus* can be kept in captivity on a diet comprised solely of *Eucalyptus andrewsii* foliage (Chilcott & Hume 1984), animals in the wild supplement their diet with leaves of various understorey species (Pahl 1984). While no seasonal food preferences have been recorded, Pahl (1984) observed that they ate more new foliage in the winter months.

The few feeding studies of *P. peregrinus* in the field indicate little relationship between preferred food species and their nutrient composition (Cork & Pahl 1984; Pahl 1984). While new foliage was often selected before mature foliage of the same species, thus increasing the nitrogen and lowering the fibre intake, young leaves had a higher condensed tannin content and a greater degree of lignification than the mature foliage. No obvious explanation for the diet selection strategy emerged.

Pseudocheirus herbertensis

The Herbert River ringtail possum (weight 700-1450g; Winter 1983a) was recorded as feeding on 26 plant species from 15 families (Seawright 1981). Sarsparilla (*Alphitonia petriei*) accounted for 45% of all feeding observations, with two trees (*Opisthiolepis heterophylla*, *Syzygium* sp. RFK 1891) and a vine (*Rhipogonum papuanum*) contributing another 23%. He also recorded a pronounced seasonal shift in the species composition of the diet. The greatest dietary change was in *Alphitonia petriei* which contributed only 4% of the autumn (March - May) feeding observations but a substantial 59% of the feeding records in winter (June - August).

This species' movements appear to be determined by its food preferences. Seawright (1981) recorded it moving through *A. petriei* trees to feed on specific individuals of the same species. In some instances, an animal would feed for up to five hours in a single tree.

Petauroides volans

The greater glider (weight: 900-1700g; McKay 1983) is the only volant arboreal folivore in Australia (Hume 1982). It is found in eucalypt forests along the east coast where it feeds extensively on leaves and buds of *Eucalyptus* species and small amounts of bark (Marples 1973). Troughton (1965) has also recorded this species feeding on *Casuarina*.

Most feeding occurs in the first half of the night, animals emerging around 8pm and returning to their dens around 3am (Tyndale-Biscoe & Smith 1969). Data on rates of stomach filling and emptying indicate that a glider consumes 20g dry weight of foliage, buds and bark each night. Using this figure, Marples (1973) calculated that *P. volans* consumes 6 kg dry weight/ha/yr or 3.2 X 10^4 kcal/ha/yr.

Phascolarctos cinereus

The koala (weight: 4.1-9.1kg; Martin 1983) is the most folivorous and arboreal of all the marsupial herbivores (Eisenberg 1978). Its diet consists almost entirely of *Eucalyptus* leaves. Over 50 species have been recorded in its diet, although several non-eucalypt species are also known to be eaten occasionally (Hume 1982; Martin & Lee 1984). Koalas prefer the foliage of *E. viminalis*, *E. punctata* and *E. tereticornis*, and tend to occur where these species are relatively common (Southwell 1978).

Most of the koala's diet is made up of mature leaves. As captive koalas preferred young foliage when offered excess food (Ullrey et al. 1981), it has been suggested that its diet of mature leaves may be due to a shortage of young foliage in the wild (Ullrey et al. 1981). Food preference in koalas has been correlated with crude protein levels (Degabriele 1981, 1983; Ullrey et al. 1981), essential oils, secondary compounds (Eberhard et al. 1975) and various trace elements (Martin 1983a). However, Hindell (1979) found no relationship between crude protein or structural compounds and preferred browse, and Southwell (1978) rejected the argument for the role of essential oils and allelochemicals in determining food choice. Overall the factors influencing food preference in the koala are still uncertain.

Dendrolagus lumholtzi

Lumholtz's tree-kangaroo (weight: 3.7-10.0kg; Johnson 1983) is a strict folivore with only 1.3% non-leaf items in its diet (Proctor-Gray 1985). It inhabits rainforest between the Herbert and Daintree Rivers in north Queensland (J.W. Winter, pers. comm.), where it is sympatric in range and habitat with the green, lemuroid and Herbert River ringtail possums, and the coppery brushtail possum *Trichosurus vulpecula johnstoni*.

In the only field study yet conducted on an Australian tree kangaroo, Proctor-Gray (1985) determined that this species prefers to feed on late succession/climax forest plants. It has been recorded to feed on 33 plant species, of which the most frequently occurring were: *Maclura cochinchinensis*, *Euroschinus falcata*, and *Elaeagnus triflora*. *Dendrolagus lumholtzi* has a less specialized diet than the sympatric *Pseudocheirus archeri*, although it appeared to be somewhat more selective in its choice of tree foliage. The dietary overlap between the two species was 18.2% (Proctor-Gray 1985).

There are no feeding data published for Bennett's tree-kangaroo, (*D. bennettianus*).

5.1.3 General considerations

Apart from a few species (eg. the leaf monkey *Presbytis senex*), most folivorous primates have been found to be less folivorous than most of the marsupials studied to date. This is due in part to the lack of work on rainforest dwelling folivorous marsupials.

The best known marsupial species are those from the nutrient poor *Eucalyptus* forests. As these forests have a relatively low floristic diversity, there is not the opportunity for the resident species to become as frugivorous as the rainforest primates with whom they are compared.

The low number of sympatric marsupial folivores found in the eucalypt forests is also a reflection of the lack of floristic diversity. Most folivores are generalists as they need to balance their nutrient and allelochemical loads. This means they have to include a diverse array of food resources in their diet. In low diversity forests there is not the *niche space* to partition the food resources finely among many folivores. This results in a rarity of folivorous guilds (Eisenberg 1978). Rainforests are more likely to have sympatric folivores as they are much more diverse habitats.

The temperate folivorous marsupials (eg. the koala) are amongst the most specialized folivores. Eisenberg (1978) classified *Phascolarctos cinereus* as the strictest folivore of any mammal species, followed closely by *Petauroides volans*. They are also more arboreal than any old world primates. This in itself may explain some of the difference in the degree of folivory between the folivorous marupials and the primates. These marsupials do not forage on the ground as some of the primates do and must obtain all their food from the trees.

Given that the three possum species studied here are rainforest folivores, their diets are constrained by the following factors which are similar to those influencing their primate counterparts:

(i) The availability of food in the forest. This is influenced by floristic diversity, the extent of feeding by sympatric folivores and the phenology of the food species.

(ii) The food preference of the species. This is based on their digestive capacity and nutritional needs plus more intangible factors such as: palatability of individual items and the previous history and physiological status of the animal (Gilmore 1967).

(iii) The spatial use of the habitat. The height at which species forage is determined in part by their food preferences and also by their body weight.

Based on the primate literature and the small amount that is known about tropical marsupial folivores, I hypothesized that these Australian species would:

(vi) have a diverse diet that changed in composition with season;

(ii) exploit preferred items intensively when they were available, while continually sampling potential food sources;

(iii) become specialized on species that provided a longterm source of more nutritious food items.

To test these expectations I collected data to determine the following:

(i) the number of plant species eaten,

(ii) the relative proportion of those species in the diet,

(iii) the proportion of leaf and non-leaf items in the diet,

(iv) the maturity of the preferred leaf items,

(v) the extent of dietary overlap between the three species,

(vi) the extent of dietary specialization, and

(vii) the extent of habitat partitioning.

5.2 METHODS

5.2.1 Duration of field work

I undertook monthly field trips between January 1982 and December 1983 and January and December 1985. I spent the first six months learning to identify the plants, and obtained feeding observations from July 1982 (Fig 5.1, 5.2).

5.2.2 Spotlighting techniques

Spotlighting is the best method for locating possums, as the *tapetum lucida* in their eyes is reflective. A red cellophane filter was swung over the beam of a 12 volt 30 watt sealed beam spotlight, as red light is less disturbing to the animals (J.W. Winter, *pers. comm.*). The light was powered by a lead-acid motorcycle battery carried in a backpack harness. A fully charged battery supplied enough power for approximately 3 hours of observation.

The ridge top snigging track that traverses the study site was used as the main spotlighting transect. As the track is about four metres wide it allows a clearer view of the forest face on each side than is available from within the forest. This track was used for spot sampling during the first 12 months of the study (July 1982 - July 1983). Spot sampling gave an indication of the diet and general activity schedules of the possum population as a whole at Longlands Gap.

Spot sampling of animals

I spent between about six and ten hours each night continuously spotlighting along the track (three to five return trips). Dusk to midnight surveys were alternated with midnight to dawn surveys. Whenever an animal was located the following data were noted:

i. Time ii. Possum species & sex iii. Tree spp/no.
iv. Activity v. Height in tree vi. Social grouping
vii. Weather viii. Location & orientation in tree.

Once I spotted an animal I spent little time watching it unless something unusual was happening, or if it was (or apparently soon would be) feeding. If the animal was feeding, details of the food item were recorded and samples collected if possible the next day.

A separate feeding record was scored for each different food item although several items may have been eaten sequentially from the same tree. The following food items were recorded as separate categories:

Leaves: i. leaf buds, ii. incompletely expanded,
iii. newly expanded, iv. mature leaves;
Flowers: i. flower buds, ii. open flowers;
Fruit: i. immature, ii. ripe.

Most primate feeding studies use length of a feeding bout as an indication of the importance of items in the primate's diet. Due to the difficulties of observing nocturnal animals in a dense canopy, the measurement of feeding intervals was not an option in this study. The best estimator of dietary importance I could obtain was frequency of feeding observations. In an attempt to weight this measure, I scored another feeding record if the same animal was feeding on the same category of food item for more than an hour. This weighting was applied to known and marked animals, and to animals which were being continuously followed. Throughout this study I have used the number of feeding observations to indicate the proportion of each food species in the diet.

Focal animal sampling

All study animals were located within a four hectare patch of forest at the western end of the main transect. Any animal living in this area qualified as a study or "focal" animal (*sensu* Altmann 1974) provided: (i) its natural fur colouration was distinctive, or (ii) it could be caught and marked (section 5.2.3). As most possum captures were made from the main spotlighting transect, the majority of focal animals included the track area in their home ranges.

Between July and December 1983 and January and July 1985, eight animals known from natural or artificial markings were followed for as long as possible each night. Known animals included a family group of three *H. lemuroides* and two distinctly patterned *P. herbertensis* plus two marked *H. lemuroides* and a marked *P. herbertensis*.

Each night I staked out the den of a different animal (chosen using random numbers), then followed the animal visually for as long as possible. Due to the difficulties of visual tracking in dense forest, animals were often lost soon after leaving their dens. Once an animal was lost another known individual of the same species would be located opportunistically and followed as soon as possible.

All activities of focal animals were noted as they were seen to occur. On a calm night, the activities of animals out of sight in the canopy could be monitored by ear until visual contact was renewed. This was only useful when the focal animal was alone.

5.2.3 Capture and marking of animals

So that animals could be unequivocally recognised, they were caught and uniquely marked. Captures were made using a hooked aluminium pole which could be extended to a length of nine metres. The hook was placed around the branch on which the animal was perched and the branch shaken vigorously until the animal was dislodged. All successful captures were made from trees overhanging the main track where there was no undergrowth into which the animals could fall and escape. When the animal fell to the ground, it was placed into a cotton bag and taken to camp to be marked. In this way four animals were caught and marked in July 1983 (two *H. lemuroides*, one *P. herbertensis* and one *P. archeri*). A further 14 animals were caught later in the study (section 5.2.4).

The animals were weighed, eartagged, sexed and measured before being marked with dye or bleach. The tails of the *P. herbertensis* and *H. lemuroides* were banded with hair bleach (Clairol Blonding Creme) and the white belly of the *P. archeri* was dyed with black permanent ink (Swann). The bleached animals were easily recognised for six months but the only *P. archeri* ever caught was not identified again.

Eartags were attached to both ears of the captured animals to increase the likelihood of a tag remaining with time. (Tag loss was very common in Seawrights' (1981) study.) Each 8mm by 2mm Monel metal fingerling tag carried an unique combination of coloured reflective Scotchlite tape. This tape could be seen with a spotlight for about 20 metres but unfortunately did not last as long as the eartags themselves. Bleaching was found to be a more reliable and permanent marking technique for these animals.

5.2.4 Telemetry techniques

During May 1985 five animals were caught (two *H. lemuroides*, three *P. herbertensis*), as previously described, fitted with radio collars and released at point of capture. This was done in conjunction with a pilot study on the water turnover rate of these species. Between August and November 1986 another nine possums (four *H. lemuroides*, five *P. herbertensis*) were caught and radio collared for doubly labelled water measurements (Chapter 7). Unfortunately, it was not possible to catch a single *P. archeri* despite four months of intense work.

The two-step SB2 transmitters (AVM, California, USA) were fitted with a 10cm whip aerial to allow the animals relatively unimpeded movement through the forest. However, this reduced the range of these transmitters to less than 50 metres. Each transmitter was powered by two lithium cells and fitted inside a leather pouch which was attached around the animal's neck and behind its forelegs with plastic covered cable ties. The double harness was essential, as the animal's neck was of a similar size to its head enabling a neck mounted transmitter to be slipped off. Reflective Scotchlite symbols were glued to the outside of the leather pouch to facilitate visual tracking once the animal was located.

The second type of two-stage transmitter, the SR-1 (Biotrack, Dorset, U.K.), was incorporated into harnesses of two designs. The first was similar to the above, with a 10 cm trailing aerial, and the second incorporated a loop aerial around the neck. Both had a 50 metre range within the forest.

Animals were tracked with an AVM LA-12DS telemetry receiver and a three element handheld yagi aerial. Both types of transmitters transmitted in the frequency range 150.7875 - 151.1625 MHz. They weighed about 20g when fitted to the animal.

While following radio-collared animals, all feeding observations were recorded. This enabled an estimate to be made of the number of tree species on which the animals fed in a night.

5.2.5 Statistical methods

All data were analysed using statistical methods as outlined in Sokal and Rohlf (1969) unless otherwise indicated. All tests were considered significant at the 0.05 level or less. All G-tests were based on actual counts and done with William's correction.

Two diversity measures were used to determine whether the species were generalist or specialist folivores. Relative diversity was also used to determine how evenly feeding observations were distributed between the different tree species. To test whether the possums were feeding on trees in the same proportion as they occurred in the forest electivity (*sensu* Petraitis 1979) was calculated. Having calculated electivities, dietary overlaps between the three possum species were determined both with and without taking resource density into account. More details are presented below.

Dietary diversity and homogeneity

There are several indices used to classify an animal as a specialist or generalist feeder. By definition a specialist has a narrower niche breadth than a generalist. The Shannon-Weaver diversity index is commonly used as a measure of niche breadth. It varies from $H'=0$, indicating a specialist diet, to $\log n$ when an animal chooses n food resources in equal proportions.

It is computed as:

$$H' = -\sum_{j=1}^{n} P_{ij} \log P_{ij}$$

Equation 1

where P_{ij} is the proportion of resource j in the diet of species i (also called proportional utilization) and n is the number of food resources used (ie. number of plant species).

Shannon evenness is a measure of homogeneity where $J'=1$ indicates an even allocation of observations into each category. This is also called relative dietetic diversity as it expresses the diversity H' as a proportion of the maximum possible diversity ie: $J'=H'/\log n$.

The Shannon-Weaver index maximizes niche breadth when all resources are used equally. In the field however, not all resources are equally available, and errors can result from this assumption (Lawlor 1980; Petraitis 1979). The Petraitis index (Petraitis 1979), which takes into account the relative availability of resources in the environment, defines a generalist as one which uses resources in the same proportion as they are available in the environment.

$$W_i = \prod (R_j/P_{ij})^{n_{ij}/N_i}$$

Equation 2

where R_j is the relative frequency of resource j in the environment (ie. relative density of tree j); P_{ij} is as defined above; n_{ij} is the number of times species i ate resource j; N_i is the total number of feeding records for species i.

Electivity

Electivity, $A_{ij}=P_{ij}/R_j$ where P and R are as defined above, measures the use of individual tree species by the three possum species. It is calculated for each tree species taking relative density of each species into account (Lawlor 1980). If $A=1$, possums are utilising a tree species in the same proportion as it occurs in the habitat. If $A<1$, they are showing relative avoidance of the species, and if $A>1$ they are showing a relative preference.

Measures of dietary overlap

Similarity, S_{ik}, measures the dietary overlap between sympatric species taking resource density into account (Lawlor 1980). The similarity measure is defined as:

$$S_{ik} = \frac{\sum A_i \quad A_k}{\sqrt{\sum (A_i)^2 \sum (A_k)^2}}$$

Equation 3

where A_i is electivity of species *i*. $S_{ik}=1$ indicates that species *i* and *k* have identical diets while $S_{ik}=0$ indicates total dietary dissimilarity. As there is no correction for biomass in this measure, the electivity of very large but rare trees is probably too large.

Dietary similarity was calculated for the three possum species using electivities calculated for tree species without taking account of foliage being of different ages. However, as the forest is evergreen this equates with electivities for mature foliage. Feeding observations were used as an indication of dietary preference.

Overlap is a similar measure to S_{ik} (Equation 3), but indicates the extent of the sharing of food items by two species without reference to resource density (Lawlor 1980).

It is calculated as:

$$O_{ik} = \frac{\sum P_i \, P_j}{\sqrt{\sum (P_i)^2 \sum (P_j)^2}}$$

Equation 4

where P_i and P_j are as defined above. Overlap is complete when $O_{ik} = 1$, and non-existent when $O_{ik} = 0$.

5.3 RESULTS

The number of feeding observations collected each month during the study varied with changing spotlighting conditions and animal visibility. Due to its cryptic colouration, dim eye-shine and alert nature, there was a definite bias against finding and observing *Pseudocheirus archeri* in the canopy. Likewise, the broken colour pattern and retiring nature of *P. herbertensis* made this species difficult to find when in the canopy of trees such as *Alphitonia*, with white-reflecting discolourous leaves. *Hemibelideus lemuroides* was much more visible than the other two species due to its glaring eye-shine and its habit of jumping noisily between trees. This allowed me to find animals in the canopy which would have been otherwise overlooked. Thus there is a bias in the number and types of my feeding observations.

While most field trips were affected by cloud and rain, six had to be totally abandoned and three more were cut short by deteriorating weather conditions. Despite these difficulties, during 165 nights of spotlighting (approximately 1100 hours; 650 hours for feeding observations, 450 hours for census/catching), 1761 feeding records were collected (118 for *P.*

archeri, 285 for *P. herbertensis*, 1358 for *H. lemuroides*; Fig 5.1).

As field work during the wet season months was the most interrupted by inclement weather, there was 55% less time spent spotlighting for feeding observatons in the wet season (n=230hrs) than the dry season months (n=418hrs). The wet season work yielded 56% of the total number of feeding observations collected (636 obs. vs 1125 obs.), thus there was no bias in the rate of data collection between the wet and dry seasons.

5.3.1 Dietary Composition

Leaves constituted the major proportion of the diet of all three species (Table 5.1). *H. lemuroides* was the most folivorous of the species (94.0% of feeding records on leaves) followed by *P. archeri* (90.7%) and *P. herbertensis* (87.7%). *H. lemuroides* included a more diverse variety of fruits and flowers in its diet (Shannon Weaver index of diversity for fruit and flowers only, $H' = 1.1139$) than *P. herbertensis* ($H' = 1.0414$) although the overall proportion of leaves and flowers in its diet was smaller (3.7% compared with 10.2% respectively). *P. archeri* was seen to feed on the fruits of two figs only (*Ficus watkinsoniana* and *F. pleurocarpa*). Overall, the differences in the proportion of feeding observations on leaves, as opposed to non-leaf items (flowers and fruits), was significant between the species (G test, G = 18.658, df = 2, $p < 0.001$).

The possums fed from a large number of plant families and species (*H. lemuroides* 21 families, 71 species; *P. herbertensis* 18 families, 50 species; *P. archeri* 12 families, 22 species). Of these, 16 or fewer species were exploited regularly. These *"core"* species made up between 71-85% of the animals' total diets (Table 5.2), and individually contributed at least 1% of the total feeding observations recorded during the study. Those species contributing less than 1% to the overall diet I called "*minor*" species. This division is purely arbitrary.

Core species component of the diets

Three tree species accounted for over 45% of the feeding observations of *H. lemuroides: Flindersia brayleyana* (19.2%), *Sloanea langii* (16.5%) and *Elaeocarpus ruminatus* (9.7%)(Table 5.2). *Alphitonia petriei* accounted for 39.3% of the feeding records of *P. herbertensis*, while *Endiandra sankeyana* (22.1%), *Ficus watkinsoniana* (20.2%) and *Cissus hypoglauca* (7.7%) together made up 50% of feeding observations for *P. archeri* (Table 5.2).

H. lemuroides

Except in January 1983, leaves made up the largest component of the diet of this species. Small amounts (ie: <5%) of fruits or flowers supplemented the diet in most months. *F. brayleyana* was a core food species, becoming most important in the diet during leaf flush. There was only one flush in 1983 (Sept.- Nov.) compared with two in 1985 (Feb./March and Sept./Oct.). The importance of young *F. brayleyana* foliage to this species can be gauged by comparing the dietary composition in March of 1983 and 1985 (Fig 5.2). *F. brayleyana* contributed 23.4% of 77 feeding records in March 1983 when only mature leaves were present, compared with 40.5% of 42 records in March 1985 during the flush peak. Of these, 70% (12 records) were on young foliage. This difference in feeding frequency however, is not significant (G test, $G = 3.679$, $df = 1$, $p > 0.05$).

H. lemuroides periodically fed on the mature leaves of *Sloanea langii* (0-12.5% of monthly records). However, when this species flushed between June and August 1983, young leaves became an important resource accounting for 17 - 27% of the monthly feeding records (eg. June mature leaves 0.6%, young leaves 25%; July mature 0%, young 27%; August mature 1%, young

17.7%). In March and April 1985 both *Sloanea* and *Flindersia brayleyana* flushed together. When presented with a choice of young foliage *H. lemuroides* fed almost exclusively on *Flindersia* (Table 5.3). The relative importance of young *Sloanea* leaves in the diet of *H. lemuroides* depends on whether young *Flindersia* is also available. The proportion of records of *H. lemuroides* feeding on *Sloanea* was significantly less in 1985 when leafing coincided in two species than in 1983 when leafing did not overlap (G-test, $G = 31.33$, $df = 2$, $p < 0.001$).

Other major food items included young leaves of *Ceratopetalum succirubrum, Litsea leefeana, E. ruminatus*, and *Endiandra* sp.62 and the mature leaves of *F. pimentaliana, Beilschmiedia aff. obtusifolia, Cryptocarya angulata, E. ruminatus* and *F. brayleyana.* In all species but *Endiandra* sp. 62, there was significant seasonality in food choice, both between wet and dry seasons and between winter, spring, summer and autumn (Table 5.4).

Flindersia brayleyana, Sloanea langii and *Ceratopetalum succirubrum* were eaten significantly more in those months in which they flushed new leaves (G-tests with 1 d.f: *Flindersia* $G = 22.013$, $p <0.001$; *Sloanea* $G = 13.012$, $p < 0.001$; *Ceratopetalum* $G = 23.447$, $p < 0.001$). *H. lemuroides* used *Flindersia pimentaliana* mainly as a source of <u>mature</u> leaves. The proportion of feeding records on the leaves of this species was significantly greater during the winter months (when there were fewer sources of young foliage available in the forest) than at other times of the year (G-test: *Flindersia* $G = 13.431$, d.f $= 1$; $p < 0.001$).

<u>P. herbertensis</u>

The feeding records for this species are distributed unevenly between months (Fig 5.3). The most detailed diet records were obtained in May 1985 when 56 feeding observations covered 21 plant species. This contrasts with

October and November 1983 where six observations accounted for six and five plant species respectively.

Alphitonia petriei was this species' most important food resource. It contributed more than 30% of the monthly feeding records for 11 out of the 18 data months. It leafs throughout the year providing a constant new leaf source for the possums. Both old and new leaves are eaten.

Although Seawright (1981) found a significant difference in the proportion of *Alphitonia* feeding observations between autumn and winter in his seven month study, I found no such difference (G-test: G = 2.172, d.f = 1, $p > 0.1$). Likewise, there was no significant difference between wet and dry season usage (G-test: G = 0.128, d.f = 1, $p > 0.75$). However, there were very significant differences in *Alphitonia* use between winter (June-August), spring (September-November), summer (December-February) and autumn (March-May) (G-test: G = 16.489, d.f = 3, $p < 0.001$) and between pooled autumn/winter and spring/summer data (G- test: G = 12.417, d.f = 1, $p < 0.001$).

Other important food species include *Elaeocarpus ruminatus*, *Polyscias murrayi*, *Elaeagnus triflora*, *Syzygium cormiflora* and *S. papyraceae*. There were no significant seasonal differences in feeding on foliage of any of these species.

P. archeri

The figs *Ficus watkinsoniana* and *F. pleurocarpa* and the laurels *Endiandra sankeyana*, *Cryptocarya rigida* and *Litsea leefeana* were the most important food species for this possum (Fig. 5.4). Both figs produced leaves regularly throughout the year between major flushing activity, providing a constant source of young foliage. Mature leaves were also eaten. *Ficus watkinsoniana* and *Endiandra sankeyana* were eaten in nine and eight months respectively of the 18 for which there are data. Total feeding observations were spread evenly between both wet and dry seasons.

There was significant seasonality in the frequency with which some core species were eaten. *E. sankeyana* and *F. pleurocarpa* were eaten significantly more during the wet season (G-tests with 1 d.f: $G = 5.456$, $p < 0.025$; $G = 12.572$, $p < 0.001$ respectively) while *F. watkinsoniana* was eaten throughout the year (G-test: $G = 0.993$, d.f $= 1$, $p > 0.25$).

P. archeri is noteworthy as the only possum species to feed on noxious or irritating plants such as the figs, which contain terpenes (Milton 1980), the stinging tree *Dendrocnide photinophylla* (Everist 1973) and the highly alkaloidal nightshade *Solanum veride*. The latter two plant species were eaten infrequently at Longland's Gap but more often at Curtain Fig State Forest nearby (Proctor-Gray 1985).

Minor species component of the diet

There were no significant differences between the wet and the dry seasons in the number of minor species utilized each month by either *H. lemuroides* or *P. herbertensis* (Mann-Whitney U test with tied ranks: *H. lemuroides* $U = 18$, d.f $= 5,6$ $p > 0.2$; *P. herbertensis* $U = 11$, d.f $= 5,6$ $p > 0.2$). Of the 18 tree species (total) from which *H. lemuroides* fed on average each month, only four to six species were eaten in large amounts. They made up between 40 and 70% of the monthly feeding records (Fig 5.2), while often the remaining 14 or more minor species were only observed being eaten once.

The low number of species included in *P. herbertensis* diet each month (average of 6.8 species) probably reflects the general paucity of data for this species. During focal animal studies in May 1985, items from 26 species of plant were eaten. This suggests that minor species may be more frequently included in the diet of this species than indicated by the records in most months (Fig 5.3).

Although there were only a few minor species recorded in the green ringtail's diet, this was probably also due to the low number of feeding observations for this species (Fig 5.4). January 1983, with 45 records (six core species, seven minor species), indicates that there are probably appreciable amounts of minor species included in the diet each month.

Non-leaf items

Fruit and flowers were included in the diets of all three possum species (Table 5.5). There were no significant differences between wet and dry seasons in the relative importance of fruits and flowers in the diet of *P. herbertensis* (G-test: $G = 0.747$, d.f = 1, $p > 0.50$). However, *H. lemuroides* ate significantly more flowers and less fruit in the dry season than the wet (G-test: $G = 24.234$, df = 1, $p < 0.001$). There are too few data to comment on *P. archeri*. Ripe figs eaten in January 1983 were the only non-leaf items this species was observed to eat.

Flowering peaked in both the wet and dry seasons (section 4.3.2), with most overstorey species blooming seasonally between July and October. There was no correlation between the number of species flowering in either the over or understorey and the number of observations of blossom feeding for *H. lemuroides* (Spearman rank correlation: $r = -0.001$, d.f = 17, $p > 0.5$). Instead, blossom feeding by *H. lemuroides* coincided with mass flowering of three food species: *Litsea leefeana* (February 1983), *Helicia lamingtoniana* (May 1985) and *Syzygium cormiflora* (July 1985). Although there were too few data to test for a similar correlation in the diet of *P. herbertensis*, blossom feeding by *P. herbertensis* appeared to coincide with widespread flowering by three preferred food species (*Syzygium leuhmannii, S.*

papyraceae, S. cormiflora) between May and July in 1983 and 1985. There were too few data to test for a similar correlation for *P. archeri*.

H. lemuroides included fruit in its diet infrequently (8/18 months) as did *P. herbertensis* (6/18 months) and *P. archeri* (1/18 months). However, there were too few data on fruit feeding to test for a correlation between the number of feeding observations on fruit by any of the possums and the number of tree species bearing ripe fruit in the forest.

5.3.2 Leafing and food preference

There was a significant difference between possum species in the proportion of young foliage in diets (G-test: $G = 23.127$, d.f $= 2$, $p < 0.001$), with *H. lemuroides* eating significantly more than the others ($G = 17.277$, d.f $= 1$, $p < 0.001$) (Table 5.6).

H. lemuroides

H. lemuroides increased its feeding activity in certain tree species when they were in leaf flush (mean phenology score for species $>=3$) (Table 5.7). For example, there was a positive correlation between the monthly phenology score for *Flindersia brayleyana* and the proportion of feeding records on that species in that month (Spearman rank correlation: $r = 0.773$, d.f $= 8$, $p < 0.01$). Likewise, increased feeding on *Sloanea langii* and *Ceratopetalum succirubrum* were similarly correlated to months of leaf flush (Spearman rank correlations with 8 d.f: $r = 0.727$, $p < 0.02$; $r = 0.647$, $p = 0.05$ respectively). A similar analysis showed that although feeding increased when *Endiandra* sp. 62 was in leaf, the increase was not significant (Spearman rank correlation: $r = 0.085$, d.f $= 8$, $p > 0.5$).

The ringtails' diets were affected by the species of trees in leaf rather than the total number of leafing species or individuals present in the forest. There was no significant correlation between the proportion of young foliage in the diet in any one month and the corresponding total number of tree species in leaf (ie. availability of young foliage) (Spearman rank correlation, $r = 0.008$, d.f = 17, $p > 0.25$). However, the overall proportion of young leaves in the diet of *H. lemuroides* did increase when core species were in leaf. For example, there were large amounts of young *F. brayleyana* leaves in the diet when it leafed in March 1985 (12/24 young leaf feeding records) but not in March 1983 (0/10 records) when it did not leaf. This difference in dietary intake of young leaves is significant (G-test: $G = 10.231$, d.f = 1, $p < 0.005$). Although there were other species in the forest producing young foliage in March 1983, they were not exploited. Instead the mature leaf component of the diet increased, indicating the animal's selectivity and dependance on specific plants to provide young leaves.

There was no significant difference in the monthly proportions of young foliage in the diet of the lemuroid ringtail between dry and wet seasons (Mann-Whitney U test: $U = 41$, d.f = 7,11, $p > 0.05$).

P. herbertensis

The major food species recorded in *P. herbertensis'* diet were *Alphitonia petriei* and *Elaeocarpus ruminatus*. Although a continuous leafing species, *Alphitonia* has pronounced periods of leaf flush in March/April and July/August (section 4.3.1). The proportion of feeding records on *Alphitonia petriei* was greater in periods of leaf flush than in other months (G-test: $G = 13.636$, d.f = 1, $p < 0.001$).

There were no significant differences in the monthly proportions of young foliage included in the diet between the wet and dry seasons (Mann-Whitney U test: $U = 42.5$, d.f = 7,11, $p > 0.20$). Additionally, neither the monthly total number of flushing tree species nor the monthly phenology scores of core food species (ie. *A. petriei, Eleaocarpus ruminatus*) were significantly correlated with the proportion of young foliage in this possums' diet in that month (Spearman rank correlations: total number of flush species r = 0.102, d.f = 17, p = 0.75; *Alphitonia* r = -0.624, d.f = 9, p> 0.1; *Elaeocarpus* r = 0.467, d.f = 9, p > 0.2).

P. archeri

Due to the low number of feeding records for *P. archeri*, the data collected over 30 months were pooled into months before being tested for seasonal changes in leaf age preference. There were no significant differences in the amount of young foliage consumed in either wet or dry season (G-test on pooled data: G = 1.929, df = 11, p > 0.1). During the study period, young leaves contributed on average 43% of all feeding records. Additionally, there was no relationship between the proportion of young leaves of all species in the diet in any one month, and the proportion of feeding records for *Ficus watkinsoniana* or *Endiandra sankeyana* (Spearman rank correlations with 11 d.f: *F. watkinsoniana* r = -0.389, p > 0.2; *E. sankeyana* r = 0.120, p > 0.5). More data are needed.

5.3.3 Dietetic diversity and homogeneity

The Shannon-Weaver index of diversity reveals that *P. herbertensis* has the least diverse diet (*H'*= 1.1331) followed by *P. archeri* (*H'*= 1.1563) and *H. lemuroides* (*H'*= 1.3774) with the most diverse. These diversity indices are significantly different between *H. lemuroides* and the other two species (t-test between diversity indices: *H. lemuroides-P. herbertensis* t = 3.357, df = 305, p< 0.001; *H. lemuroides-P. archeri* t = 2.564, df = 124, p< 0.02) (Zar 1984). However, there is no significant difference between the diversity indices of the two *Pseudocheirus* species (t-test: t = 1.876, df = 284, n.s). Of the three species *P. herbertensis* has the most heterogenous diet (*J'* = 0.6669) i.e. the most uneven distribution of observations in the different species categories. This is followed by *H. lemuroides* (*J'* = 0.7442) and *P. archeri* (*J'* = 0.8078).

The Petraitis index of diversity tests whether the animals are using food species in the same proportions as they occur in the environment. The diversity score indicates that *H. lemuroides* is the least discriminating of the three species (W = 0.2964), followed by *P. herbertensis* (W = 0.1245) and *P. archeri* (W = 0.0797).

Both diversity indices therefore show that *H. lemuroides* is more of a generalist than either *P. herbertensis* or *P. archeri*.

H. lemuroides has the highest dietary diversity and is the least discriminating of the three species (ie. using food species in similar proportions to their occurrance). *P. archeri* has a less diverse diet than *H. lemuroides*, is far more discriminating and thus appears to be more of a specialist than the lemuroid ringtail. Likewise, *P. herbertensis* has a low diversity, unevenly distributed diet and is more specialist than *H. lemuroides*.

H. lemuroides

There was no correlation between the monthly dietary diversity index (Fig 5.5) and the number of flushing tree species (phenology scores >= 3) in the forest (Spearman rank correlation: r = -0.067, d.f = 10, p > 0.5). However diversity did decrease whenever *Sloanea* or *Flindersia* were leafing. During 1983, monthly diversity scores for *H. lemuroides* were significantly negatively correlated with the proportion of young *Sloanea* leaves in the diet in that month (Spearman rank correlation, r= -0.658, d.f = 10, p <

0.05). In 1985, there was no correlation between *Sloanea* and diversity, as both core species flushed simultaneously and the animals fed mainly on *Flindersia* (see above). As these two core species are not used independantly (ie. one replaces the other when both are available) the feeding observations for both species were pooled for 1985. There is then a very strong negative correlation between monthly dietary diversity and the corresponding proportion of *Sloanea* plus *Flindersia* in the diet ($r = -0.873$, d.f = 17, $p < 0.001$).

The largest single species components of the overall diet of *H. lemuroides* were *Flindersia brayleyana* (15.4%) and *Sloanea langii* (15.2%) (Table 5.7). Although only *Flindersia* individually affected dietary evenness (Spearman rank correlations with 17 d.f: *F. brayleyana* $r = -0.503$, $p < 0.05$; *S. langii* $r = -0.115$, $p > 0.5$) when pooled they had a more significant affect ($r = -0.717$, d.f = 17, $p< 0.002$). Overall, the homogeneity and the diversity of the diet were affected by the phenology of the core food species.

P. herbertensis

There were large variations in the dietary diversity of this species from one month to the next (Fig 5.5). These monthly variations did not correlate with monthly sample size (Spearman rank correlation: $r = 0.021$, d.f = 17, $p > 0.5$) and therefore were probably not due to variation in the number of feeding observations on which the data were based. The decrease in monthly diversity was pronounced in July and August 1983 (months with low numbers of feeding observations), but with over three times the number of feeding observations in July 1985 (41 in 1985 compared to 12 in 1983) a similar decrease in diversity was still apparent. There was no significant difference in monthly dietary diversity between the wet and dry seasons

(Mann-Whitney U test: $U = 57$, d.f = 7,11,$p > 0.05$). Diversity averaged $H' = 0.6603$.

Overall *P. herbertensis* has a relatively homogenous diet. J' ranged from 0.75 - 0.95 for all months except for September 1982 and August 1983 (Fig 5.5). Most of the heterogeneity ($1-J'$) is due to *Alphitonia*. It made up 43.5% of all feeding observations, while the other 49 food species accounted for the remainder. The marked drop in J' coincided with extensive feeding on *Alphitonia* during those months, after which it decreased in the animal's diet (Fig 5.3). There was a significant correlation between the number of *Alphitonia* feeding records and evenness (Spearman rank correlation $r = -0.651$, $n=17$, $p < 0.01$) but not diversity ($r = -0.336$, $n=17$, $p > 0.1$). In 1983, Shannon evenness was negatively correlated with the flush periods of both *Alphitonia* (Spearman rank correlation between monthly phenology scores and J': $r = -0.625$, $0.02 < p < 0.05$) and *E. ruminatus* (Spearman rank correlation as above: $r = -0.855$, $p < 0.001$).

P. archeri

Due to the low number of feeding observations recorded for this species, observations were pooled into a 'representative' 12 month period (Fig. 5.5). Feeding observations collected incidentally in December 1985 were also included in this data set. Despite pooling the data, diversity was significantly correlated with sample size ($r = 0.709$, $n=12$, $p < 0.01$) preventing further analysis.

5.3.4 Use of individual tree species

The wide range of electivity values, represented in Fig. 5.6 and listed in Appendix B, Table 1, indicates that there is considerable variation in the use of individual tree species by the three species of possum. Some common trees are avoided by some or all of the possum species (eg: *Neolitsea dealbata, Darlingia ferruginea, Stenocarpus sinuatus, Flindersia bourjotiana* and *Euodia* sp. nov.) while some less common species were actively sought after (eg. *Beilschmiedia aff. obtusifolia* and *F. pimentaliana* by *H. lemuroides; Syzygium leuhmannii* by *P. herbertensis*). None of the trees have high elective values for all three possum species. Indeed, most tree species are positively selected by only one of the folivores and avoided by the other two (eg: *Sloanea langii, Endiandra sankeyana)*.

Some common food species were vines (eg. *Cissus* species). As the relative density of vines was very difficult to estimate, electivities for these plants could not be calculated. This does not affect the dietary indices for *H. lemuroides* as it feeds mainly on canopy tree species (vines = 0.15% of feeding records). Both *P. herbertensis* and *P. archeri*, however, made more frequent use of vines (4.2% and 7.1% of feeding records respectively). Overall though this is probably not enough to invalidate diversity or similarity indices for these species.

The most sought after food species used by *H. lemuroides* were *Sloanea langii, Flindersia pimentaliana, Ceratopetalum succirubrum* and *Beilschmiedia aff. obtusifolia*. They were used between five and eight times more freqently than would be predicted by chance. *Flindersia brayleyana*, although one of the largest components in the diet of this species, was eaten only slightly more often than predicted. It is one of the most common trees in the forest.

P. herbertensis actively selects *Alphitonia petriei, Syzygium luehmannii, S. papyraceae* and *Planchonella brownlessiana*. The elective value of the latter may be overly high, as some individuals of this shrubby species were too small to be included in the tree census. *Alphitonia* has a very clumped distribution, occurring predominantly alongside the old snigging tracks. Within relatively undisturbed areas it is quite rare. Due to its clumped habit, I may have underestimated the elective value of this species.

P. archeri fed on both *Ficus watkinsoniana* and *F. pleurocarpa* many times more frequently than expected based on tree density. Other species such as *Endiandra sankeyana* and *F. leptoclada* were also highly sought.

5.3.5 Dietary overlap between species

Family overlap

Overall *H. lemuroides* was observed to use 71 species belonging to 21 plant families (excluding lichen), *P. herbertensis* used 50 species from 18 families and *P. archeri* 27 species from 12 families (Table 5.8). Of these families, *H. lemuroides* shared eleven with *P. herbertensis* and seven with *P. archeri*, while the latter shared six with *P. herbertensis*. Only four of the 31 families were used by all three species (ie. Lauraceae, Proteaceae, Rhamnaceae, Rutaceae).

Most of the families which are unique to one of the species are used very infrequently. An obvious exception to this generalization is the extensive use of the Moraceae by *P. archeri*.

Species overlap

Despite the large overlap of food plant families, only four of the 29 core plant species eaten by the three species were shared (Table 5.9). Of the total of 100 plant species used by the possums, 37 were shared: *P.*

herbertensis - *P. archeri* 7 species, *P. herbertensis* - *H. lemuroides* 29 species, *P. archeri* - *H. lemuroides* 14 species. Only seven food species out of 100 were shared by all three possum species.

Lawlors' (1980) overlap measure was applied to those food species that contributed at least 1% to the total diet of the species (ie. "core" food species). The diet of *H. lemuroides* overlapped most with that of *P. herbertensis* (18.99%) and *P. archeri* (5.75%). *P. herbertensis* and *P. archeri* diets only overlapped by 2.86%. The plant species contributing most to the dietary overlap between the species include *Litsea leefeana*, *Syzygium cormiflora* and *Elaeocarpus ruminatus*.

When resource density is taken into account (ie. S_{ik}), the same order of dietary similarity results: *P. herbertensis* - *H. lemuroides* (S_{ik}= 0.144), *P. herbertensis* - *P. archeri* (S_{ik}=0.00134), *P. archeri* - *H. lemuroides* (S_{ik}= 0.00249). The overlap and similarity measures show that the diets of *P. herbertensis* and *H. lemuroides* are the most alike followed by the diets of *P. archeri* and *H. lemuroides*. There is almost total dietary dissimilarity between the congeners, *P. archeri* and *P. herbertensis*. Overall there is very little dietary overlap between the three possum species due to significant partitioning at the plant species level.

5.3.6 Seral partitioning

In addition to partitioning of food species and items between the possum species, there were significant differences in the successional status of preferred species (G-test: G = 71.22, d.f = 2, $p < 0.001$ Table 5.10). *H. lemuroides* core food species belonged to the late secondary succession or mature climax stages (types C,D). *P. archeri* obtained most of its food from mature climax trees; smaller amounts from pioneer and early succession plants (types A_1,B). *P. herbertensis* depended significantly on both mature climax species and early succession species (type B).

5.3.7 Feeding activity

While it was relatively easy to track the radio-collared animals in the canopy, it was virtually impossible to maintain visual contact with them for extended periods. As a result, reliable records of the number of species eaten by individual animals in a night are few (Table 5.11). There are no data for *P. archeri*.

H. lemuroides feeds on between five and ten species per night. The two animals which were observed for the longest periods each fed on seven species during the nights foraging (Table 5.11).

There are too few data to make many comments about *P. herbertensis*. One animal ("Spot") was followed for almost seven hours and only fed from three species. The following night the same animal fed from six species in four hours. Such variability may be common in a species which includes so much of one food plant (*Alphitonia petriei*) in its' diet.

The timing of feeding activity in the possum population varies throughout the night and with the species. Thus which part of the night is monitored for feeding activity affects the figures on proportion of total time spent feeding. The data suggest that in the first part of the evening *H. lemuroides* spends approximately 45% of the time feeding (Table 5.11). This increases from about 0200hrs to between 50-60%. These different feeding intensities coincide with the periods of major feeding activity during the night (Fig 5.7). When the entire night is monitored, the average time spent feeding is between 35-50%.

The relationship between peaks of feeding activity and feeding intensity is not so clear for *P. herbertensis*. The small number of data suggest that the percentage time this species spends feeding varies from

50% to 70%, possibly falling towards the end of the night (Table 5.11).

As it was not possible to track *P. archeri* little is known about the proportion of time this species feeds in a night. Unlike the other species however, *P. archeri* starts feeding as soon as it becomes active. This is followed by periods of inactivity until it resumes feeding again between 2200 and 2300. Its major feeding activity occurs between 0300 and 0500 prior to retiring before dawn (Fig. 5.7).

Neither *P. herbertensis* nor *H. lemuroides* feed immediately upon becoming active but instead spend most of the first hour of the evening sitting, grooming and moving to feeding trees, especially in the wet season (Fig 5.7). There are three major feeding periods during the night: (i) within two hours of emerging, (ii) between 2200hrs and 0100hrs, and (iii) several hours before retiring to the den.

There is some movement of the feeding peaks with season. During the shorter wet season nights, most feeding occurs in the first half of the night, dropping to a lower but steady proportion of activity until the animals' retire. As the nights get longer feeding is concentrated into two main periods, the first soon after emergence. This is followed by a variable period of sitting and/or moving until feeding activities increase again in the latter half of the night.

5.3.8 Feeding heights

The three possum species were active at all heights between the shrub layer and overstorey (ie. 2 - 30 metres). However, there was a significant difference between the species in the average height at which they fed (G-test: $G = 110.084$, $d.f = 10$, $p < 0.001$).

H. lemuroides most commonly fed at heights between 11 and 20 metres (63.7%) (Fig. 5.8). This corresponded with feeding in *F. brayleyana, E.*

ruminatus and *Endiandra* sp. 62. The substantial group of observations between 6 and 10 metres (18.4%) is due to feeding in understorey species (eg. *S. langii*, *H. lamingtoniana*, and *L. leefeana*).

The bimodal distribution of *P. herbertensis* feeding heights (Fig 5.8) also closely reflects its preferred food trees. About half of all feeding observations (47.9%) were made at heights less than 11m in young *Alphitonia petriei*, *Acmena resa* and *Polyscias murrayi*. The second, smaller peak in the range 16-20m (25.%) reflects canopy feeding in mature *Alphitonia* and *E. ruminatus*.

The feeding heights recorded for *P. archeri* peak in the 6-10m range (32.3% of all sightings) and reflect feeding on understorey plants such as *E. sankeyana*, *L. leefeana* and *Solanum veride* (Fig 5.8). This species is most often seen in the understorey as its cryptic colouration and poor eyeshine reflection make it very difficult to locate when feeding in figs or in the canopy. For this reason observations of this animal at higher levels in the forest are probably under-represented.

Overall, both *P. archeri* and *P. herbertensis* feed predominantly in the understorey (6-10 metres), although the former is probably found more commonly than indicated in the overstorey. *P. herbertensis* is also found quite often (25.3%) between 16 and 20 metres. Here it overlaps in height with *H. lemuroides* which feeds primarily in overstorey trees.

5.4 DISCUSSION

5.4.1 Evaluating the foraging strategies

The three species utilize two foraging strategies: they swap between generalist (wet season) and specialist (dry season) strategies as the phenology of food plants change in response to the seasons. As expected, all three have diverse diets, especially during the late dry and early wet seasons. However during most of the dry season they have each specialized on plants which leaf over many months. These core species provide young foliage when few other plants are leafing. *H. lemuroides* uses several staple food species which leaf discreetly. The other possum species have specialized on continuous leafing plants which provide them with a constant source of young foliage.

There are many minor species in the animals' diets, some of which were only observed to be used once a month or less. Although minor species may be used as sources of limiting nutrients or minerals, their presence also suggests that the animals may be monitoring or sampling potential food items. Sampling and monitoring behaviour has been recorded for the howler monkey *Alouatta palliata* (Glander 1978) and is probably fairly widespread amongst the folivorous primates (Milton 1980). I expect it is also common amongst generalist folivorous marsupials.

H. lemuroides

Although *H. lemuroides* is the most generalist of the three species, it is still very selective. It does not select food species or seasonal items in the same proportion which they occur in the forest, nor does it utilize plants in equal proportions. Active selection occurs.

H. lemuroides eats significantly more mature leaves than the other possum species. However, unlike primate mature leaf specialists (eg. *Presbytis senex*), dietary diversity increases as the proportion of mature leaves in its diet increases. Some primate studies show a significant decrease in diversity with an increasing mature leaf component (eg. Hladik 1977a). I suggest that in contrast to primates such as *P. senex* it is necessary that this possum eats a more diverse array of less optimal items to balance the nutrient and allelochemical content of its diet. When preferred species leaf, there is intense feeding on young leaves and a significant decrease in dietary diversity. Presumably young foliage is better able to satisfy the animal's nutritional demands than mature leaves, and increased diversity is not necessary.

P. herbertensis

P. herbertensis has a more specialist diet than *H. lemuroides*. The large amount of young foliage in its diet also separates it from *P. archeri*, although both *P. archeri* and *P. herbertensis* specialize on continuous leafing species. Extensive feeding on trees which leaf year-round enables both *P. herbertensis* and *H. lemuroides* to become more narrowly specialist than *H. lemuroides* which must swap amongst discrete flushing staples during the year.

Many primate species spend considerable time searching for seasonal items such as young foliage. *P. herbertensis* has side stepped this problem by specializing on *Alphitonia* foliage, both young and old. As young leaves are available throughout the year this species can maintain a high young leaf component in its diet at no extra search cost.

The proportion of *Alphitonia* in the animal's diet dropped at the end of 1983. While this drop and the accompanying increase in diversity may be due to lack of data, it is suggestive of a real change in diet for two reasons: (i) other months with low numbers of feeding records still have a high proportion of *Alphitonia* present in the diet, (ii) despite the low number of feeding records, the dietetic diversity remains high. The only months of similarly high diversity are October and November 1982. Overall the general trend, although not significant (G test: $G = 0.129$, d.f $= 8$, p

> 0.5), is for an increasing use of *Alphitonia* through the year, decreasing rapidly in September as the diversity of food plants included in the diet increased.

Dietary diversity increases at the end of the dry season when the proportion of *Alphitonia* decreases in the diet, although the amount of young foliage in the diet remains the same. The sudden increase in feeding on other species coincides with the pre-rains flush seen in many plants at that time (section 4.4.1). Whether this flush has some influence on the diet is unknown. Presumably the increased costs in searching for young leaves are offset by some nutritional gain from a more diverse diet. As search costs for generalists are lower when many species are leafing together, the timing is important. Seawright (1981) noted the shift in diet between September 20th and 27th 1981. During this study, the shift occurred between 22nd September and 9th October in 1982 and between September 16th and 24th in 1983. The very small variability in timing between years suggests a link with light induced phenological changes (Chapter 4). Thus the onset of the pre-rains flush may trigger the dietary shift.

P. archeri

P. archeri is the most selective of the three species, feeding extensively on fig leaves. The very high elective values for *Ficus* suggests that this species may be a fig specialist. Unlike the other species, *P. archeri* also appears to be a family specialist, as partitioning of the diet occurs mainly at this level. *P. archeri*, includes three fig species in its diet.

One reason for feeding extensively within a single family is the cost of inducing and maintaining sets of detoxification pathways (Chapter 6). Latex, which is rich in terpenes, is one of the characteristics of the

Moraceae and is probably used as a defence against herbivores (Milton 1980). It is possible that there is more energy tied up in the detoxification pathways of a *Ficus* diet than would be necessary for other diets. As it is costly maintaining a variety of pathways, the animal may be better off to retain only a few. As this species' diet is the least diverse of the three it probably maintains fewer detoxification enzyme systems and saves on energy expenditure.

5.4.2 Competition

At present there appears to be very little competition occuring between the three species. There is partitioning between *H. lemuroides* and *P. herbertensis* on the species and item level, and between these species and *P. archeri* on the family level. Additionally, there are significant differences in the heights at which the three species feed and the timing of nightly feeding peaks. This all serves to reduce present levels of competition.

Of the three species, the feeding height data is most accurate for *H. lemuroides*. This is partly due to the relatively large numbers of this species in the study area, and also due to this species' habit of jumping between trees making them easier to locate. By contrast, the two *Pseudocheirus* species are more conservative in their movements and present in lower numbers. Such a difference in relative visibility between the species may lead to a bias in the results, with fewer overstorey observations for the more cryptic species. Such a bias could lead to a greater than actual feeding height separation between them. Only more radio-telemetry work will reveal whether my data is significantly biased by visibility differences.

Dietary overlap is least between the congeners and greatest between *H.*

lemuroides and *P. herbertensis*. However the extent of the overlap appears to be small enough that there is little direct competition occurring between them.

The data indicate that the food preferences of these rainforest possums diverge during the most difficult season, ie. when the diversity and abundance of preferred food items is low. It is then that the animals make greatest use of their staple food species and become more specialist. At the beginning of the wet season when many plants are flushing, diets become more diverse as animals eat more widely. This is predicted under the hypothesis that interspecific competition determines resource partitioning patterns (Smith et al. 1978). Foraging strategy theory, however, predicts the reverse: that in times of food scarcity, animals become less selective and take a wider range of items. The data do not support this prediction.

Consumptive competition is the most common form of competition that occurs between herbivores, ie. where one competitor utilizes a resource, making it unavailable to another (Schoener 1983). There is no evidence of this presently occurring between the three folivores. However it may have operated in the past, especially during the dry season, and may have prevented possum species increasing dietary diversity when food is scarce. Many studies implicate this type of competition as the causal mechanism influencing different patterns of resource utilization (reviewed by Schoener 1983).

Another likely mechanism that explains the large differences between the diets of the three species is that they became specialized to exploit chemically diverse resources. As plants protect their leaves with complex chemical defences it is necessary for a predator to evolve detoxification mechanisms to counter these defences (Chapter 6). Detoxification specialization enables the possum species to feed on food species for which they are enzymatically best adapted and so obtain maximum benefit. Given the high probability that coexisting folivores would develop enzyme systems around different chemical entities (of which there are thousands), this would lead to differences in preferred food species. Although folivores are enzymatically flexible, once feeding on divergent food resources consumptive competition would encourage the animals to remain with their particular food habits, especially in times of food scarcity.

Table 5.1

The proportion of plant items in the diets of *P. herbertensis*, *P. archeri* and *H. lemuroides*. Figures in brackets are percentages.

Species	Total	Number of Observations Leaf	Fruit	Flower	Unknown
H. lemuroides	1358	1277 (94.0)	15 (1.1)	35 (2.6)	31 (2.3)
P. herbertensis	285	250 (87.7)	14 (4.9)	15 (5.3)	6 (2.1)
P. archeri	118	107 (90.7)	8 (6.8)	0	3 (2.5)

Table 5.2

Core food plants in the diets of *H. lemuroides*, *P. herbertensis*, and *P. archeri*. ? = unknown food item.

H. lemuroides

Species	Family	Overall % in diet
Flindersia brayleyana	*Rutaceae*	19.2
Sloanea langii	*Elaeocarpaceae*	16.5
Eleaocarpus ruminatus	*Elaeocarpaceae*	9.7
Castanospora alphandii	*Sapindaceae*	5.9
Endiandra #62	*Lauraceae*	5.4
Litsea leefeana	*Lauraceae*	5.2
Ceratopetalum succirubrum	*Cunoniaceae*	4.7
F. pimentaliana	*Rutaceae*	4.5
Helicia lamingtoniana	*Proteaceae*	3.2
Beilschmedia bancroftii	*Lauraceae*	2.4
Syzygium cormiflora	*Myrtaceae*	1.8
Euodia sp. 305	*Rutaceae*	1.7
Cryptocarya angulata	*Lauraceae*	1.4
Alphitonia petriei	*Rhamnaceae*	1.2
A. whiteii	*Rhamnaceae*	1.1
Acmena resa	*Myrtaceae*	1.0
Total of overall diet		84.9%

P. herbertensis

Species	Family	Overall % in diet
A. petriei	*Rhamnaceae*	39.3
E. ruminatus	*Elaeocarpaceae*	9.7
A. resa	*Myrtaceae*	4.7
S. cormiflora	*Myrtaceae*	3.1
S. leuhmannii	*Myrtaceae*	3.1
Acronychia crassipetala	*Rutaceae*	3.1
S. papyraceae	*Myrtaceae*	2.3
Polyscias murrayi	*Araliaceae*	1.9
Planchonella brownlessiana	*Sapotaceae*	1.9
C. alphandii	*Sapindaceae*	1.9
Total % of overall diet		71.0%

P. archeri

Species	Family	Overall % in diet
Endiandra sankeyana	*Lauraceae*	22.1
Ficus watkinsoniana	*Moraceae*	20.2
Cissus hypoglauca	*Vitiaceae*	7.7
L. leefeana	*Lauraceae*	6.7
F. pleurocarpa	*Moraceae*	5.8
Cryptocarya rigida	*Lauraceae*	4.8
Carnavonia sp. 231	*Proteaceae*	3.9
H. lamingtoniana	*Proteaceae*	3.9
A. whiteii	*Rhamnaceae*	1.9
Solanum veride	*Solanaceae*	1.9
Total % of overall diet		78.9%

Table 5.3

The proportion (%) of young foliage from two core species (*Flindersia brayleyana, Sloanea langii*) in the diet of *H. lemuroides*. During 1983 leafing did not overlap; in 1985 leafing coincided in both species.

Month	1983 *Sloanea*	 *Flindersia*	1985 *Sloanea*	 *Flindersia*
March	9.1	23.4	0 *	40.5*
April	19.2	8.5	10.0*	27.5*
May	—	—	15.0	25.0*
June	27.8*	16.6	—	—
July	27.2*	11.1	7.5	5.9

* species producing new leaves

Table 5.4

Seasonality in frequency of feeding on core food species by *H. lemuroides*. Numbers are feeding records. Seasons: Wet = Nov - Apr; Dry = May - Oct; Spring = Oct, Nov, Dec; Summer = Jan, Feb, Mar; Autumn = Apr, May, June; Winter = July, Aug, Sept.

Species	Wet	Dry	Total	Winter	Spring	Summer	Autumn
Flindersia brayleyana	80	158	238	59	82	11	86
Sloanea langii	152	51	203	112	33	19	39
Litsea leefeana	34	27	61	12	17	11	21
Elaeocarpus ruminatus	91	31	122	49	49	20	4
Ceratopetalum succirubrum	36	25	61	7	29	10	15
Flindersia pimentaliana	39	17	56	32	3	6	15
Beilschmedia aff. obtusifolia	38	13	51	23	16	5	7
Endiandra sp. 62	54	28	82	25	28	12	17

Table 5.5

Non leaf items included in the diets of *H. lemuroides*, *P. herbertensis* and *P. archeri*. Numbers refer to the total number of feeding observations. Percentages are proportions of total feeding observations.

Species	*H. lemuroides*		*P. herbertensis*		*P. archeri*	
	fruit	flower	fruit	flower	fruit	flower
Ficus pleurocarpa					3	
Ficus watkinsoniana					5	
Elaeocarpus ruminatus			4			
Amylotheca sp.	1					
Litsea leefeana		6				
Doryphora aromatica		2				
Acmena resa	3		1			
Syzygium cormiflora	2	5	2	8		
S. luehmannii	3		4			
S. papyraceae		4				
Darlingia ferruginea				1		
Helicia lamingtoniana				13		
Alphitonia petriei	11	1		1		
A. whiteii		1				
Acronychia crassipetala			2			
Euodia sp. 305			1			
Arytera divaricata			1			
Castanospora alphandii		3				
Symplocus cochinchinensis	3					
Planchonella brownlessiana				1		
	1.69%	1.62%	5.26%	8.42%	6.78%	0

Table 5.6

The proportion (%) of young and mature age leaves in the diets of *H. lemuroides*, *P. herbertensis* and *P. archeri*.

Species	Young Leaves	(n)	Mature Leaves	(n)	Total (n)
H. lemuroides	40.9	(555)	59.1	(803)	1358
P. herbertensis	56.6	(161)	43.4	(124)	285
P. archeri	43.0	(51)	57.0	(67)	118

Table 5.7

Percentage of young leaf feeding records in the diet of *H. lemuroides* during flush periods compared with the overall proportion of young leaf feeding records for this species for the whole study.

Species	No. Months in Flush	Feeding records for flush months % Flush spp. GL/total GL in month	% Flush spp. GL/total L in month	% spp. in diet overall
Sloanea langii	3#	75.5#	23.3#	15.2
Flindersia brayleyana	4	45.5	26.2	15.4
Ceratopetalum	5	16.7	7.8	5.2
Endiandra sp.62	2	27.4	10.1	6.0

GL = young leaves   L = leaves of all ages   # = For 1983 data only

Table 5.8

The families of plants used for food by the three possum species. Those families that are unique to the diet of one possum species are marked *. The number in brackets is the % of total feeding records for that species that the family represents. The number outside the brackets represents the number of plant species that are eaten from that family.

Families	*H. lemuroides*	*P. herbertensis*	*P. archeri*
Apocynaceae			1*(.85)
Araliaceae		4*(4.9)	
Burseraceae	1*(5.3)		
Cunoniaceae	6 (25.7)	4 (9.8)	
Elaeocarpaceae		1*(1.8)	
Eleagnaceae	2 (.29)	3 (2.8)	
Flacourtiaceae	2 (.43)	1 (.35)	2 (.85)
Lauraceae	18 (20.2)	5 (2.1)	4 (28.9)
Loranthaceae	1*(.06)		
Meliaceae	1 (.22)	1 (.35)	
Menispermaceae		1*(1.4)	
Mimosaceae	1 (.22)	1 (.35)	
Monimonaceae	2 (.51)		(.85)
Moraceae			4*(34.7)
Myrsinaceae	1*(.15)		
Myrtaceae	8 (4.1)	7*(14.38)	
Ochnaceae	1*(.07)		
Proteaceae	7 (6.2)	5 (3.16)	5 (11.0)
Rhamnaceae	2 (2.5)	1 (43.5)	2 (2.5)
Rosaceae	1*(.07)		
Rubiaceae		1*(.35)	
Rutaceae	8 (24.8)	4 (5.3)	1 (.85)
Sapindaceae	3 (5.2)	5 (4.6)	
Symplocaceae	1*(.3)		
Sapotaceae	2 (.29)	4 (3.5)	
Smilacaceae	1*(.07)		
Solanaceae			1*(1.7)
Sterculiaceae	1 (.29)		1 (.85)
Urticaceae			1*(.85)
Vitiaceae		1 (.35)	2 (11.0)
Unidentified			–(4.2)
No. of unique families	7	5	4
(% of total feeding records contributed by unique families)	6.5	9.2	38.1

Table 5.9

Core food species shared by two or more possum species shown as number of feeding records. ? = unknown food item.

Species	Flower			Leaf			Fruit			?		
	Hl	*Ph*	*Pa*	*Hl*	*Ph*	*Pa*	*Hl*	*Ph*	*Pa*	*Hl*	*Ph*	*Pa*
Elaeocarpus ruminatus				130	16			4		3	5	
Sloanea langii				206	1							
Beilschmeidia bancroftii				35	2					6		
Cryptocarya rigida				17	1	5						
Endiandra sankeyana				4		25				2		
Litsea leefeana	8			61	1	7						
Acmena resa				13	7		3	1			1	
Syzygium cormiflora	5	8		20	2		2	2				
S. luehmannii					2		3	4				
S. papyraceae				2	2			4				
Carnavonia sp. 231			3		4							
Helicia lamingtonia	13			24	1	4				2		
Alphitonia petriei	1	1		17	122	1	11				1	
A. whiteii	3			10		2						
Acronychia crassipetala				1	5			2				
Euodia sp. 305	1		21	6	1							
Flindersia brayleyana				208	1					1		
Castanospora alphandii	3			63	5					2		
Planchonella brownlessiana		1		2	4						1	

Hl = H. lemuroides   *Ph = P. herbertensis*   *Pa = P. archeri*

Table 5.10

The seral classification of core food plants eaten by the three possum species. Numbers are % of feeding observations; in brackets, number of feeding observations. Classification is according to Hopkins et al. (1977). A1 = pioneer species, 1-3 years longevity, 1-2m high; A2 = pioneer species , 5-15 years, 4-8m high; B = early secondary succession species, 15-50 years, 10-25m high; C = late secondary succession species, 50-100 years, 10-25m high, D = mature climax species, > 100 years longevity.

	% Seral Type (n)				
	A1: Short lived pioneers	A2: Long lived pioneers	B: Early 2° succession	C: Late 2° succession	D: Mature Climax
H. lemuroides	0	0	0	28.9 (320)	45.1 (680)
P. archeri	1.9 (2)	0	2.8 (3)	0	67.7 (80)
P. herbertensis	0	1.9 (5)	44.3 (126)	0	24.8 (71)

Table 5.11

Number of plant species eaten and percent feeding time (in one night) of radio-tracked animals. M = male, F = female.

Date		Individual	Sex	Time Period	No. of Species	% Feeding: Total Minutes
3/7	*H. lemuroides*	Babe	F	1835-0500	7	35.4
28/10		Non-TT	M	2100-0220	8	43.4
29/7		Mum	F	1825-0011	8	43.9
27/6		Mum	F	1908-2303	5	38.2
27/6		Dad	M	1908-2303	5	43.9
17/6		Dad	M	2041-0033	4	46.3
17/6		Dad	M	0038-0300	2	61.3
17/6		Mum	F	0038-0300	2	60.6
30/10		B/Y Male	M	0300-0445	6	62.9
20/6		Mum	F	0128-0410	4	56.8
5/9		Ethelred	F	2120-0430	7	54.7
4/7	P. herbertensis	Spot	M	1830-2300	3	48.8
16/8		Whiteleg	F	1932-2035	1	41.4
5/7		Spot	M	2040-2210		
				2330-0200	6	69.9
9/5		C-male	M	0330-0440	1	14.3

Figure 5.1

TOP: Number of days per month spent in the field during 1982, 1983 and 1985. Where number of days per month is < 4, only phenology observations were collected due to inclement weather. The four longest field trips coincided with possum catching trips for telemetry and isotope work.

BOTTOM: Total number of feeding observations collected each month during 1982, 1983 and 1985.

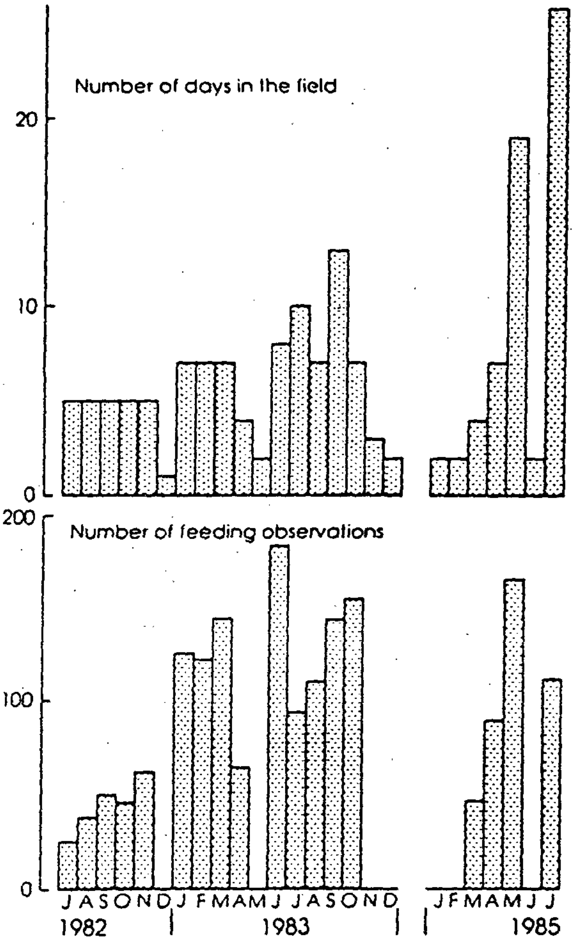

Number of days in the field
20
10
0
200
Number of feeding observations
100
0
J A S O N D J F M A M J J A S O N D
1982
1983
J F M A M J J
1985

Figure 5.2

Monthly feeding records of core food species collected for *H. lemuroides* during the study. **n** is the total number of feeding observations collected; black indicates young foliage, white is mature foliage; vertical lines separate wet and dry seasons.

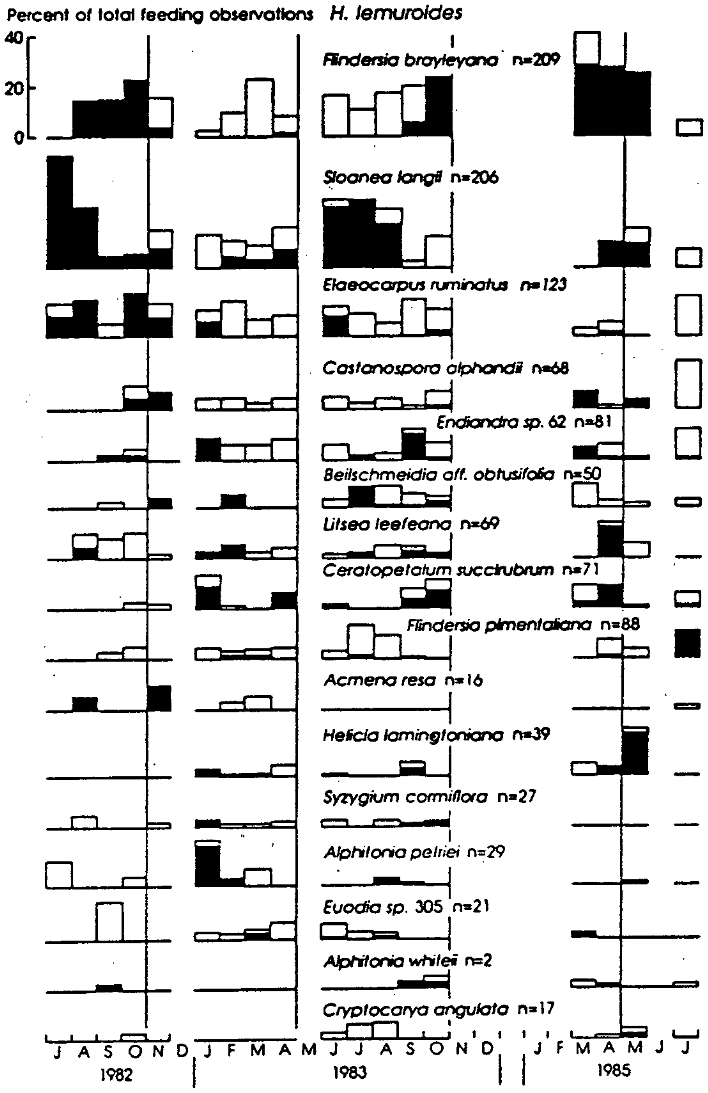

Percent of total feeding observations
H. lemuroides
40
20
0
Flindersia brayleyana n=209
Sloanea langii n=206
Elaeocarpus ruminatus n=123
Castanospora alphandii n=68
Endiandra sp. 62 n=81
Beilschmeidia aff. obtusifolia n=50
Litsea leefeana n=69
Ceratopetalum succirubrum n=71
Flindersia pimentaliana n=88
Acmena resa n=16
Helicia lamingtoniana n=39
Syzygium cormiflora n=27
Alphitonia petriei n=29
Euodia sp. 305 n=21
Alphitonia whitei n=2
Cryptocarya angulata n=17
J A S O N D J F M A M J J A S O N D J F M A M J J
1982
1983
1985

Figure 5.3

Monthly number of feeding records of core food species collected for *P. herbertensis* during the study. **n** is the total number of feeding observations collected; black indicates young foliage, white is mature foliage; vertical lines separate wet and dry seasons.

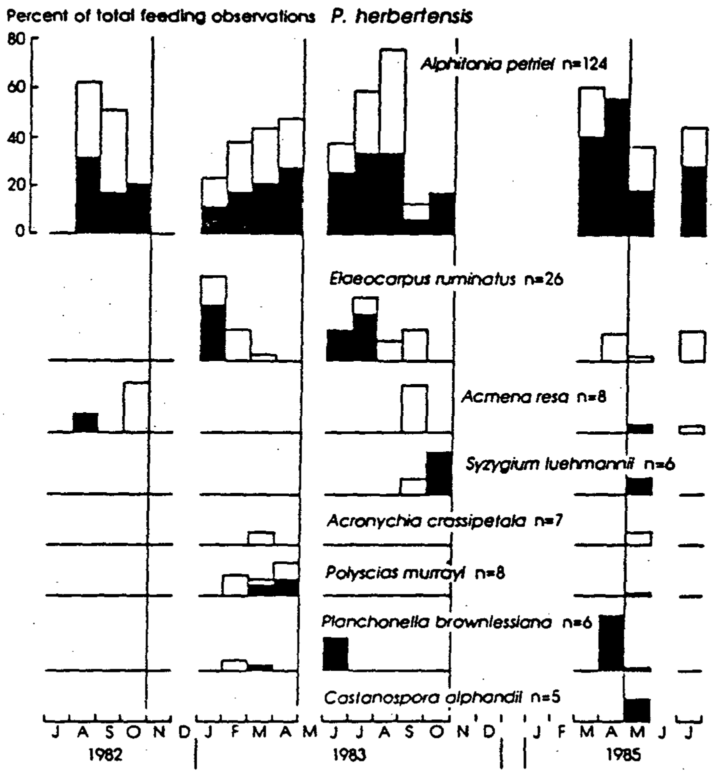

Percent of total feeding observations
P. herbertensis
80
60
40
20
0
Alphitonia petriei n=124
Elaeocarpus ruminatus n=26
Acmena resa n=8
Syzygium luehmannii n=6
Acronychia crassipetala n=7
Polyscias murrayi n=8
Planchonella brownlessiana n=6
Castanospora alphandii n=5
J A S O N D J F M A M J J A S O N D J F M A M J J
1982
1983
1985

Figure 5.4

Monthly number of feeding records of core food species collected for *P. archeri* during the study. **n** is the total number of feeding observations collected; black indicates young foliage, white is mature foliage; vertical lines separate wet and dry seasons.

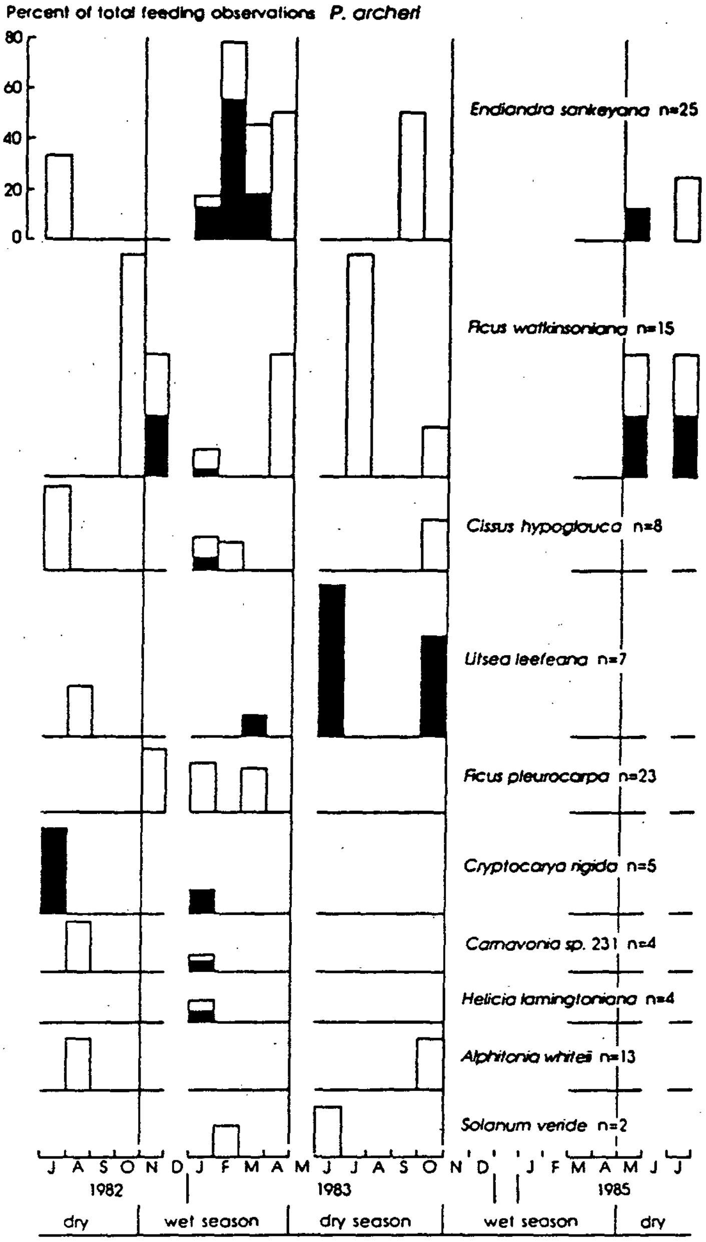

Percent of total feeding observations *P. archeri*
80
60
40
20
0
Endiandra sankeyana n=25
Ficus watkinsoniana n=15
Cissus hypoglauca n=8
Litsea leefeana n=7
Ficus pleurocarpa n=23
Cryptocarya rigida n=5
Carnavonia sp. 231 n=4
Helicia lamingtoniana n=4
Alphitonia whitei n=13
Solanum veride n=2
J A S O N D J F M A M J J A S O N D J F M A M J J
1982
1983
1985
dry
wet season
dry season
wet season
dry

Figure 5.5

TOP: Dietary diversity and eveness indices for *H. lemuroides*.

MIDDLE: Dietary diversity and eveness indices for *P. herbertensis*.

BOTTOM: Dietary diversity and eveness indices for *P. archeri*. Data were pooled into a "representative" 12 month period due to lack of feeding observations.

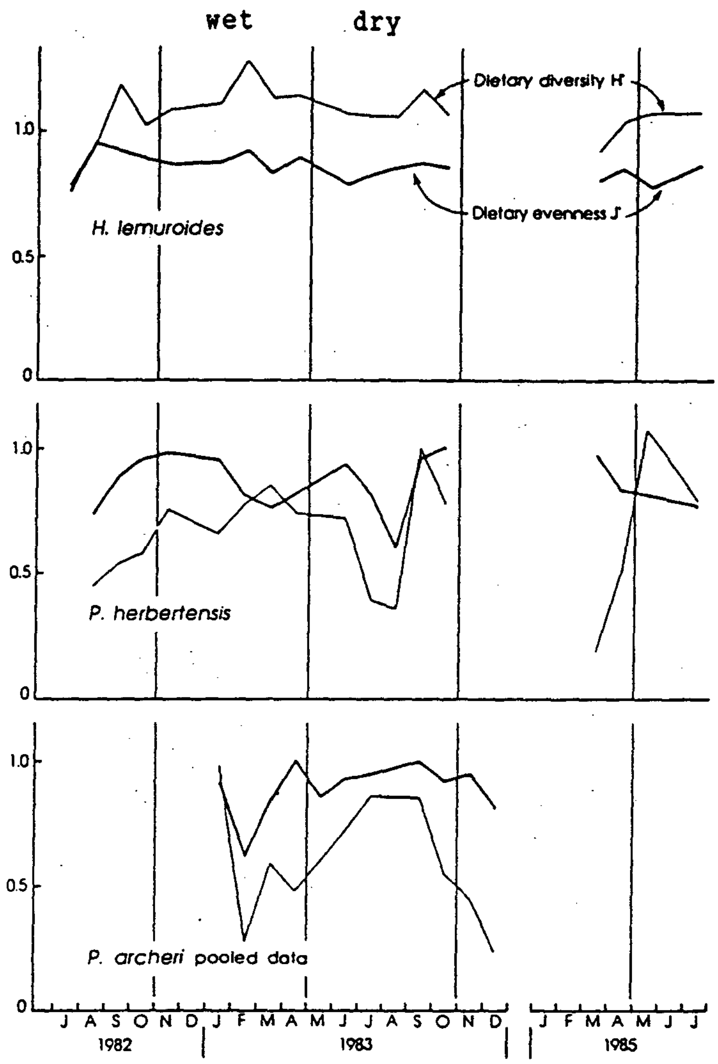

wet
dry
Dietary diversity H'
Dietary evenness J'
H. lemuroides
P. herbertensis
P. archeri pooled data
1.0
0.5
0
J A S O N D J F M A M J J A S O N D J F M A M J J
1982
1983
1985

Figure 5.6

Feeding electivities (A_{ij}) of the three possum species and relative densities (%) of common tree species at Longland's Gap State Forest. Increasing length of line represents increasing importance. For complete data refer to Appendix B, Table 1.

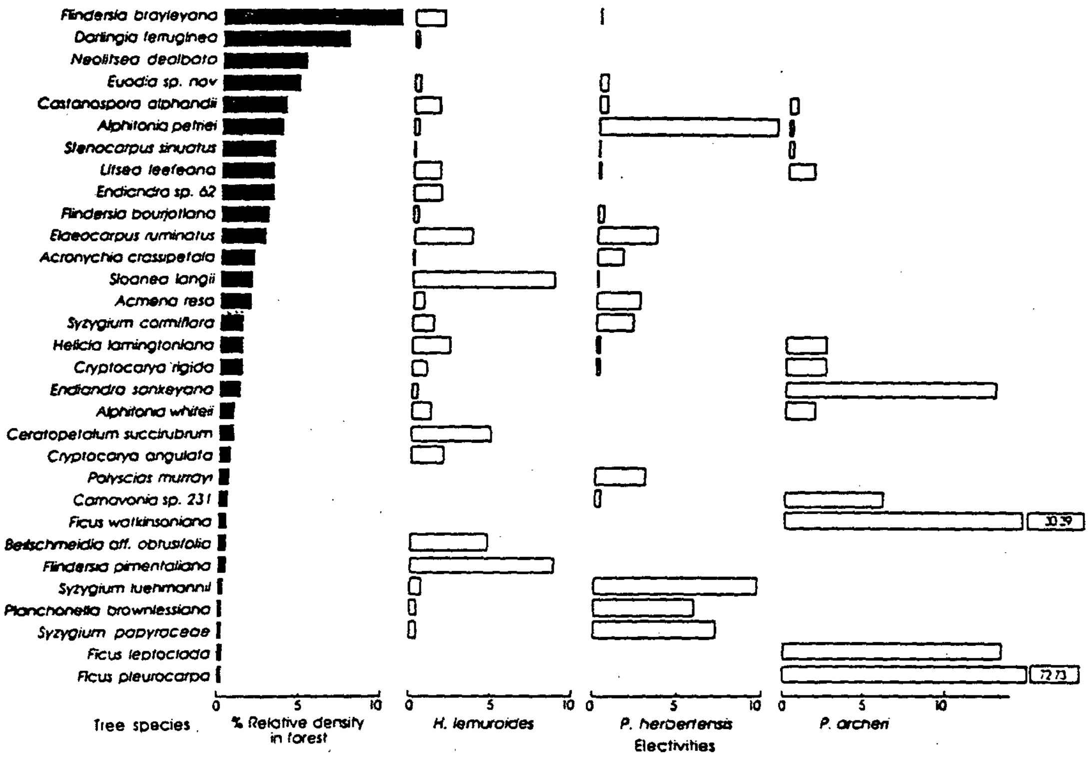

Flindersia brayleyana
Darlingia ferruginea
Neolitsea dealbata
Euodia sp. nov
Castanospora alphandii
Alphitonia petriei
Stenocarpus sinuatus
Litsea leefeana
Endiandra sp. 62
Flindersia bourjotiana
Elaeocarpus ruminatus
Acronychia crassipetala
Sloanea langii
Acmena resa
Syzygium cormiflora
Helicia lamingtoniana
Cryptocarya rigida
Endiandra sankeyana
Alphitonia whitei
Ceratopetalum succirubrum
Cryptocarya angulata
Polyscias murrayi
Carnarvonia sp. 231
Ficus watkinsoniana
Beilschmeidia aff. obtusifolia
Flindersia pimentaliana
Syzygium luehmannii
Planchonella brownlessiana
Syzygium papyraceae
Ficus leptoclada
Ficus pleurocarpa
30.29
72.73
0
5
10
0
5
10
0
5
10
0
5
10
Tree species
% Relative density in forest
H. lemuroides
P. herbertensis
P. archeri
Electivities

Figure 5.7

(i) Activity schedule of *H. lemuroides* in (TOP) the wet season, and (BOTTOM) the dry season. Dry season: dusk 1800 hrs, dawn 0630 hrs. Wet season: dusk 1840 hrs, dawn 0530 hrs.

(ii) Activity schedule of *P. herbertensis* in (TOP) the wet season, and (BOTTOM) the dry season. Dry season: dusk 1800 hrs, dawn 0630 hrs. Wet season: dusk 1840 hrs, dawn 0530 hrs.

(iii) Activity schedule of *P. archeri*. Wet and dry seasons were combined due to lack of activity data.

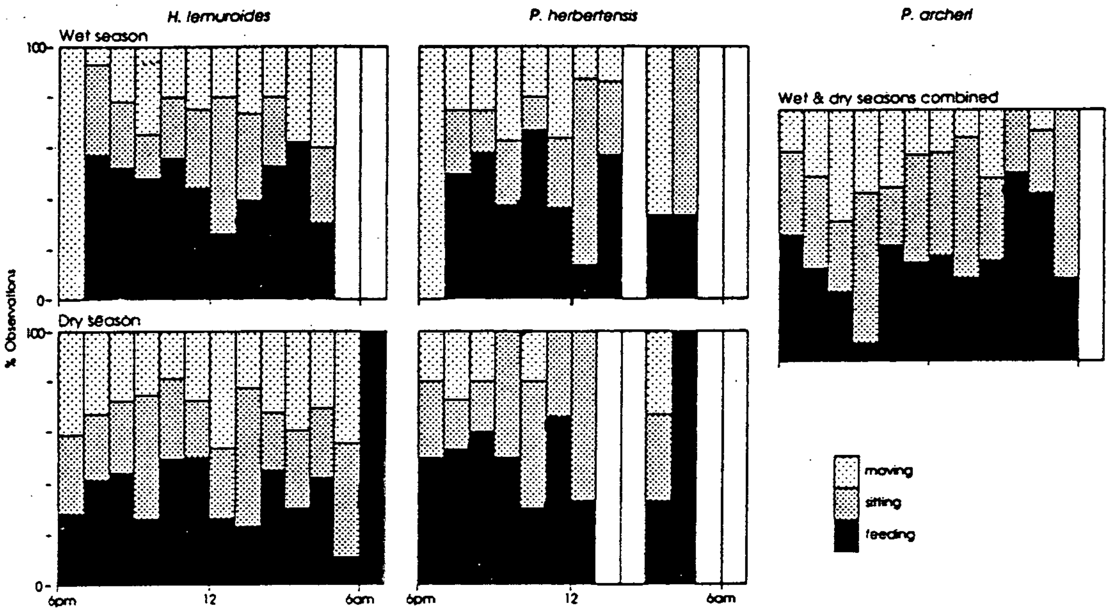
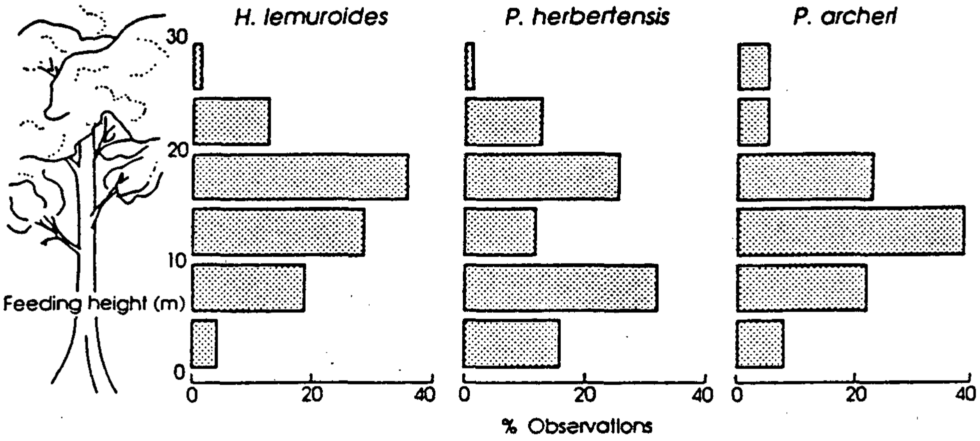

H. lemuroides
P. herbertensis
P. archeri
Wet season
Dry season
Wet & dry seasons combined
% Observations
100
0
6pm
12
6am
moving
sitting
feeding

Figure 5.8

Feeding heights in trees of *H. lemuroides*, *P. herbertensis* and *P. archeri*.


H. lemuroides
P. herbertensis
P. archeri
30
20
10
0
Feeding height (m)
0
20
40
0
20
40
0
20
40
% Observations

CHAPTER 6. FOOD QUALITY

6.1 INTRODUCTION

6.1.1 Factors governing leaf choice

Of the various factors which have been suggested as most likely to affect leaf choice by generalist folivores, protein, fibre, leaf toughness and allelochemical content are the most frequently cited (Cork & Pahl 1984; Fox & Macauley 1977; Freeland & Janzen 1974; Lowman & Box 1983; Macauley & Fox 1980).

Milton (1979) extrapolating from studies on domestic animals estimated that howler monkeys (*Alouatta palliata*) needed 9-12% crude protein by dry weight of food to maintain nitrogen balance. As most mature leaves available to these primates contain less than this minimum concentration, they have to be very selective in their choice of food items. Koalas, on the other hand, can survive on a diet of mature leaves containing 6% crude protein (Cork 1981). Thus the degree of selectivity necessary for survival varies between species depending on their physiological and behavioural adaptations.

Young leaves generally contain more protein than mature leaves (Cork & Pahl 1984). The protein content of mature leaves usually varies between 7-15% depending on the plant species (Glander 1981; A. Hladik 1978; Milton 1979; Ullrey et al. 1981). While some leaf buds and growing leaves contain 25-35% protein by dry weight and leguminous species often as much as 55%, most young foliage contains about 20% protein dry weight (A. Hladik 1978). However, although many studies show that young leaves have a higher nitrogen (ie. protein) content and are preferred over mature leaves, herbivore preferences are rarely related to total nitrogen content of food plants (Glander 1981; C.M Hladik 1978; Milton 1979; Oates et al. 1980). This suggests that there is more to diet selection than choosing species with the highest protein content.

The cell walls of plant tissues consist of cellulose, hemicelluloses and lignin in varying amounts. Typically plant tissues contain between 30% and 60% dry weight of structural compounds (Freeland & Janzen 1974) which have to be degraded by the action of symbiotic bacteria in the gut. Lignin, however, is regarded as being totally resistant to digestion by either (domestic) mammalian or microbial enzymes (Van Soest 1977). Additionally, it slows down digestion rates in small grazing ruminants and reduces the digestibility of protein, hemicellulose and cellulose (Harkin 1973; Phillipson 1970; Van Soest 1982). However, lignin does not reduce the digestion rate in some folivorous non ruminants (eg. *Pseudocheirus peregrinus*, *Phascolarctos cinereus*) feeding on *Eucalyptus* leaves. These species can digest 26% and 19% of the lignin respectively from their high fibre diets (Chilcott & Hume 1984; Cork et al. 1983). This digestion occurs despite the higher overall fibre and lignin content of foliage compared to herbage (Short et al. 1974), for although the ratio of lignin to cellulose correlates with herbage digestibility (Parra 1978; Van Soest 1964), the same does not apply to foliage. This may be due to the different chemical composition of lignin in dicotyledons (Sarkanen & Ludwig 1971; Wilson 1977) enabling folivores to digest some of it.

The degree of lignification varies with plant species and tissue age. There is generally less lignin in young foliage than in mature foliage (A. Hladik 1978), but this is not always the case (Cork & Pahl 1984). Most studies have found that folivores preferentially select leaves with low cell wall content, and more especially, low lignin content (eg. Clutton

Brock & Harvey 1977; Oates et al 1977). Once again however, there are exceptions amongst the marsupial folivores (eg. *Pseudocheirus peregrinus*: Chilcott & Hume 1984; Cork et al. 1983).

The concentration of allelochemicals in plant tissues depends upon several factors. Mature leaves of colonizing plants generally contain lower concentrations of defensive chemicals than those of later successional species (Cates & Orians 1975; Coley 1983a, 1983b, 1986). Deciduous species also tend to contain more allelochemicals than evergreen species (Opler 1978). Young foliage has often been reported to be high in qualitative defences (alkaloids) but low in quantitative defences (phenolics) compared with mature foliage (Dement & Mooney 1974; Feeny 1970, 1976; Lawton 1976; McKey 1979; Rhoades & Cates 1976). However there are many exceptions to this general rule (Coley 1983b; Macauley & Fox 1980; Milton 1979). The concentration of both leaf phenolics and toxins increases in forests growing on poor soil as it is relatively more costly for plants to replace predated leaves (Coley 1983b; Coley et al. 1985; Grime 1986; Muller et al. 1987; Southwood et al. 1986). Thus the relative numbers and diversity of animals living in such forests and the degree of folivore damage tends to be lower than for forests growing in richer soils (McKey et al. 1978; Southwood et al. 1986; Struhsaker 1978).

Of the many groups of allelochemicals present in plants, the compounds which reduce their digestibility (eg. tannins) are found more commonly in the woody, rather than herbaceous, plants (Rhoades & Cates 1976; Marks et al 1988). They are therefore of particular relevance to arboreal folivores. There are two major groups of tannins: hydrolysable and condensed. The former have a carbohydrate core which is bound by ester linkages to a number of phenolic, carboxylic acids (McLeod 1974). They can be hydrolysed into the constituent phenols and sugars and absorbed from the gut. Condensed tannins have no carbohydrate core, are resistant to both chemical and enzymatic digestion in the gut and are unlikely to be absorbed through the gut wall (McLeod 1974).

Phenolic compounds have often been implicated as an influence on food selection by generalist herbivores (Freeland & Janzen 1974; McKey et al.1978; Oates et al. 1977, 1980; Rosenthal & Janzen 1979; Waterman et al. 1980). There is evidence that they complex with proteins in acid stomachs (Feeny 1970; Swain 1965; Waterman et al. 1980, 1984), cause mineral depletion and erosion of intestinal epithelium (Freeland et al. 1985), and deactivate digestive enzymes (McKey et al. 1978). Some studies have found, however, that phenolic concentrations in foliage are less of a deterrant to herbivores than leaf toughness and fibre (Coley 1983b; Lowman & Box 1983), especially when leaves also have a high nutritive value (Cork & Pahl 1984). McArthur (1988) found that tannins did not reduce the apparent digestibility of nitrogen in *P. peregrinus*. She suggested that marsupial folivores which regularly include large amounts of tannin rich leaves in their diet may have an increased capacity to counteract the effects of tannins. Selective retention of digesta in the caecum may be the key to such an adaptation.

6.1.2 Adaptations to a folivorous diet

Most folivores have behavioural and morphological adaptations to allow them to exist on a leafy diet. Many species are very selective, choosing only seasonal items such as leaf buds which are high in positive (eg. protein) nutrients and low in fibre and allelochemicals (Hume 1982; Milton 1980). In addition, most folivores have developed digestive specializations to aid in the breakdown of structural and allelochemical compounds.

Among the arboreal folivores, fermentation of cellulose has been achieved either through the evolution of forestomach fermentation chambers eg. *Colobus, Macaca* and *Presbytis* monkeys (Bauchop & Martucci 1968; Freeland & Janzen 1974; Hladik 1967) or by the development of an enlarged caecum and/or colon (ie. hindgut fermentation in *Pseudocheirus, Phascolarctos, Lepilemur, Indri, Alouatta*: Cork 1981; Hladik 1967; Milton et al. 1980). Some relatively small arboreal species (eg. *Colobus*) are foregut fermenters, and it has been suggested than this may be due to the accompanying advantages of microbial detoxification (saving microsomal conjugation molecules) and vitamin synthesis (Milton 1980). Foregut digestion, however, has a number of disadvantages. The first being the lack of control over rate of passage due to the seive-like qualities of the reticulo-omasal orifice. In ruminants this leads to a depression of voluntary intake and inability to survive on very fibrous foods (Clutton Brock & Harvey 1977). The second problem is the fermentation of glucose in the foregut to produce volatile fatty acids (VFA). As only one VFA is glucogenic this leads to glucose intolerance and the inability to fast for any significant period (Janis 1976). However, unlike hindgut fermentation, all the products of digestion are absorbed in the small intestine. As the products of hindgut fermentation are formed distal of the usual site of absorption, there are several strategies used to prevent loss of valuable nutrients. Some animals, such as lagomorphs, some rodents and the common ringtail possum (*Pseudocheirus peregrinus*) are coprophagic, that is, they reingest their faeces and absorb the bacterial protein in the second pass (Chilcott & Hume 1984; Janis 1976). Others have greatly enlarged the surface area of the proximal colon and/or the caecum to act as sites of nitrogen/amino acid absorption (Janis 1976; Parra 1978).

Hindgut fermenters use two main digestive strategies. The first is colonic fermentation, where there is no separation of the fluid and small particulate matter from the less digestible particles. This is in contradistinction to caecal fermentation, where easily digested matter is selectively retained and fermented in the caecum (Hume & Warner 1980). Those species which practice colonic fermentation are usually animals of larger mass as they have lower mass-specific nutrient requirements (Hume 1982), however, the common brushtail possum *Trichosurus vulpecula* is in this group (Wellard & Hume 1981). Most caecal fermenting species are small with higher mass-specific energy needs. Shunting less digestible particles into the distal colon allows a higher intake, a faster rate of passage, and the ability to feed on more fibrous foods (Wellard & Hume 1981).

There are two methods by which herbivores detoxify allelochemicals: microsomal enzymes and gut microbes. The former are most active in the liver and kidneys. The biocide undergoes a two step process: enzymatic oxidation, reduction or hydrolysis, followed by conjugation with glucose, a sulphate group or an amino acid. This makes the compound water soluble and often less toxic, allowing it to be more easily excreted (Freeland & Janzen 1974). Most herbivores conjugate biocides with glucose (Baudinette et al. 1980). The second method, detoxification in the gut, only occurs in animals with a diverse gut flora, ie. those with foregut digestion. Microbes have been shown to degrade many compounds (Scheline 1968), however the enzymes needed to detoxify novel biocides have to be induced. This necessitates ingesting small amounts of the novel food. If too much is sampled before the enzymes are in sufficient quantity, both the gut flora and the animal can suffer (Freeland & Janzen 1974).

6.2 METHODS

Leaves were collected in the field at first light from 37 species of rainforest trees (Table 1; Appendix D), sealed in plastic bags and transported on ice to Townsville. The samples were frozen at -20°C within six hours of being collected, and stored this way until dried immediately prior to analysis. Mature leaves were collected in the wet and dry seasons from all species, while young foliage of the same trees was collected when it was available. Leaf samples of food species were collected from individual trees known to be browsed by possums whenever possible. Prior to analysis, mature leaves of some species were cut from the branchlets about a third of the way up the leaf from the petiole. This imitated the feeding pattern of the folivores, as only the distal two thirds of the leaves of these species were eaten.

Leaves were classified as either mature or young. Mature leaves were distinguished by their darker colouration, tougher texture and well developed structure. Only those without a coating of epiphyllae were taken; this corresponded with leaves between about one and twelve months old. Any leaf less than about three weeks old which was still soft (ie. lacking a heavy cuticle) and without adult pigmentation was classified as young foliage. Most were collected before the blade had completely expanded.

6.2.1 Analytical Methods

All samples were run in duplicate except for fibre which was run in quadruplicate.

Total phenols

Drying and storage are known to lower total phenol concentrations (McKey et al. 1978); however attempts to grind leaves under liquid nitrogen proved unsuccessful. Therefore leaves were dried for approximately 48 hours at 50°C then ground in a Wiley mill prior to extraction. As all samples underwent the same drying and storage treatments, values of total phenols should be regarded as relative rather than absolute.

Approximately 0.2 grams of the dried ground samples were extracted for three days in 20ml of 50% v/v methanol then filtered through a Whatman's Grade 1 filter paper. One ml of each extract was then made up to 10 ml with 50% v/v methanol in a volumetric flask. Aliquots of the samples (0.4ml) were then tested colorimetrically with Folin-Ciocalteau reagent for total phenols using the "reduced volume improved procedure" of Singleton and Rossi (1965; page 156). To each aliquot was added 14.6ml of distilled water and 1ml of Folin-Ciocalteau reagent (obtained from laboratory chemical suppliers). This was vortexed and left for three minutes before 4ml sodium carbonate reagent was added. After exactly two hours, the maximum absorbance of each sample was read against a blank (containing only the reagents) at a wavelength of 765nm on a Pye Unicam SP6-200 spectrophotometer using a flow through cuvette assembly. I found absorbance to be greatest at this wavelength, although other studies have used different wavelengths (eg. 750nm, Lowman & Box 1983). While sitting, some samples developed a white precipitate which affected their absorbance readings. Once centrifuged, however, absorbance was not significantly different from replicates which did not develop the precipitate. Anhydrous gallic acid was used as the standard.

Condensed tannins

Dried, ground foliage was extracted as above and tested for condensed tannins using the *leuco*-anthocyanidin (LA) test of Swain and Hillis (1959; page 64). Into test-tubes of even diameter and thickness was added 1ml of each extract and 10ml of LA reagent (25ml of 36% w/w HCl diluted to 500ml with *n*-butanol in a volumetric flask). The tubes were vortexed, placed in a covered boiling water bath and stoppered three minutes later. After 40 minutes the test tubes were cooled under cold running water to stop the reaction, and their absorbances read at 550nm against blanks of unheated reagents on a Hitachi 101 spectrophotometer. Quebracho tannin, often used as a standard when determining condensed tannin content, was not used here as it has been shown to be a poor source of condensed tannins (Mole & Waterman 1987c). Instead, freeze dried and ground *Eucalyptus regnans* kino was used as it is known to be rich in condensed tannins (Claire McArthur, *pers. comm.*).

Alkaloids

Alkaloids were tested using the field method of Culvenor and Fitzgerald (1963). Three grams of fresh leaf material were finely ground under liquid nitrogen in a mortar and pestle. To this was added 10ml of ammoniacal chloroform (N/20 with respect to ammonia) which was mixed well and filtered. Dilute sulphuric acid (0.5ml, 2N) was added to the filtrate which was then left to sit until the two phases separated. Several drops of the aqueous solution were tested with Mayer's reagent for the presence of tertiary alkaloids. The density of precipitate that formed was assessed as + to ++++: + = a slight milkiness, ++ = cloudy with no precipitate, +++ = light to moderate precipitate, ++++ = heavy precipitate. Although this very simple method does not detect quaternary alkaloids, it does detect all significant amounts of tertiary alkaloids. When compared with hot ethanolic extraction, Culvenor and Fitzgerald (1963) found that 90% of the field tests gave identical results; the remaining 10% of field tests indicated higher alkaloid concentrations than those determined by ethanolic extract.

Protein

Nitrogen was determined using the micro-Kjeldahl technique. The results were multiplied by the standard 6.25 conversion factor to obtain an estimate of crude protein content. Fresh leaves were dried at 50^0C for 48 hours until about 95% dried. One gram samples were then dried for one hour at 100^0C, reweighed, wrapped in cigarette paper and digested overnight in 3ml conc. sulphuric acid, to which half a Kjeldahl tablet and boiling bead had been added. The clear digestate was made up to 50ml with distilled water in a volumetric flask and read on a Technicon autoanalyser using the indophenol method of Clare and Stevenson (1964). I wore gloves to prevent contamination of samples and paper whenever they were handled.

Fibre determinations

Neutral and acid detergent fibre (NDF and ADF respectively), permanganate lignin, insoluble ash and cellulose were determined sequentially by the standard detergent procedures (Goering & Van Soest 1970). Leaves were oven dried for 48 hours at 50^0C to minimize the possibility of artifact lignin and cutin forming (Mould & Robbins 1981), ground in a Wiley mill then processed. NDF is thought to represent total cell wall constituents, minus pectin. When this residue is treated with acid detergent it then ideally contains only cellulose, lignin and insoluble minerals (ADF). If not previously treated with neutral detergent much of the original pectin may also be present in the ADF residue. The residue is then treated with permanganate to oxidise the lignin leaving only cellulose, and insoluble minerals. Lignin content is determined as the difference. The residual mineral content is determined by ashing the residue, and cellulose is lost as the difference.

Leaf toughness

Two mature and two young leaves of 21 favoured food species were randomly collected from the sampled trees. The leaves were measured for leaf toughness immediately upon collection using a penetrometer modelled after that of Feeny (1970). The surface of each leaf was pierced four times (two distal, two proximal) with a 5mm diameter brass plunger. The plunger was weighted by water poured into a beaker after the method of Lowman & Box (1983). The average weight of water required to puncture the leaf was used as the index of leaf toughness.

6.2.2 Statistical Methods

Analysis of variance, t-tests and Newman-Keuls multi-range test (Zar 1984) were used to test the significance of differences in nutrient content between leaves and between animal's preferred diets. The nutritional content of food items was correlated with feeding observations for each possum species using Spearman rank correlation. A polythetic divisive strategy to 20 splits was used to sort out the two major fibre/protein groups using NTP (Numerical Taxonomy Package) software (Dr. W.T. Williams, pers. comm.).

6.3 RESULTS

6.3.1 Variability of leaf quality

The concentrations of allelochemicals (Table 1; Appendix D) and primary compounds (Tables 2, 3; Appendix D) in the leaves tested varied greatly (total phenols: 0.07 - 2.57 ml/mg standard, coefficient of variation V=0.785; condensed tannins: 0 - 0.84 ml/mg standard, coefficient of variation V=2.773; protein: 7.44 - 26.94% dry weight, coefficient of variation V=0.335; lignin: 3.01 - 29.22% dry weight, coefficient of variation V=0.458). However, no significant differences were detected due to the age of the leaves. Both mature and young leaves had similar concentrations of condensed tannins (t-test: $t = 1.352$, d.f 47, $p > 0.1$), total phenolics ($t = 0.2026$, d.f 54, $p > 0.5$), lignin ($t = 1.6006$, d.f 54, $p > 0.1$) and protein ($t = 0.0188$, d.f 54, $p > 0.5$). When the tree species were grouped according to successional status (after Hopkins et al. 1977), there was no difference in the concentrations of condensed tannins in leaves of climax (D), early (B) or late successional (C) forest tree species (ANOVA: $F = 2.259$, d.f 2,34, $p > 0.1$). However, there was a significant difference in the concentrations of total phenols in the leaves of the different successional groups (ANOVA: $F = 7.354$, d.f 2,37, $p < 0.0025$). The difference in total phenols between climax (D) and early successional (B) species was significant (Newman-Keuls test with unequal sample sizes: $q = 7.081$, error d.f 37, $n = 20,11$, $p < 0.001$).

6.3.2 Food quality and feeding preferences

Factors influencing initial food choice

To determine which factors were the most important influences on diet selection by the three folivores, the ten most preferred food items (i.e. those which made up the largest or most constant food source with time; see Table 4, Appendix D) for each species of possum were tested against eight items of seven common species of plants which were never observed to be eaten by any of the possums (Table 6.1). In all cases there were significantly more total phenols in the preferred food items than the rejected items (for details see Table 6.1). Therefore total phenols (T.P) do not appear to negatively influence food selection by any of the species.

Condensed tannin content (C.T) however, was significantly different between the preferred and rejected items and may play a major role in diet selection by all species. Preferred food items generally had less than 0.2% condensed tannin content (range 0 - 0.6%; coefficient of variation: *H. lemuroides* V = 0.893; *P. herbertensis* V = 2.268; *P. archeri* V = 1.079).

The protein content of food items appears to positively influence only the diet of *P. herbertensis*. The other two species have significantly less protein in their food items than those they ignored.

Lignin content and total cell walls (NDF) do not negatively influence food selection by *P. archeri* as it's preferred diet contains significantly greater amounts of these antinutrients. They may be significant factors however, to the other species with between 15-60% less lignin and 5-32% less cell walls in preferred food items (Table 6.1).

Cellulose content may negatively influence diet selection by all three species, with between 5-30% less cellulose in preferred foods. Alkaloids may influence only the two *Pseudocheirus* species (63-144% less alkaloids).

Factors influencing ranking of food items

The leaf items (young and mature leaves) eaten by the three species of possum were ranked separately according to frequency of feeding observations and tested against total phenols, condensed tannins, crude protein, lignin content, ADF, NDF, cellulose, lignin to crude protein ratio and leaf toughness (Table 5, Appendix D). The ranking of food items in *H. lemuroides* preferred diet is correlated with reduced amounts of total cell walls (NDF) and lignin (Spearman rank correlation, $r= 0.3968$, $r= 0.3948$ respectively, $n= 25$, $p< 0.05$), while in *P. herbertensis* diet preferred items had lower condensed tannin contents ($r= 0.5474$, $n= 16$, $p< 0.02$). The ranking of preferred food items in *P. archeri*'s diet is correlated with high neutral detergent fibre content ($r= 0.6218$, $n= 13$, $p< 0.02$) and high lignin to protein ratios ($r= 0.6218$, $n= 13$, $p< 0.02$).

Although protein content was not significantly related to feeding preferences between plant species, there was a trend by both *P. herbertensis* and *P. archeri* to select the items with highest protein content within a species. Thus, when feeding on mature and young leaves of a single species, young, higher- protein leaves ranked higher than old leaves in *P. herbertensis* diet 67% of the time, in *P. archeri*'s diet 71% of the time, but in *H. lemuroides* diet only 30% of the time. This again suggests that protein is not a factor influencing diet selection by *H. lemuroides* and reflects the low protein status of preferred food species, such as *Sloanea langii*, *Flindersia brayleyana* and *Ceratopetalum succirubrum*.

To discover if rainforest plants could be grouped on the basis of their food quality, all 55 plant species for which nutrient data were available were subjected to a polythetic divisive strategy to 20 splits. (Alkaloids were not included in the analysis due to an incomplete data set). The resulting dendrogram (Fig. 6.1) reveals two major types of food plants, those with generally high nitrogen, low fibre and variable phenolic content (which I called Type I) and those with generally low nitrogen, high fibre and variable phenolic content (Type II). In addition there were several outlying plant items which did not fit either group (Table 2, Appendix D).

The proportions of Type I and Type II plant species in the animals' diets differed for each possum species (G-test: $G = 71.75$, d.f = 2, $p < 0.001$). Type I and Type II plants were approximately equally represented in the diet of *P. herbertensis* (Table 6.2). Eighty seven per cent of the items analysed in the diet of *P. archeri* had a high fibre content (majority Type II), while 72% of the items analysed from the diet of *H. lemuroides* had low fibre (majority Type I).

Between species comparison of nutritional factors

Foraging strategy predicts that the core food items on which the animals are most specialized will be more nutritious than those on which they feed less often. To test this prediction, the means of the most influential anti-nutrients in the top four food items of each species were tested against the means for those same anti-nutrients in the minor food species (Table 6.3). Condensed tannins, total cell walls, cellulose and lignin content were selected as the nutrients, as they have the most influence on diet selection by these species (Table 6.1). For each possum species, the top four food items were both the young and mature leaves of two plants i.e. *Sloanea langii*, *Flindersia brayleana* (*H. lemuroides*); *Elaeocarpus ruminatus*, *Alphitonia petriei* (*P. herbertensis*); *Ficus watkinsoniana*, *Cissus hypoglauca* (*P. archeri*). Overall, the animals specialized on items that were of better nutritional quality than those species on which they fed less frequently (minor species). *H. lemuroides* specialized on items that were significantly more "palatable" in all respects, while *P. herbertensis* displayed less selectivity and *P. archeri* the least.

When the main nutritional characteristics (protein, fibre) of the items on which each species specializes are compared, the following appears: *P. archeri* and *H. lemuroides* both have a lower protein content in their food than *P. herbertensis* (ANOVA: $F = 29.587$, d.f 2,9, $p < 0.001$; Newman Keuls test, d.f 9: *P. herbertensis*-*P. archeri* $q = 10.376$, $p=3$, $p < 0.001$; *P. herbertensis*-*H. lemuroides* $q = 8.0217$, $p=2$, $p < 0.001$), while the food of *H. lemuroides* has a lower lignin content than that of *P. herbertensis* (ANOVA: $F = 4.779$, d.f 2,9 $p < 0.05$; Newman Keuls test, d.f 9: $q = .956$, $p=3$, $p < 0.05$). The total cell wall content of the food of *H. lemuroides* is also less than that found in the food of the other two species (ANOVA: F = 5.081, d.f 2,9, $p< 0.05$; Newman Keuls test, d.f 9: *H. lemuroides*-*P. archeri* q = 4.1022, p=3, $p< 0.05$; *H. lemuroides*-*P. herbertensis* q = 3.3925, p=2, $p < 0.05$). Additionally, *P. archeri* has a higher cellulose content in its food than *H. lemuroides* (ANOVA: F = 25.344, d.f 2,9 $p< 0.001$; Newman Keuls test, d.f 9: q = 4.5006, p=3, $p < 0.05$). Therefore the species favour food items with significantly different nutritional qualities.

6.3.3 Gut measurements

The three species have significantly different gut dimensions based on weighted, non volumetric measurements (Table 6.4). (The carcass weights of the possums from which the gut length data were collected are unknown so all gut lengths were divided by the average weight of the species, as given in Winter (1983a,b,c), to try to correct for the different body sizes of the species. Average weights are: *H. lemuroides* 966g, *P. herbertensis* 1070g, *P. archeri* 1190g). There are no differences in the dimensions of the stomachs or distal colons between the species. Of the three, *P. archeri* has a longer and wider proximal colon than *P. herbertensis*, and a shorter caecum and small intestine than *H. lemuroides* (for tests and significance refer to Table 6.4).

6.4 DISCUSSION

6.4.1 Diet selection

While tannins may be a major factor influencing diet selection, there are some short comings in the chemical methodology used to determine condensed tannin (C.T) content which could affect the validity of this result. The *leuco*-anthocyanidin method yields both cyanidin and/or delphinidin anthocyanidin pigments depending on the nature of the tannin present (Mole & Waterman 1987c). These pigments have different absorbances, delphinidin absorbing significantly more than cyanidin. This leads to a marked overestimation of C.T content when there is a high pro-delphinidin content. This is most likely the cause of the greater than 100% CT/TP values obtained for *Opisthiolepis heterophylla*, *Brackenridgea nitida* and *Aglaia sapendina*. That both young and mature foliage of these species register such high CT/TP values lends support to this suggestion. Additional problems with the phenolic determinations include the varying degree of reactivity of condensed tannins to the LA reagent depending on the degree of tannin polymerization (Goldstein & Swain 1963), and the differences in reactivity of condensed and hydrolysable tannins to the Folin-Ciocalteau (FC) reagent. Also, the FC reagent reacts with non-tannin compounds with reducing properties, especially those with phenolic hydroxyl groups (Mole & Waterman 1987c; Lowman & Box 1983). Thus the results of phenolic determinations must be interpreted with caution in the light of these problems. It is unfortunate that more reliable tests are not yet available for mass screening of diverse plant groups.

If the results from the phenolic determinations are accepted as a guide to relative quantities of tannins in the leaves, condensed tannin does influence diet selection by all species, but total phenols do not. *Colobus* monkeys are also sensitive to condensed tannins. Oates et al. (1977) found that voluntary intake was depressed when concentrations exceeded 0.2%. Interestingly, neither condensed tannins nor total phenols influenced diet selection by howler monkeys (Milton 1979). Sensitivity to phenolics appears to vary with species and lends support to McArthur's (1988) suggestion that some folivorous species may be able to counteract their effects.

Cellulose influences diet selection by all three species, although *P. archeri* specializes on leaves with higher levels than the others. *P. archeri* is not negatively influenced by lignin or total cell wall content which are avoided by the other species, especially *H. lemuroides*.

The lack of correlation between leaf toughness and feeding preference is not unexpected. Studies, such as that of Lowman and Box (1983), which implicate this factor as important to diet selection have been concerned with invertebrate folivores. The strength of the mouth parts relative to the leaf probably result in the observed correlations. As possums have sturdy jaws, it is not surprising that leaf toughness has no significant influence on food preference.

There are some tree species and items that appear to be high quality food, but which are ignored or avoided by the possums (eg. *Euodia* mature and young leaves; *Neolitsea* young leaves). Why the animals avoid these items is not clear. Further chemical investigation may prove profitable.

The ranking of the food items from most to least preferred depends on the number of times animals were seen feeding on each species. For the rankings to accurately reflect the animals' preference, each species would have to be similarly visible in all feeding situations. This is obviously not true in a rainforest. To overcome visibility problems I started radiotracking individuals over entire weeks. Unfortunately these data were collected at the end of the study and represent only a small proportion of the total feeding records. Only long term tracking will enable more accurate diet preferences to be calculated. Problems with inaccurate rankings may account for some of the failures to explain feeding preferences of nocturnal or cryptic species in terms of nutritional and allelochemical contents of foods.

6.4.2 Foraging strategies

The three species of folivores have different strategies for diet selection and this is partly reflected in their digestive physiologies. *H. lemuroides* selects food items of low fibre and condensed tannin content and high soluble cell contents. The significantly longer small intestine of this species may correlate with the preference of *H. lemuroides* for foods with high soluble cell contents. The large size of the proximal colon and caecum of *H. lemuroides* is unexpected considering the relatively low fibre diet of this species. Such a digestive morphology appears better suited to a high fibre intake, and may indicate a behavioural rather than morphological restraint in diet selection. This point needs to be investigated further.

P. herbertensis feeds on high protein, low cellulose foods. It appears to be the least well adapted of the three species to a fibrous diet, with little colonic expansion and a caecum of similar size to that of *H. lemuroides*. Most fermentation probably occurs in the caecum.

The relatively great expansion of the proximal and distal colon enables *P. archeri* to survive on a high fibre diet. The small size of its caecum suggests that the colon may be the more important fermentation site for this species.

The limited number of gut measurements available to date provides correlative evidence that the three species of rainforest ringtails exhibit different degrees of morphological adaptation to a fibrous diet. This will remain unproven until the husbandry techniques necessary to maintain these animals in captivity are developed. Only systematic work on digestive capabilities will reveal if there are species differences in fibre digestibiity and if, like the common brushtail *T. vulpecula*, these species practise colonic fermentation.

As predicted by foraging strategy theory, the items on which *H. lemuroides* and *P. herbertensis* specialize are more nutritious than those species they eat only occasionally (ie. the minor species). *H. lemuroides* specializes on food items which are nutritionally superior in most respects, containing fewer structural carbohydrates and condensed tannins. This indicates greater reliance on behavioural adaptations to a foliage diet. *P. herbertensis* specializes on items with lower condensed tannin concentrations than found in other food items. With the few feeding data presently recorded for *P. archeri*, there appears to be no difference between the foods on which it specializes and the minor species in its diet. I suspect this is, in part, a function of a need for further data.

6.4.3 Distribution of secondary compounds

Apparency theory (Feeny 1976) suggests that climax species and old leaves (apparent plant tissues) are defended against predation by tannins, while ephemeral tissues such as young foliage and leaves of colonising plants have higher concentrations of qualitative defences (alkaloids) and escape in time and space (Feeny 1976; Rhoades & Cates 1976). I have found, however, that there is no significant difference in the amount of qualitative or quantitative defences in mature or young foliage which I examined, an observation that runs counter to prediction. Although there is an increase in total phenolic content with successional stage, this would appear to provide little protection against folivorous mammals. The data suggest that condensed tannins confer more protection to a plant, however maximum concentrations are not found in the climax species as predicted by apparency theory. These data suggest that apparency may not be the only factor controlling distribution of plant defences against mammalian folivores.

6.4.4 Conclusions

Attempts to explain the feeding preferences of animals in terms of the allelochemical content of their foods have met with mixed success. Some studies found a negative correlation between food preference and secondary compounds (Fitzgerald 1978, Glander 1978; McKey 1978; Oates et al. 1977). Others found that primary compounds were a better predictor of preference (C.M Hladik 1978; Milton 1979; Oates et al. 1980). There would appear to be more factors involved in food preference than have so far been identified. Overall, I found the following:

1. *H. lemuroides* selects food with low fibre, protein and condensed tannins and high soluble cell contents. When compared with the other species it specializes on food items with much less fibre. Both the caecum and the proximal colon probably function in fibre fermentation.
2. *P. herbertensis* selects food with low cellulose and condensed tannins but high protein content. When compared with the other species, its diet has significantly more protein. With its small proximal colon, most fibre fermentation probably occurs in the caecum.
3. *P. archeri* selects food high in fibre but low in condensed tannin. Comparison between the species again indicates the relatively high fibre diet. The significantly larger colon and smaller caecum suggests the colon plays a major role in fibre fermentation.

These species all avoid foods high in condensed tannins and react differently to the protein and fibre content of various plant items. Given this, and the lack of consensus between different studies of folivore food preference, it may well be impossible to advance a general rule relating the role of primary and secondary compounds that will predict the diet of the majority of folivores.

Table 6.1

Comparison of the nutritional factors between the ten leaf items most preferred by each species (Table 4, Appendix D) and eight items never eaten. Avoided leaf items are: mature leaves of *Polyosma rhytophloia, Neolitsea dealbata, Brackenridgea nitida, Scolopia braunii, Rhodomyrtis trineura* and young foliage of *Macarangia inamoena, N. dealbata, Aglaia ferruginea*. Comparison by t-test, significance: * $p < 0.01$; ** $p < 0.001$. TP is total phenols; CT is condensed tannins.

Factor	Ave. 10 Preferred Items	Ave. 8 Never Eaten Items	t Value	Influence
H. lemuroides				
T.P.	0.6415	0.3344	5.236**	-
C.T.	0.1539	0.2761	3.274*	+
PROTEIN	11.571	13.001	19.19**	-
LIGNIN	10.445	16.646	8.826**	+
ALKALOIDS	0.6667	1.625	2.112n.s.	o
CELL WALLS	38.521	50.973	12.60**	+
CELLULOSE	18.401	23.686	11.17**	+
P. herbertensis				
T.P.	0.5787	0.3344	4.753**	-
C.T.	0.0974	0.2761	2.990*	+
PROTEIN	15.751	13.001	18.09**	+
LIGNIN	14.497	16.646	6.975**	+
ALKALOIDS	1.000	1.6250	3.099*	+
CELL WALLS	48.499	50.973	12.63**	+
CELLULOSE	18.244	23.683	11.02**	+
P. archeri				
T.P.	0.4238	0.3344	5.509**	-
C.T.	0.1510	0.2761	3.761*	+
PROTEIN	10.675	13.001	15.66**	-
LIGNIN	17.624	16.646	10.55**	-
ALKALOIDS	0.8571	1.6250	3.195*	+
CELL WALLS	52.843	50.973	15.68**	-
CELLULOSE	22.590	23.686	12.29**	+

Table 6.2

The proportion of feeding observations from Type I and II foods. Percentages do not total 100% as animals included food items in their diets which were not tested for nutritional quality. Chi square test on combined yearly data, d.f = 1, significance: * $p < 0.01$, ** $p < 0.001$.

Species	Year	Total	Type I	Type II	Significance
					x^2 value
P. herbertensis	1982	32	8	12	
	1983	140	40	49	
	1985	113	32	32	
	overall	285	80	93	0.98 n.s.
H. lemuroides	1982	170	84	35	
	1983	895	416	147	
	1985	293	129	61	
	overall	1358	629	243	170.87**
P. archeri	1982	19	4	6	
	1983	82	4	27	
	1985	17	7	3	
	overall	118	15	36	8.65*

Table 6.3

A comparison of the mean nutritional quality of the top four food itmes on which the species are most specialized, with the mean nutritional quality of the minor species in the diet. T-test, significance: * $p < 0.05$; ** $p < 0.02$; *** $p < 0.001$. Fibre in % dry weight, condensed tannin in mg/ml. NDF is neutral detergent fibre; C.T is condensed tannins; CELL is cellulose.

	NDF	C.T	CELL.	LIGNIN
H. lemuroides				
Specialist items (n = 4)	28.500	0.088	13.875	5.103
Minor food items (n = 18)	52.78	0.417	24.89	16.22
t values	5.799	2.348	4.243	3.848
Significance	***	**	***	***
d.f.	20	16	20	20
P. herbertensis				
Specialist items (n = 4)	43.930	0.0005	15.840	15.244
Minor food items (n = 12)	50.65	0.345	22.106	17.159
t values	1.095	2.804	1.928	0.339
Significance	n.s	**	n.s	n.s
d.f.	14	14	14	14
P. archeri				
Specialist items (n = 4)	47.158	0.015	19.248	13.873
Minor food items (n = 6)	46.155	0.374	21.308	13.573
t values	0.100	0.212	0.409	0.761
Significance	n.s	n.s	n.s	n.s
d.f.	8	8	8	8

Table 6.4

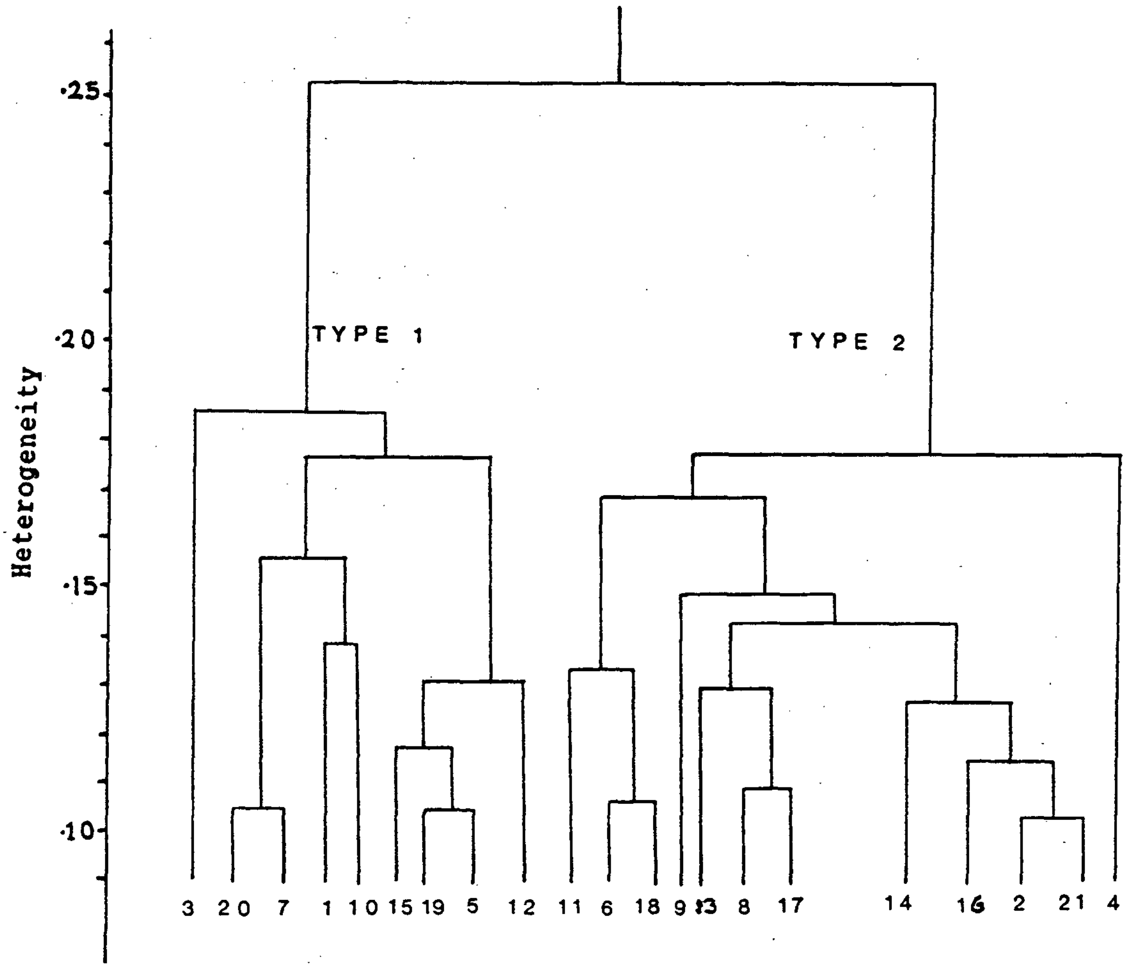
Average lengths of parts of the digestive tract of adult specimens of the three species in centimetres (ave. = s.d.). All measurements have been corrected for the size differences between the species by dividing each by the average weight of the species (given in Strahan 1983). Significance of Kruskal-Wallis test (H) and nonparametric multiple comparison test (Q) : * p , 0.05; ** $p < 0.02$; *** $p < 0.001$.

	H. lemuroides (n = 6)	*P. herbertensis* (n = 5)	*P. archeri* (n = 3)	H	Q
STOMACH					
Length	11.69±1.962	11.81±1.926	11.06±0.642	n.s	
Width	3.67±0.489	4.73±0.550	4.19±0.194	n.s	
SMALL INTESTINE					
Length	224.66±29.927	185.42±45.062	132.27±22.430	7.230**	2.647*
Width	0.94± 0.133	1.19± 0.277	1.27± 0.085	n.s	
CAECUM					
Length	34.42±4.500	33.61±2.259	23.39±3.613	6.621*	2.424*
Width	2.95±0.392	3.08±0.461	2.28±0.283	n.s	
PROX. COLON					
Length	45.81±4.189	28.78±2.274	61.07±5.947	18.186***	3.056**
Width	1.39±0.214	1.11±0.293	1.64±0.276	7.154**	2.662*
DIST. COLON					
Length	75.36±20.869	97.66±11.049	118.63±29.782	n.s	
Width	1.14±0.215	0.92±0.075	0.97±0.034	n.s	

#Data from Jan Gipps, pers. comm. 1982

Figure 6.1

Dendrogram resulting from cluster analysis of nutritional data. A polythetic divisive strategy to 20 divisions was used on all leaf nutritional data except for alkaloid content. See Appendix C for complete list of members belonging to the two groups. Type I leaves generally have high protein and low fibre content and Type II leaves generally have low protein and high fibre. Phenolic content in both leaf groups is variable.


Heterogeneity
·25
·20
·15
·10
TYPE 1
TYPE 2
3
20
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1
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CHAPTER 7 ENERGETICS

7.1 INTRODUCTION

Interest in animal energetics has been spurred in the last 20 years by the development of the doubly labelled water method for measuring energy expenditure of free-living animals. Until this development, rates of basal or standard metabolism (BMR) were used to indicate the relative energetic status of animals. However, as basal metabolism is measured while animals are post-absorptive, resting and at thermoneutrality, BMR has little relevance to an animal's performance in the field.

The development of the doubly labelled water technique followed the discovery by Lifson, in the late 1940's, that the oxygen of expired CO_2 was in isotopic equilibrium with the body water of rats and mice. Over the following 20 years, Lifson and his co-workers developed the method. But it was not until the past decade with large drops in the cost of isotopes, the streamlining of techniques and a thorough evaluation of errors (Nagy 1980; Nagy & Costa 1980) that the method has become widely used.

7.1.1 The doubly labelled water method

The metabolic rates of free-living animals can be measured by the decline in the specific activity of hydrogen and oxygen isotopes with time. As the oxygen in body water and exhaled CO_2 are in isotopic equilibrium, the decline in isotopic oxygen in body water is related to CO_2 loss as well as body water loss (Nagy 1980). If the rate of body water loss (through excretion and evaporation) and dilution (eating, drinking, oxidative metabolism) is known, the rate of CO_2 production can be calculated (Lifson

& McClintock 1966; Nagy & Costa 1980). This is best measured by labelling the body water with either tritium or deuterium; the difference in the turnover rates of O^{18} and H^3 isotopes then measures the rate of CO2 production.

Rates of water flux in mammals measured using tritiated water (HTO) have been shown by laboratory experiment to be within 10% of actual flux rates (Nagy & Costa 1980). However large errors can occur when animals are measured in an uncontrolled environment. Lifson and McClintock (1966) list assumptions which, if violated, can lead to significant errors in measuring water flux (Table 7.1). Some sources of error are negligible or avoidable; others can cause errors exceeding 100% (Nagy & Costa 1980). Similarly, laboratory measurements of CO_2 production using doubly labelled water have been validated to within 8%, but may be much less accurate when measured in the field (Nagy 1980).

7.1.2 Field metabolic rate

Improved radio-tracking technology has led to an increasing use of the doubly labelled water method (HTO^{18}, HDO^{18}) to measure metabolic rates of freeliving animals. This in turn has led to the proposal of a series of allometric relationships of body water to water flux and metabolic rate in eutherian and marsupial mammals, birds and reptiles (Nagy 1982a, 1982b; Green et al. 1986; Nagy 1987). The field metabolic rate (FMR) for medium-sized (240-550g) mammals and birds is similar. However, outside this size range the slope of the regression between FMR and body mass is different for the following endothermic subgroups: rodents, passerine birds, herbivorous eutherians, herbivorous marsupials, desert eutherians, desert birds and seabirds (Nagy 1987).

Table 7.1

Assumptions made in measuring water and energy flux using the doubly labelled water method (Lifson & McClintock 1966).

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1. Body water volume remains constant during measurement period.
2. Constant water and carbon dioxide flux rates, ie. influx=efflux.
3. Isotopes label only body water and carbon dioxide.
4. Isotopes are lost only as carbon dioxide and water.
5. H^3 and O^{18} isotopes do not fractionate upon leaving the body.
6. There is no water or carbon dioxide input via the lungs and skin.

7.2 METHODS

7.2.1 Field methods

This study ran from August 4th to October 18th 1986, coinciding with the end of the dry season. Possums were initially captured from low trees over the spotlighting track using a catching pole. After capture, animals were placed in cotton bags, weighed, measured and given separate intraperitoneal injections: 1.0 ml HTO (500uCi) and 0.3 ml 95% atom excess H^3O^{18}. After allowing three hours for isotope equilibration, animals were sedated with halothane and about 1.0ml of blood collected by cardiac puncture. The blood samples were sealed in plastic vialls and frozen until analysis.

To facilitate recapture and identification, animals were uniquely tail marked using bleach and fitted with radio transmitters (SR-1 two stage, 151.1MHz; Biotrack Pty Ltd, Dorset U.K.) which were mounted over their shoulders (section 5.2.4). All were released at point of capture.

Nine of the twelve injected animals (five *P. herbertensis*, four *H. lemuroides*) were recaptured 3-22 days later. Animals were recaptured during the day from their dens. Trees were climbed with the aid of tree surgeon's spikes (A. A. Arborists and Tree Surgeons, Melbourne), an eight metre extension ladder and a ten metre wire caving ladder (Frontispiece). All dens were within 20m of the ground. Several known dens were fitted with wire doors that could be closed from the ground. However this was not a successful capture method as animals abandoned these dens for the duration of the study. Recaptured animals were weighed upon removal of their collar and a second blood sample taken before they were released.

7.2.2 Laboratory methods

The frozen sealed blood samples were flown on ice to Canberra for analysis by Dr. B. Green (CSIRO, Lyneham, ACT). Serum was drawn off the clotted blood samples and both serum and cellular fractions stored frozen (-20°C) in plastic vials until analysis.

Tritium

Water was extracted from the cellular fractions by lyophilisation (Vaughan & Boling 1961). To 3.0ml of PCS scintillation cocktail was added 100ul subsamples of the water and the HTO levels were measured in a liquid scintillation counter (Beckman Model LS 2800). Standards were prepared by diluting (1:1000) a sample of the injected HTO solution and counting 100ul subsamples.

Oxygen-18

To determine the O^{18} levels in this water, 0.5ml samples were heated (80°C) in Urey tubes with a fixed volume of standard CO_2. Equilibration of the oxygen atoms in the water and CO_2 occurs after about 15 hours. Once equilibrated, gas samples were drawn out of the Urey tubes and the O^{18} levels assayed in an isotope ratio spectrometer (V.G.903).

Rates of water flux and CO_2 production were calculated using the modified equations of Lifson and McClintock (1966)(Nagy 1980; Nagy & Costa 1980). It was assumed that the mass specific pool sizes of the animals were unchanged between successive blood samples and that changes in their body mass were linear (Lifson & McClintock 1966; Nagy 1980; Nagy & Costa 1980).

7.2.3 Equations

Food consumption

The feeding rates of the possums were calculated from the allometric equation relating rate to body mass for marsupial herbivores (Nagy 1987).

Basal metabolism

There are two standard equations used to predict mean basal metabolic rate (BMR) from body mass; both have the form BMR = $K.Wt^{\cdot 75}$. The value of the constant K changes from 3.34 for the Kleiber (1961) mean for eutherian mammals to 2.33 for the Dawson and Hulbert (1970) mean for marsupials (in SI units $W.kg^{-0.75}$). I used the latter.

7.3 RESULTS

7.3.1 Free water availability

Although no rainfall was recorded in the study site while isotope turnover measurements were made, heavy fog was common between mid August and early September. Therefore preformed water was available to animals eating wet leaves and grooming wet fur, although drinking as such was never observed. The fog disappeared on September 9th and was replaced by dry, clear weather for the remainder of the study period.

7.3.2 Field production of carbon dioxide

Measurements of CO_2 production were made on four *P. herbertensis* (three females, one male) and two *H. lemuroides* (two females). Due to the small sample sizes and their composition, it was not possible to test for differences in FMR between the sexes of each species. The mean rate of carbon dioxide production in *P. herbertensis* was 0.816 ml CO_2 prod./g.h (SD=0.0265; n=4) and for *H. lemuroides*, 1.102 ml CO_2 prod./g.h (SD=0.269; n=2).

The regression of carbon dioxide produced per gram per hour on the mean percentage daily change in body mass for *P. herbertensis* was not significant ($F = 0.436$, $n=4$ $P> 0.1$). Thus FMR was not correlated with rates of gain and loss of body mass. Likewise, the regression between the log of body mass (grams) and the log of CO_2 production (ml/h) for this species was not significant (F test, $n = 4$, $P> 0.1$). Thus body size apparently did not correlate with energy expenditure in the field.

The mean carbon dioxide production per day for each species of free-living possums during August/September is taken to be the mean rate of production. On this basis the mean metabolic cost of free existence in September for an average sized *P. herbertensis* (mass = 1103g) is 433 kJ/day; for *H. lemuroides* (mass 1026g) 546 kJ/day. This assumes a caloric equivalent of 20.1 kJ per litre of CO_2 produced and 4.184 J/cal (Nagy 1983; Schmidt-Neilsen 1983).

7.3.3 Water turnover in the field

The rate of water influx by *P. herbertensis* (both sexes combined) in the field in August/September was 130.6 ml/kg.d (SD=10.41; n=4; average body mass 1103g); for females 136.1 ml/kg.d (SD=4.9; n=3; average body mass 1090g). Corresponding figures for H. lemuroides were 159.3 ml/kg.d (SD=23.47; n=4; mean body mass 1026g, both sexes combined); 168.1 ml/kg.d (SD=20.45; n=3; mean body mass 1077g, females only) (Table 7.2). Separate male calculations could not be done due to small sample sizes. Although two male *P. herbertensis* were measured, the second animal had a turnover rate twice the average for that species and has been excluded from all subsequent calculations.

There was no significant difference in the mean water turnover rates between the species (using the data for both sexes combined; Mann Whitney U-test: U = 14, n_1n_2 = 4,4, $p > 0.05$). Likewise there was no significant difference between the two species when the data from the females only were examined (Mann Whitney U-test: U = 9, n_1n_2 = 3,3, $p = 0.1$). The slope of the regression line describing the relationship between the water influx and average daily percentage change in body mass was not significant for either species (Spearman rank correlation: *H. lemuroides* $r = -0.400$, $n = 4$, $p > 0.5$; *P. herbertensis* $r = 0.200$, $n = 4$, $p > 0.5$; data from both sexes combined). As there was no relationship between body mass change and water turnover, the water influx values for both possum species in August/September have been represented by the mean values of 159ml/kg.d (*H. lemuroides*) and 130ml/kg.d (*P. herbertensis*) in subsequent calculations.

7.3.4 Relationship between CO_2 production and water influx

It is to be expected that there would be a significant relationship between water influx and CO_2 production in the absence of free drinking water in animals in an energetic steady-state. The water influx under these conditions would come from water formed during energy metabolism and from water from food plants. However, there was no significant relationship found when CO_2 production was correlated with water influx (Spearman rank correlation, $r = -0.400$, $n = 4$, n.s) for *P. herbertensis.* The *H. lemuroides* sample was too small to test for a significant relationship. More data are needed for both species before a significant relationship can be expected to appear.

7.3.5 Metabolic scope

Assuming that the mean basal metabolic rate for *P. herbertensis* based on the equation of Dawson and Hulbert (1970) is correct (ie: BMR = 218.49 $kJ/kg^{0.75}.d$; mass = 1.103kg), the HTO results suggest a metabolic scope of 2.3. The corresponding figure for *H. lemuroides* is 3.2 (BMR = $206.95 kJ/kg^{0.75}.d$; mass = 1.026kg).

7.3.6 Food consumption

The feeding rate for each injected possum was calculated using Nagy's (1987) allometric equations for marsupial herbivores, y(g/d) = 0.321W0.676 and $y(kJ/d) = 6.36W^{0.644}$ where W is body mass in grams (Table 7.3). Thus an average-sized *H. lemuroides* (mass = 1026g) is predicted to ingest 34.85g dry mass per day and an average *P. herbertensis* (mass = 1103g) 36.31g dry mass per day. There is no significant difference between the feeding rates of these two species.

As the average water content of the leaves commonly eaten by both species is between about 60-70% (Table 3, Appendix D), the possums in August/September probably ate between 100-120g fresh weight of leaves daily, or about 10% of their body weight in foliage. In the course of a year an average Herbert River ringtail would consume about 13.3kg dry mass and a lemuroid ringtail about 12.7kg dry mass of leaves. Using Seawright's (1981) mark/resight population density estimate of 8.9 *P. herbertensis* per hectare (9.8kg/ha biomass) and my estimate of 10 *H. lemuroides* per hectare (10.3kg/ha biomass) results in an annual food consumption of 118 and 127 kg dry mass per hectare per year respectively.

7.4 DISCUSSION

7.4.1 Carbon dioxide production

When labelled animals den in confined spaces, errors can occur in the measurement of isotope turnover rates. Carbon dioxide can accumulate in the den and enter the animal via skin or lungs. This labelled CO_2 entering from outside is then measured by the isotopes along with that produced endogenously. This violates one of the assumptions of the doubly labelled water method and can lead to a serious underestimate of CO_2 production (Nagy 1980). If an injected animal dens with unlabelled animals and breathes in unlabelled CO_2 this can lead to an overestimate of metabolic rate (Nagy 1980).

There was no error caused by absorbing CO_2 in the case of the labelled P. herbertensis. Each animal denned alone, except for very small pouch young in the case of the females. Dens were usually in epiphytes which were open to the free flow of air. The possibility of an error was more likely with the lemuroid ringtail which dens in tree hollows. This may account for the variability between the two animals measured. Ethelred (CO_2 production = 1.37ml/g.h) denned alone on top of a dead stump for the duration of the measurement period and was unlikely to absorb CO_2 from her surroundings. The other animal, Mrs Cyclops (CO_2 production = 0.833ml/g.h), denned with a male in a small hollow. Her mate was labelled but not recaptured until his isotopes were close to background level. The isotope concentration of the labelled CO_2 that accumulated in Mrs Cyclops small den would not have changed as rapidly as that in the animal's body. Nagy (1980) found that this situation leads to a serious underestimate of metabolic rate. The difference between the two lemuroid ringtails' CO_2 production rates is possibly due to this.

7.4.2 Basal metabolic rate

While there has been some doubt expressed that a low basal metabolic rate (BMR) is evolutionarily conservative (McNab 1966, 1974, 1978a), there is a statistically significant difference between marsupial and eutherian rates (Hume 1982). In general, marsupials have basal rates which overlap only the lower part of the eutherian range.

Low basal rates in marsupials have been attributed to phylogeny (Dawson 1973; Hulbert & Dawson 1974; Nicol 1978) and climate and diet (McNab 1978a, 1980; Hume 1982; Thompson & Nicoll 1986). Food habits in particular appear to be strongly correlated with basal rates (McNab 1974, 1978a, 1978b, 1980). When therian species were divided into six groups based on habitat and diet, McNab (1978b) found that terrestrial marsupials generally have a BMR lower than their eutherian counterparts. This difference disappears however in the two arboreal categories - the folivores and the frugivore/omnivores which have similarly very low basal rates. Factors which may relate to this phenomenon include the reduced muscle mass of arboreal animals (Grand 1978) and the allelochemical content and generally poor nutritional quality of a folivorous diet (McNab 1978a, 1978b).

7.4.3 Field metabolic rate

There are few published accounts of the field metabolic rate (ie: BMR plus the energetic costs of thermoregulation and activity) of possums. Those that are available are presented in Table 7.4. Nagy (pers. comm.) found field metabolic rates (FMR) for the folivorous common ringtail possum, *P. peregrinus*, from Melbourne averaged 1.49ml CO_2/g.h or 556kJ/day for adults (mean body mass 717g) and 1.72ml CO_2/g.h or 249kJ/day for juveniles (mean body mass 278g). This is higher than the metabolic costs of free existence for average sized adult *P. herbertensis* (0.816 ml CO_2/g.h) or *H. lemuroides* (1.102 ml CO_2/g.h). As the cost of thermoregulation in temperate climates would be greater than for animals in warmer climates, it is reasonable that tropical possums would have a lower FMR than temperate species (mean yearly temperature range, x (SD): eastern Melbourne 18.9 (4.31)^{0}C - 10.05 (2.48)^{0}C (Victorian Yearbook 1985); Herberton 25.6 (2.78)^{0}C - 14.4 3.02)^{0}C (Tracey 1982). In addition, the more actively-moving *H. lemuroides* would be expected to expend more energy than the relatively sedentary *P. herbertensis* in the course of a night's activity as suggested by my results.

The sugar glider, *Petaurus breviceps* (mean body mass 128g; Dawson & Hulbert 1970) is an arboreal possum feeding primarily on exudates and insects (Smith 1980). It has a basal metabolic rate of 0.69 ml 0_2/g.h (Dawson & Hulbert 1970) and a scope of 4.5 (Nagy & Suckling in A.P Smith 1980) in spring giving it a FMR of about 2.5 ml CO_2/g.h (using RQ 0.8). The closely-related Leadbeater's Possum, *Gymnobelideus leadbeateri* (mean body mass 129g; Smith et al. 1982), is also an exudate feeder and overlaps in its distribution with *P. breviceps* (Smith et al. 1982). It expends 2.91 ml CO_2/g.h in free existence which is 5.8 times its calculated BMR (Smith et al. 1982). Both these species show very high metabolic rates for such small animals.

The only energetics data available for a tropical folivorous possum is that pertaining to the spotted cuscus, *Phalanger maculatus* (mean body mass 4250g; Dawson & Degabriele 1973). A slow moving rainforest species, this large possum has been likened to a sloth due to its low BMR (0.26 ml O_2 /g.h) and highly insulative fur. Although there are no data available on its FMR, only one of the 42 marsupials listed by McNab (1978b), the red kangaroo *Megaleia rufa* (mean body mass 32.5kg; Dawson & Hulbert 1970), has a lower BMR. This low BMR coupled with the cuscus' very sedentary habits suggests it has a low FMR.

The low field metabolic rates of the folivorous possums relative to the more omnivorous exudate feeding gliders are in agreement with the literature. The three folivorous possums *Pseudocheirus occidentalis, Trichosaurus vulpecula* and *P. maculatus* have a mean BMR only 59% of the Dawson & Hulbert (1970) mean (McNab 1978b). As possums and gliders are arboreal and therefore all have a reduced muscle mass (23% of total body mass compared with 53% for terrestrial species; Grand 1978), the differences in metabolic rate between the onmivorous compared to folivorous possums can probably be explained by dietary differences.

Although leaves have a high percentage of carbohydrates, most are structural and not available until processed by gut symbionts. They therefore have a low available caloric density compared with plant exudates. The need for extended processing of a fixed bulk of food (Westoby 1978) limits the daily energy intake of a folivore below that expected from the Kleiber curve relating body mass to BMR (McNab 1978a). In addition, plant defensive compounds (Chapter 6) may drain valuable resources, such as glucose molecules, which are needed for conjugation and subsequent detoxification. This further decreases the energy available to the folivore.

7.4.4 Scope of metabolism

The metabolic scope, ie. the factor by which an animal raises its metabolic rate above basal in the field, is low for both the rainforest possum species I studied. The exudate/insect feeding petaurids have scopes in spring of 4.5 (*P. breviceps*; Nagy & Suckling in Hume 1982) and 5.8 (*G. leadbeateri*; Smith et al. 1982). Likewise, small insectivorous dasyurids have been reported to expend between 4 and 4.5 times their basal energy requirements on maintenance (Cowan, O'Riordan & Cowan 1974; Macmillan & Nelson 1969; Nagy et al. 1978). By constrast, herbivores generally have a lower maintenance requirement of about twice BMR. For example Nagy and Milton (1979) found that the FMR of wild howler monkeys (*Alouatta palliata*) averaged twice the BMR or 355kJ/kg.d. Hume (1974) found the maintenance energy requirements of the euro (*Macropus robustus*) and the red kangaroo (*Megaleia rufa*) to be about twice basal. Using the Dawson and Hulbert (1970) mean to estimate BMR for the two ringtail possums, the resultant scopes are close to those of other herbivores.

However, if the rainforest possums have a lower BMR than the estimates obtained from the Dawson and Hulbert (1970) equation, the estimated scopes will be too low. Other folivorous possum species have basal rates 59% of that estimated from the equation. Using this figure, metabolic scope increases to 5.4 for *H. lemuroides* and 3.9 for *P. herbertensis*. Only measurements of the BMR of these species will result in more accurate figures.

7.4.5 Water relations

Marsupials generally have lower water turnover rates than eutherians

(Dawson et al. 1975; Denny & Dawson 1975). For example, there is a 27% difference in the water turnover rate (WTR) of five species of macropods (98 = 21 ml/kg$^{0.8}$.d; Denny & Dawson 1975a) when compared with seven species of eutherians (134 = 32 ml/kg$^{0.8}$.d; Richmond et al. 1962). This is not unreasonable given the lower BMR of marsupials, as metabolic rate indirectly influences the rate of water loss from the body (Macfarlane et al. 1971). However Nicol (1978) found that this difference was not quite significant and that the strongest correlation was not with phylogeny but with habitat. Generally, equivalent eutherians and marsupials in the same habitat have similar water fluxes.

As water balance is correlated with habitat, it is governed by the availability of water (preformed and metabolic) and the extent of water loss due to thermoregulation and excretion. Those species which evolved in moist climates (eg. *Antechinus stuartii*, 539 ml/kg.d in July; Nagy et al.1978) have higher water turnovers compared to xeric evolved species (eg. *M. rufa*, 39.5 ml/kg.d; Dawson et al. 1975; desert bandicoot *Macrotis lagostis* 45.5 ml/kg.d; Hulbert & Dawson 1974). Some species appear out of place, such as *Sminthopsis crassicaudata* which has secondarily invaded more arid areas in times of increased water availability (Morton 1980). This is explained by the conservative rate of change of basic ecophysiology causing animals to retain ancient patterns of water and energy turnover which seem inappropriate to their present habitat (Macfarlane 1976).

The weight-adjusted water turnover rate for the two rainforest possums are amongst the highest recorded for arboreal and/or herbivorous marsupials (Table 7.5). The predicted daily water turnover using Nicol's (1978) equation $T = 102.2\text{kg}^{0.82}$ (regression coefficient $r = 0.97$) is 104.4 and 110.8 ml/kg$^{0.82}$ for *P. herbertensis* and *H. lemuroides* respectively. These turnovers are lower than the actual fluxes, indicating that both ringtails evolved in a moist habitat without the need for strict water constraints. (Their upland rainforest distribution lends support to this point). As these possums have not been seen drinking water in the field they probably satisfy their water needs from their leafy diet; some preformed water may be obtained from wet leaves and grooming wet fur. The water content of core food species varies between 56.2% (SD 8.3, n=8; mature leaves) and 67.5% (SD 7.3, n=8; young leaves) for *H. lemuroides* and 67.8% (SD 1.7, n=4; mature leaves) and 74.6% (SD 3.0, n=7; young leaves) for *P. herbertensis*.

7.4.6 Food consumption

The estimated annual food consumption rates of the two possum species (*P. herbertensis* 118 kg dry mass/ha/yr; *H. lemuroides* 127 kg dry mass/ha/yr) are considerably higher than that found for the howler monkey (*Alouatta palliata*) on Barro Colorado Island (90 kg dry mass/ha/yr, Nagy & Milton 1979; 70kg dry mass/ha/yr, Leigh & Smythe 1978). As the howlers eat about three times as much fruit as leaves (Nagy & Milton 1979) this leads to a lower carrying capacity and a lower per hectare impact in terms of biomass eaten. The animals must range over a larger area to obtain the necessary amount of fruit. By contrast,mature leaves are an ubiquitous resource for the well adapted folivore, allowing higher population densities.

Nagy's (1987) equations to calculate feeding rates do not include an increment for producing new biomass and as such may underestimate the actual rates for reproducing females. All females except Genevieve were lactating and carrying small pouch young. In rodents, lactating females have metabolic and feeding rates that are up to twice those of non-reproductive females (Grodzinski & Wunder 1975). However, as the possums have smaller litters (1-2 young) and a slower growth rate than rodents, the increased metabolic and feeding rates in the two possum species due to reproduction may be less.

The lemuroid possum, Mrs Cyclops, had the largest single young of the injected females (193.5g). She was in medium/good condition and heavy for a *H. lemuroides* (Table 7.6). It is unfortunate that this animal's metabolic rate was probably in error. The other female carrying a large weight of pouch young, Madame (body mass 1080g without young; two young: 97g, 100g), was in good condition and had the <u>lowest</u> FMR of any possum measured. These data suggest that pouch young up to 20% of mothers body mass may not induce an elevation of their mother's metabolic and feeding rates to the extent observed in some rodents. Mammal populations do not generally invest more than 2% of their ingested energy in new biomass in a year (Turner 1979). If this applies to these possum species, then the estimated annual food consumption should be increased by about 2%.

7.5 CONCLUSIONS

The water turnover rates of both ringtail possums are those of animals which evolved in a moist habitat. As the possums do not drink free water, they must obtain sufficient water from their diet, metabolic water and from water gleaned incidentally through grooming wet fur.

The field metabolic rate of both species is lower than that of the common ringtail possum in Melbourne.The difference is probably due to the higher cost of thermoregulation in temperate as opposed to tropical environments. Overall, the metabolic costs of free existence for the two rainforest species reflect their folivorous diet and arboreal habits.

Table 7.2

Metabolic rate and water turnover in free-living *P. herbertensis* and *H. lemuroides* in August/September at Longlands Gap State Forest, north Queensland.

Individual	Species	Sex	Days between captures	Mass (g)		FMR (CO_2 prod/g.h)	Water Influx (ml/kg.d)	Water Efflux (ml/kg.d)	Water Influx (ml/kg $^{0.8}$.d)
				1st capture	2nd capture				
Bruno	*H. lemuroides*	M	19	870	900	—	132.589	132.650	128.947
Dolly		F	22	1090	1095	—	145.159	145.200	147.683
Ethelred		F	3	1022	1025	1.3707	194.837	195.163	195.687
Mrs Cyclops		F	3	1120	1122	0.8334	164.416	165.011	168.185
MEAN				1028		1.1021	159.250		160.126
STD DEV				96.5		0.2687	23.466		24.781
Geronimo	*P. herbertensis*	M	4	1210	1215	0.8431	114.175	114.382	119.402
Madame		F	4	1203	1230	0.8018	142.092	142.298	147.442
Whiteleg		F	4	1032	1102	0.7792	130.056	115.764	130.878
Genevieve		F	6	1060	1010	0.8386	136.174	142.454	137.770
Spot #		M	3	1010	930	—	256.764	257.107	257.275
MEAN				1103		0.8157	130.624		133.873
STD DEV				86.1		0.0265	10.407		10.219

Not included when calculating the mean and standard deviation of water turnover and metabolic rate.

Table 7.3

Estimated food consumption and energy metabolism of free-living possums.

H. lemuroides

INDIV	MEAN BODY MASS(g)	DAILY MASS CHANGE %	METABOLIC RATE		FEEDING RATE	
			ml CO_2/g.h	kJ/kg.h	kJ/kg.d	g dry/kg.d
Bruno@	885	+0.18	-	-	567.99	35.62
Dolly	1092	+0.0002	-	-	527.05	33.28
Ethelred	1023	+0.09	1.3707	646.36	539.44	33.99
Mrs Cyclops	1121	+0.06	0.8334	358.64	522.15	32.99
MEAN				502.49	539.16	33.97
SD				143.86	17.80	1.02

P. herbertensis

INDIV	MEAN BODY MASS(g)	DAILY MASS CHANGE %	METABOLIC RATE		FEEDING RATE	
			ml CO_2/g.h	kJ/kg.h	kJ/kg.d	g dry/kg.d
Geronimo	1213	+0.10	0.8431	335.29	507.69	32.16
Madame	1216	+0.56	0.8018	318.08	507.25	32.14
Whiteleg	1067	+1.67	0.7792	352.28	531.41	33.52
Genevieve	1035	-0.79	0.8386	390.86	537.20	33.86
MEAN				349.13	520.89	32.92
SD				26.96	13.57	0.78

@ subadult

Table 7.4

Comparison of metabolic rates of forest dwelling, arboreal marsupials *Trichosurus vulpecula*, *Phalanger maculatus*, *Petaurus breviceps*, *Phalanger occidentalis*, *Gymnobelideus leadbeateri*, *Pseudocheirus peregrinus*, *Pseudocheirus herbertensis*, *Hemibelideus lemuroides*.

Species	Diet	Mass (g)	BMR $ml/O_2/g.h$	FMR $ml\ CO_2/g.h$	Source
Phalangeridae					
T. vulpecula	LF	1982	0.32		Dawson & Hulbert 1970
P. maculatus	LF	4250	0.26		Dawson & Degabriele 1973
Petauridae					
P. breviceps	F-O	128	0.69		Dawson & Hulbert 1970
P. occidentalis	L	860	0.33		Kinnear & Shield 1975
G. leadbeateri	E-I	129	0.62	2.91	Smith 1980
P. peregrinus	L	717		1.49	Nagy 1987
Pseudocheiridae					
P. herbertensis	L	1103		0.816	This study
H. lemuroides	L	1026		1.102	This study

(After McNab 1978b) L = leaves, F = fruit, O = omnivore, I = insects, E = exudates

Table 7.5

Comparison of water turnover rates in forest dwelling marsupials: *Pseudocheirus herbertensis*, *Hemibelideus lemuroides*, *Perameles nasuta*, *Pseudocheirus peregrinus*, *Gymnobelideus leadbeateri*, *Trichosurus vulpecula*, *Potorous tridactylus*, *Phascolarctos cinereus*.

Species	Diet	Water turnover (ml/kg.d)	Water turnout (ml/kg$^{0.8}$.d)	Body mass (g)	Source
P. herbertensis	F	133.9	130.6	1.103	This study
H. lemuroides	F	160.1	159.3	1.026	This study
Perameles nasuta	F	72.5	72.5	1.000	Hulbert & Dawson 1964
P. peregrinus	I	138.5	148.0	.717	Nagy pers. comm.
G. leadbeateri	E-I	162.1	242.0	.135	Smith et al 1982
T. vulpecula	F-O	96.0	104.4	1.520	Kennedy & Heinsohn 1974
Potorous tridactylus	H	105.9	113.3	1.400	Denny & Dawson 1975
Phascolarctos cinereus	F	179.0	112.9	10.0	Cork 1981

F = folivore, I = insectivore, E-I = exudate feeder, O = omnivore, H = herbivore.

Table 7.6

Weight of pouch young and condition of lactating ringtail possums.
Condition was a subjective assessment taken on each captured animal and was based on whether or not the vertebral processes in the tail (near the base) could be easily felt (poor condition), just felt (medium) or not felt (good).

Individual	Body Mass Female (g)	Body Mass Young (g)	Sex of Young	Date of Measurement	Condition of Female#
Dolly	1090	50	F	28/09/86	good
	1095	111	F	20/10/86	good
Whiteleg	1102	18	M	23/08/86	good
Madame	1080	97	F	22/08/86	good
	1090	100	M	26/08/86	good
Ethelred	1022	38	F	30/08/86	poor
	1025	37.5	F	03/09/86	poor
Mrs Cyclops	1140	193.5	F	07/10/86	med-good

CHAPTER 8 ASSESSING THE POSSUM FORAGING STRATEGIES

Classical foraging strategy theory (eg. Emlen 1966; MacArthur & Pianka 1966) predicts that animals will select food items in order to maximize their energy intake per unit foraging time. This is not a successful predictive theory for herbivores, as potential food items vary significantly in their content of primary and secondary compounds. Westoby (1974) instead proposed that generalist herbivores should optimize the nutrient mix within a total bulk of food. He concluded that food quality rather than availability is the most important factor in diet selection by herbivores. Therefore food availability should only affect diet selection when food is less abundant.

The concentration and type of secondary compounds found in plant tissues is also predicted to influence diet selection by primary consumers (Freeland & Janzen 1974). Although they are equipped with microbial and microsomal enzymes to degrade and excrete biocides, herbivores are still limited by these detoxificatory mechanisms. Freeland and Janzen (1974) therefore suggest that herbivores may (1) need to include a variety of foods in their diet to avoid an overload of toxins, and (2) eat high nutrient foods to counteract the effects of compounds which complex with proteins and/or reduce digestibility. They also predict that herbivores will continue to feed on an established set of "safe" food items for as long as possible.

Due to the variable and relatively unpredictable nutrient and anti-nutrient content of their foods, herbivores have a much more complex task of diet selection than that described by classical foraging models.

Other factors which also influence diet selection by herbivores include the overall energy demands of the animals, the efficiency and extent of digestive modifications, and the costs of locating food (Milton 1980).

8.1 Food selection by possums

The frequency with which the possums fed upon different tree species was not related to the density of those species in the forest (5.3.2). Some very uncommon species (eg. *Flindersia pimentaliana*, *Ficus pleurocarpa*) were heavily exploited, while other very common species (eg. *Neolitsea dealbata*, *Aglaia ferruginea*) were ignored or avoided. This suggests that possums are not selecting food items due to availability but because of some other factor or factors, perhaps food quality. Proctor-Gray (1985) thought that food quality may influence dietary selection by Lumholtz tree kangaroos (*Dendrolagus lumholtzii*), as this species also obtains most of its food from several uncommon plant species.

Although all three species of rainforest possums ate a significant amount of mature foliage, they were selective in their choice, avoiding items with a high condensed tannin content (6.3.2). The other factors which apparently affected diet selection varied with the possum species. Although *H. lemuroides* was the most generalist feeder and included larger amounts of mature foliage in its diet than the others, it was still very selective. Favoured food items (eg. *Flindersia brayleyana*, *Sloanea langii*) contained significantly less fibre than those of the other species (eg. *Elaeocarpus ruminatus*, *Cryptocarya rigida*). Unlike *P. herbertensis* and *P. archeri*, *H. lemuroides* did not specialize on plants which leafed year round, but included significant amounts of young foliage in the diet from two long leafing species (*Flindersia brayleyana*, *Sloanea langii*). *P. herbertensis* specialized on a continuous flushing species (*Alphitonia* *petriei*), which allowed its diet to include almost 60% of young leaves. Due to the clumped growth habit of *Alphitonia*, the search costs that *P. herbertensis* incurred were reduced allowing the animal to obtain a high quality resource for minimum effort. Unlike the other two species, *P. herbertensis* selected food items of higher protein content. *P. archeri* had the most specialized diet of the three, although it appeared to be the least nutritionally selective. It selected a high fibre, low protein diet despite the year round availability of young *Ficus* foliage. The younger foliage contained much less fibre than the mature foliage that it ate in quantity. This strategy is comparable to the low cost/low return strategy of the leaf monkey *Presbytis senex* (Hladik 1978).

None of the possum species fed on seasonal items (eg. young leaves) in the same proportions that they were available (5.3.2). Instead they were influenced by the leafing phenology of only a few species. For example, *H. lemuroides* included more mature leaves in its diet when favoured young leaf sources were not flushing despite the continued availability of young leaves of other species. The resultant increase in the mature leaf component in the diet may indicate that the cost of specializing on young foliage is too great (whether in search, digestion or detoxification costs). This strategy of switching to mature leaves in the absence of preferred species of young leaves may be common to all three species. The other two have less energy to spend due to their lower quality diet (*P. archeri*) and higher field metabolic costs (*P. herbertensis*), thus searching for other sources of young leaves may be even less of an option for them.

The lack of correlation between the amount of seasonal foods included in the possums' diets and availability of seasonal foods in the forest (5.3.2) contrasts with the strong correlation Milton (1980) found between availability of seasonal foods and the dietary composition of howler monkeys (*Alouatta palliata*). However, both howler monkeys and the rainforest ringtails appear to switch to less preferred items when favoured food sources become scarce, and it is energetically difficult to locate them. Both groups therefore appear to be under similar energetic constraints, although their dietary strategies are dissimilar.

In accordance with Freeland and Janzen's (1974) predictions, the three possum species included a variety of food items in their diets. This variety may have been to minimize possible toxin overloads and/or to maximise nutrient intake. Protein, however, was not a nutrient that was optimized, as it did not correlate with ranked food preferences between food species (6.3.2). There are not enough data to indicate whether the possums are exploiting a variety of leaf sources to minimize the costs of detoxification. For whatever reasons, all three are exercising great selectivity in dietary choice.

Sampling novel or changing food items is predicted by foraging theory (Westoby 1974) and would account for the large number of species in the possums' diets which were only eaten very infreqently. As the phenological status of many plant species changes relatively unpredictably, monitoring potential food sources for nutritional and allelochemical content would be essential to diet selection. Additionally, the dynamic nature of rainforest communities makes it adaptively important for folivorous animals to maintain dietary flexibility rather than becoming narrowly specialist on foods which may become increasingly scarce over time. Thus, the large number of minor species included in the possum's diets may serve a two fold function.

8.2 Energetic considerations

As expected, the field metabolic rates of *H. lemuroides* and *P.*

herbertensis are lower than similar sized omnivorous possums (eg. *Gymnobelideus leadbeateri*; Smith et al. 1982). However, there is a significant difference in energy expenditure between the two rainforest species. *H. lemuroides* requires 35% more energy than *P. herbertensis* to maintain itself in the field (7.3.2). As both species have a similar rate of food consumption, *H. lemuroides* needs to ingest higher quality items to acquire sufficient energy for maintenance (7.3.6).

Compared to the field energy requirements of the folivorous common ringtail (*P. peregrinus*) in southern Victoria, these rainforest species require less energy to survive. The reduced energy demand may be due to the lower costs of thermoregulation in the tropics or perhaps to greater behavioural and/or digestive adaptations. Whatever the reason, a lower energy requirement allows the two tropical species to survive on a more folivorous diet than that of the southern species.

Although there are no field metabolic rate data for *P. archeri*, this species probably has the lowest energy requirements of the three. It spends considerable periods resting during the night, remaining curled up for several hours at a time. It also has a diet which is higher in fibre than the other species. Additionally it does not use fixed dens, but rests in the open wherever it finishes the nights' activity. As it does not return to a den, this reduces the distance the animal must travel. The energy saved by reducing travel presumably is more than the increased cost of thermoregulation incurred due to lack of a daytime den. *H. lemuroides* is very loyal to its den hollow, returning to it each night regardless of where it has been foraging. Although *P. herbertensis* uses a den during the day, the animal changes it almost daily thereby reducing the distance it must travel. As tree hollows are not generally numerous, the den requirements of this species are more flexible than those of *H. lemuroides*.

It utilizes hollows, epiphytic ferns and nests which it constructs. Thus den requirements seem to mirror the relative energy needs of the three species.

8.3 Food procurement

The cost of obtaining food in a highly heterogenous environment generally increases with increasing selectivity. Costs also increase when food items are patchily distributed in time and space. To minimize these costs, the possums have developed behavioural and morphological adaptations which allow them to utilize patchily distributed food resources.

All three species obtain food from diverse sources rather than from a single source. This increases the likelihood of an animal encountering a food species and thus cuts search and travel costs. In any one night *H. lemuroides* and *P. herbertensis* feed from between five and ten species, and may utilize more than one food type from each species. It is probable that *P. archeri* also feeds from several species nightly. In addition, although both *Pseudocheirus* species specialize on continuously leafing trees, they do not feed on these species to the exclusion of everything else. This means that the cost of seeking out new food sources is balanced by the advantages to the animal of diversifying its diet.

The animals also have very flexible diets which change to accomodate different species as they come into leaf (5.3.2). This is most apparent in the case of *H. lemuroides* which depends on several long leafing species to supply young leaves during the dry season. During the wet season, all species become more opportunistic as many plants flush new foliage. Such dietary flexibility allows the animals to utilize high quality seasonal food items throughout the year.

Although the possums do have diverse diets, during the dry season when there is less new foliage available they become more specialized on core food species. This specialization results in minimum overlap at the species and item levels in the most difficult season. During the wet when there are more species flushing, there is also more overlap in food species. Despite the increased overlap there are no obvious competitive interactions between or within the species. *H. lemuroides* occur in the highest density in Longland's Gap State Forest,and feeds on some of the most common species which also flush synchronously. As both old and new leaves of these trees are eaten, this may be a case where there is so much food available that it is not worth defending (Schoener 1971). Likewise *P. herbertensis* feeds on relatively common but very clumped resources where both old and new leaves are eaten; the same may well explain the lack of intra-species defence. *P. archeri* feeds on relatively uncommon fig species which have a very large biomass. As biomass is not taken into account when electivities are calculated, my estimates of the electivities of these fig trees are too high. Due to the sheer volume of leaves available, several individuals could live and feed in each tree, especially as it is mainly mature leaves which are eaten. Again, the resource may be too abundant to be worth defending.

Another benefit of specialization is that the species on which the animals specialized generally have a more favourable nutrient and allelochemical content than those species they ignored. In addition, the costs of detoxification are probably lower as they do not continually have to be induced. As foraging strategy predicts (Freeland & Janzen 1974), it is these "safe" staples retained in the diet for long durations that form the main basis of the animals' diet.

Freeland and Janzen (1974) suggest that herbivores should have body sizes and search strategies that "optimize the number and types of foods available with respect to the total amount of food that can be eaten". The small body sizes of the possum species allow them to reach the outer canopy of trees which some of the larger, heavier folivores cannot exploit (eg. tree kangaroos). As most canopy trees bear young growth apically, small size enables the possums to better exploit this food source. However, as the rate of food processing increases with the square of a size dimension and metabolic requirements increase as the cube (Hume 1982), small size can limit the throughput and thus the type of foods on which an animal can survive. Behavioural adaptations such as increased dietary selectivity and reduced distances which must be travelled to obtain food and shelter allow these small animals to survive on an almost completely foliage diet.

In addition to behavioural adaptations to reduce energy requirements, digestive modifications allow more energy to be obtained from a fibrous diet. Of the three species, weighted linear measurements of their digestive tracts suggest that *P. archeri* and *H. lemuroides* are the most specialized for fermenting fibre, although *H. lemuroides* selects a low fibre diet. All species show some development of the caecum and/or colon (6.3.3) although major sites of fermentation probably differ between species (6.4.3). A detailed study of the digestive physiology of these species would be valuable in determining the extent and importance of such modifications and the value of fermentation products to their overall energy budgets.

8.4 Possum ecology: Implications for conservation

This study has several implications for the longterm conservation of these three ringtail possum species on the Atherton uplands. The first is the need for a balance of primary and secondary regrowth and climax species in forests supporting these animals. The possums all feed on a mixture of trees characteristic of different seral stages. As rainforest is a dynamic ecosystem composed of diverse species from different successional stages, this balance is normally met.However, where extensive clearing or disturbance has resulted in a significant increase in pioneering and regrowth species (eg. *Alphitonia petriei, Acacia melanoxylan*) at the cost of reduced overall diversity, and especially of climax-species diversity, a decrease in the density and species composition of the possum fauna is likely to occur. The lemuroid possum appears to be the most at risk from logging disturbance, as its' diet includes many valuable cabinet species of late secondary and climax stages (eg. *Flindersia* species).

In addition to simplification of the forest structure following repeated disturbance, forest patch-size and diversity are also implicated in possum distribution on a more local scale. Fragmentation of once continuous habitat has resulted in locally reduced plant diversity, especially in smaller patches (Pahl 1979). The study by Pahl (1979) indicates that as patches become increasingly reduced in size, the density and species diversity of these ringtail possums drops. My study suggests that the reduced plant diversity, and thus the lack of an adequate food supply in small patches may be a causal factor leading to local possum extinctions. To have a diverse and seasonally changing diet necessitates having a species rich forest with many individuals of the same species present. This allows animals to choose between individuals which are allelochemically, and thus nutritionally, dissimilar. Additionally, those species which depend on a continuous young leaf supply from food species which are phenologically out of synchrony, or on a complex of species which leaf sequentially, are going to be most at risk following fragmentation and disturbance of their habitat.

Additional to their feeding requirements, the dependance of *Hemibelideus lemuroides*, and to a lesser extent *Pseudocheirus herbertensis*, on tree hollows for daytime shelter may limit their population densities in forests where large trees have been removed. Tree hollow loss may result from logging practises or from cyclonic disturbance. Due to their reliance on tree hollows, *H. lemuroides* is the most at risk in disturbed or regenerating forests while *P. herbertensis* is less affected, and *P. archeri* not at all. This order of impact is identical to that found by Pahl (1979) in his fragmentation study where *H. lemuroides* was the first species to disappear from forest following fragmentation or disturbance, and *P. archeri* the last. A study of hollow usage and possum carrying capacity of northern tropical forests, similar to that done by Menkhorst (1984) in southern Australian forests, would be a valuable aid in managing our northern possum species. It may be found that possums can survive in disturbed patches despite the decreased diversity or changed seral balance of the forest once supplemental hollows are added.

8.5 The original hypotheses

Based on foraging strategy theory I predicted (section 1.4) that the rainforest ringtails would select foliage with low concentrations of fibre and secondary compounds, but which were high in protein (Hypothesis 1, section 1.4). This prediction was only partly validated. All three species of possum specialized on foods containing lower concentrations of condensed tannins than found in foods they ate less frequently. However my predictions regarding primary compounds were not correct. *H. lemuroides* preferred leaves with less protein, while *P. archeri* specialized on high fibre foods. Of the three ringtail species, *P. herbertensis* specialized on a diet closest to that which I predicted, ie. higher protein and lower fibre than less favoured food items. While inaccuracies in ranking of preferred food species may explain some of the departure from prediction, I doubt it explains all.

Dietary overlap (Hypothesis 2) was least between congeners, and greatest between *H. lemuroides* and *P. herbertensis*. Overall, however there was little overlap evident. This may be explained due to competition in the past, or maybe due to the development of detoxification pathways particular to certain food species on which the different possum species specialise. Whatever the proposed cause, overlap of food species between rainforest ringtails is small.

The third hypothesis, that all three species would show similar adaptations to folivory and small size, is supported by the data. All three species have behavioural and morphological adaptations to a low energy diet and limited digestive capacity. However, these adaptations do not result in identical field energy requirements, as there is some variation between species.

In keeping with their highly folivorous diet both *Hemibelideus lemuroides* and *Pseudocheirus herbertensis* proved to have low field energy requirements as predicted (Hypothesis4).

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Appendix A Phenology trees

List of families and species of plants observed at monthly intervals. Refer to text (Chapter 4) for explanation of phenological terms. Plant families and species after Clifford & Ludlow (1972) and Hyland (1982).

	No. of trees	#No.of trees /ha.	Season of			Forest Storey
			Leaf	Flower	Fruit	
Amylothecaceae						
Amylotheca sp.	*1*		*dis*	*wet*	*dry*	*u/s*
Apocynaceae						
Ochrosia poweri	*5*		*wet*	*extend*	*wet*	*u/s*
Araliaceae						
Polyscias murrayi	*6*	*3.6*	*cts*	*wet*	*extend*	*u/s*
Cunoniaceae						
Ceratopetalum succirubrum	*4*	*3.2*	*?*	*wet*	*extend*	*o/s*
Elaeocarpaceae						
Elaeocarpus arhmenicus	*1*	*1.1*	*dis*	*wet*	*wet*	*o/s*
E. ruminatus	*13*	*8.8*	*wet*	*dry*	*extend*	*o/s*
Sloanea langii	*7*	*4.9*	*dis*	*dry*	*wet*	*u/s*
Euphorbiaceae						
Aleurites moluccana	*2*	*0.8*	*cts*	*wet*	*dry*	*u/s*
Flacourtiaceae						
Casearia sp.	*5*	*6.7*	*cts*	*?*	*?*	*o/s*
Lauraceae						
Beilschmeidia aff obtusifolia	*3*	*3.5*	*dis*	*wet*	*extend*	*o/s*
Cryptocarya rigida	*6*	*3.9*	*wet*	*extend*	*dry*	*u/s*
Endiandra muelleri	*2*	*4.2*	*dry*	*?*	*?*	*u/s*
E. sankeyana	*4*	*1.8*	*wet*	*wet*	*dry*	*u/s*
E. tooram	*3*	*2.5*	*dis*	*?*	*?*	*u/s*
Endiandra sp. code 62	*8*	*14.4*	*dis*	*extend*	*extend*	*o/s*
Litsea leefeana	*8*	*10.2*	*cts*	*wet*	*extend*	*u/s*
Neolitsea dealbata	*7*	*9.8*	*dry*	*extend*	*wet*	*u/s*
Meliaceae						
Aglaia sapendina	*1*	*0.3*	*wet*	*?*	*?*	*u/s*
A. ferruginea	*4*	*?*	*wet*	*wet*	*wet*	*u/s*
Dysoxylum klanderi	*2*	*1.1*	*cts*	*extend*	*?*	*o/s*
Mimosaceae						
Acacia melanoxylan	*4*	*1.4*	*dry*	*wet?*	*?*	*o/s*
Archidendrani vaillanti	*1*	*0.35*	*dry*	*dry*	*?*	*o/s*

Moniminaceae							
Daphnandra repandula	*3*	*1.4*	*wet*	*extend*	*dry?*	*u/s*	
Moraceae							
Ficus leptoclada	*3*	*1.1*	*wet*	*extend*	*dry*	*u/s*	
F. pleurocarpa	*3*	*1.1*	*cts*	*?*	*extend*	*o/s*	
F. watkinsoniana	*4*	*2.1*	*cts*	*?*	*extend*	*o/s*	
Myrtaceae							
Acmena resa	*6*	*7.4*	*dry*	*extend*	*extend*	*o/s*	
Syzygium cormiflora	*8*	*5.3*	*dis*	*dry*	*wet*	*o/s*	
S. luehmannii	*2*	*1.1*	*dis*	*wet*	*wet*	*o/s*	
S. papyraceae	*3*	*1.1*	*dry*	*?*	*?*	*u/s*	*u/storey*
Rhodomyrtis trineura	*4*	****	*cts*	*wet*	*wet*	*u/s*	
Rhodamnia blaireana	*2*	*0.7*	*cts*	*wet*	*wet*	*u/s*	
Ochnaceae							
Brackenridgea nitida	*3*	*0.7*	*dry*	*?*	*?*	*u/s*	
Proteaceae							
Cardwellia sublimis	*6*	*5.6*	*dry*	*wet*	*?*	*o/s*	
Carnavonia sp.	*5*	*1.8*	*wet*	*?*	*?*	*u/s*	
Carnavonia sp. code 231	*4*	*2.8*	*wet*	*wet*	*dry*	*o/s*	
Helicia lamingtoniana	*8*	*5.6*	*wet*	*extend*	*dry?*	*u/s*	
Lomatia fracsinafolia	*4*	*2.1*	*cts*	*wet*	*?*	*u/s*	
Opisthiolepis heterophylla	*5*	*3.5*	*cts*	*wet?*	*?*	*u/s*	
Stenocarpus sinuatus	*6*	*12.3*	*cts*	*wet*	*dry*	*o/s*	
Rhamnaceae							
Alphitonia petriei	*17*	*10.5*	*wet*	*dry*	*wet*	*o/s*	
Rutaceae							
Acronychia crassipetala	*5*	*8.1*	*cts?*	*wet*	*wet*	*u/s*	
Euodia sp. code 305	*5*	*18.6*	*cts*	*extend*	*extend*	*o/s*	
Flindersia bourjotiana	*5*	*9.1*	*dis*	*extend*	*extend*	*o/s*	
F. pimentaliana	*4*	*2.1*	*dis*	*?*	*?*	*o/s*	
F. brayleyana	*10*	*48.8*	*dis*	*dry*	*wet*	*o/s*	
Halfordia scleroxyla	*5*	*7.7*	*dry*	*wet*	*dry*	*u/s*	
Sapindaceae							
Arytera lauterana	*8*	*3.2*	*wet*	*dry*	*dry*	*u/s*	
Synima cordieri	*5*	*7.0*	*dis*	*extend*	*dry*	*o/s*	
Castanospora alphandii	*7*	*13.7*	*wet*	*dry*	*dry*	*u/s*	
Saxifragaceae							
Polyosma rhytophloia	*6*	*3.6*	*wet*	*dry*	*wet*	*u/s*	
Symplocaceae							
Symplocus cochinchinensis	*4*	*1.4*	*dis*	*extend*	*wet*	*u/s*	
Smilacaceae							
Smilax australis	*1*	****	*dis*	*extend*	*extend*	*u/s*	
Solanaceae							
Solanum veride	*2*	*1.1*	*cts*	*extend*	*extend*	*u/s*	

Vitiaceae						
Cissus hypoglauca	*1*	****	*dis*	*dry*	*wet*	*o/s*

= greater than 20cm DBH
** = all under 20cm DBH
wet season: November-April
dry season: May-October
cts = continuous leafing
dis = discreet leafing
extend = in both wet and dry seasons.
u/s = understorey species
o/s = overstorey species
? = unknown

Appendix B Table 2

Feeding records for *H. lemuroides*, *P. herbertensis*, *P. archeri*. Number of leaf feeding observations are denoted by L, blossum feeding records B, fruit feeding records F and unknown items ?. Species names after Hyland (1982); families after Clifford and Ludlow (1972).

Plant family and species	*P. archeri*	*P. herbertensis*	*H. lemuroides*
Apocynaceae			
Melodinus australis	*L*		
Araliaceae			
Cephalaralia sp.		*2L*	
Polyscias australiana		*2L*	
P. elegans		*2L*	
P. murrayi		*8L*	
Burseraceae			
Canarium baileyanum		*2L*	
Cunoniaceae			
Ceratopetalum succirubrum			*69L 2?*
Elaeocarpaceae			
Elaeocarpus arnhemicus			*8L*
E. foveolatus		*L*	*4L*
E. largiflorens			*2L 2?*
Sloanea langii		*L*	*206L*
S. macbrydeii			*L*
S. australis		*L*	
Elaeagnaceae			
Elaeagnus trifolia		*4L*	
Euphorbiaceae			
Aleurites moluccana		*L*	
Glochidion hylandii		*4L*	*2L ?*
Macarangia inamoena		*2L*	
M. subdentata			*L*
Flacourtiaceae			
Casearia sp.		*L*	*4L*
Scolopia braunii	*L*		*2L*
Lauraceae			
Beilschmiedia aff. obtusifolia			*9L*
B. bancroftii		*2L*	*35 6?*
Cryptocarya angulata			*17L*

C. corrugata			*L*
C. aff. corrugata			*L*
C. hypoglauca			*8L*
C. rigida	*5L*	*L*	*17L*
C. oblata		*L*	
C. triplinervis			*L*
Cryptocarya sp. code 1201			*L*
Cinnamomum laubatii			*L*
Endiandra sp. code 347			*L*
Endiandra sp. code 62			*81L*
E. muelleri		*L*	*12L*
E. palmerstonii			*3L*
E. sankeyana	*25L*		*4L 2?*
E. tooram	*L*		*10L*
Litsea leefeana	*7L*	*L*	*61L 8B*
Neolitsea dealbata			*2?*
Loranthaceae			
Amylotheca sp.			*4L 3? F*
Meliaceae			
Aglaia sapendina		*L*	
Synoum muelleri			*3L*
Menispermaceae			
Hypserpa sp.		*L*	
Mimosaceae			
Acacia melanoxylan			*3L*
Archidendrani vaillantii		*4L*	
Moniminaceae			
Daphnandra repandula	*L*		*5L*
Doryphora aromatica			*2B*
Moraceae			
Ficus destruens	*2L*		
F. leptoclada	*?*		
F. pleurocarpa	*20L F*		
F. watkinsoniana	*10L 5F*		
Mysinaceae			
Streblus glabar			*2L*
Myrtaceae			
Acmena resa		*7L F ?*	*1L 3F*
Syzygium cormiflora		*2L 8B 2F*	*20L 2F 5B*
S. kuranda			*6L*
S. luehmannii		*2L 4F*	*3F*
S. papyraceae		*2L 4B*	*2L*
S. trachyphloia		*2L*	
S. wesa		*L*	*L*
Rhodomyrtus trineura		*5L*	*L*
Ochnaceae			
Brackenridgea nitida			*L*

Proteaceae			
Cardwellia sublimis			12L
Carnavonia sp.	2L	3L	
Carnavonia sp. code 231	4L		3L
Darlingia ferruginea			11L B ?
Helicia lamingtoniana	4L	L	24L 13B 2?
Lomatia fracsinifolia		L	L
Opisthiolepis heteropylla	L	3L	15L
Stenocarpus sinuatus	2L	L	3L
Rhamnaceae			
Alphitonia petriei	L	122L B ?	17L 11F B
A. whiteii	L ?		13L B
Rosaceae			
Prunus turnerana			?
Rubiaceae			
Morinda sp.		L	
Rutaceae			
Acronychia crassipetala		5L 2F	L
Euodia sp. code 305	?	6L ?	21L
Flindersia bourjotiana		3L	9L ?
F. acuminata			4L
F. brayleyana		L	208L ?
F. pimentaliana			88L
Halfordia scleroxyla			L
Melicope fareana			L
Sapindaceae			
Arytera lauterana		L	2L
A. divaricata		L F	
Castanospora alphandii		5L	63L 3B 2?
Diploglottis bracteata		4L	5L
Synima cordieri		L	
Symplocaceae			
Symplocus cochinchinensis			L 3F
Sapotaceae			
Planchonella brownlessiana		4L B ?	2L
P. papyraceae		L	
P. xerocarpa		L	2L
Pouteria sp.		L	
Smilacaceae			
Smilax australis			L
Solanaceae			
Solanum veride	2L		
Sterculiaceae			
Brachychiton acerifolia	L		4L

Urticaceae		
Dendrocnide photinophylla	*2L*	
Vitiaceae		
Cissus hypoglauca	*8L*	
C. penninervis		*L*
Cissus sp.	*5L*	
unidentified tree #1256	*4L*	

Appendix C

Members of the 21 groups of plants identified by cluster analysis (polythetic divisive strategy to 20 divisions, using Numerical Taxonomy Package software kindly made available by the Australian Institute of Marine Science). The results of all food quality tests but that for alkaloids were included in the test.

Group 1

Casearia sp. - mature leaves

Group 2

Sloanea langii - mature leaves

Group 3

Flindersia bourjotiana - young leaves
Ficus watkinsoniana - young leaves
Cardwellia sublimis - young leaves

Group 4

Ceratopetalum succirubrum - young leaves
Elaeocarpus ruminatus - young leaves
Carnavonia sp. - mature leaves

Group 5

Opisthiolepis heterophylla - young leaves
Carnavonia sp 231 - young leaves

Group 6

Euodia sp. 305 - young leaves

Group 7

Flindersia brayleyana - mature leaves, young leaves

Group 8

Euodia sp. 305 - mature leaves
Polyscias murrayi - mature leaves, young leaves
Neolitsea dealbata - young leaves
Flindersia pimentaliana - mature leaves
Polyosma rhytophloia - mature leaves
Alphitonia petriei - young leaves

Group 9

Sloanea langii - young leaves

Group 10

Scolopia braunii - mature leaves
Carnavonia sp. code 231 - young leaves

Group 11

Neolitsea dealbata - mature leaves
Litsea leefeana - mature leaves
Cryptocarya rigida - young leaves
Stenocarpus sinuatus - mature leaves
Rhodomyrtus trineura - mature leaves

Group 12

Aglaia ferruginea - young leaves
Diploglottis bracteata - mature leaves

Group 13

Acmena resa - young leaves

Group 14

Litsea leefeana - young leaves

Group 15

Brackenridgea nitida - young leaves

Group 16

Alphitonia petriei - mature leaves

Group 17

Carnavonia sp. 231 - mature leaves
Cissus hypoglauca - mature leaves
Ficus watkinsoniana - mature leaves

Group 18

Endiandra sankeyana - young leaves
Opithiolepis heterophylla - mature leaves
Planchonella brownlessiana - young leaves
Cissus hypoglauca - young leaves

Group 19

Brackenridgea nitida - mature leaves
Castanospora alphandii - mature leaves, young leaves
Acmena resa - mature leaves
Lomatia fracsinofolia - young leaves
Rhodomyrtis trineura - young leaves
Ceratopetalum succirubrum - mature leaves
Arytera lauterana - mature leaves

Group 20

Macarangia inamoena - young leaves
Cryptocarya aff. corrugata - mature leaves
Elaeocarpus ruminatus - mature leaves
Acacia melanoxylan - mature leaves
Arytera lauterana - young leaves

Group 21

Elaeagnus triflora - mature leaves

APPENDIX D FOOD QUALITY

Table 1

The allelochemical content of leaves of selected species. Total phenols and condensed tannins measured in mg/ml of standard and alkaloids assessed on a 0 to 4 scale of increasing concentration. Leaf ages: 1. young foliage less than three weeks old; 2. mature leaves between one and 12 months.

Species	Leaf age	T.P#	C.T*	Alk.	%C.T/T.P.
Flindersia brayleyana	*2*	*.108*	*.104*	*0*	*96*
	1	*.398*	*.237*	*0*	*60*
Sloanea langii	*2*	*1.51*	*.001*	*0*	*0.1*
	1	*1.62*	*.000*	*0*	*0*
Elaeocarpus ruminatus	*2*	*.665*	*.000*	*0*	*0*
	1	*.845*	*.000*	*0*	*0*
Castanospora alphandii	*2*	*.322*	*n.d*	*1*	*n.d*
	1	*.229*	*n.d*	*0*	*n.d*
Endiandra sp. 62	*2*	*.268*	*.115*	*1*	*43*
Litsea leefeana	*2*	*.595*	*.534*	*0*	*90*
	1	*.939*	*.403*	*2*	*43*
Ceratopetalum succirubrum	*2*	*.379*	*n.d*	*n.d*	*n.d*
	1	*.164*	*n.d*	*n.d*	*n.d*
Flindersia pimentaliana	*2*	*.550*	*.233*	*4*	*42*
Acacia melanoxylan	*2*	*.449*	*n.d*	*2*	*n.d*
Euodia sp. 305	*2*	*.250*	*.000*	*2*	*0*
	1	*.170*	*.000*	*2*	*0*
Cryptocarya rigida	*2*	*.506*	*.403*	*0*	*80*
	1	*.542*	*.372*	*0*	*69*
Alphitonia petriei	*2*	*.631*	*.002*	*1*	*0.3*
	1	*.555*	*.000*	*2*	*0*
Acmena resa	*2*	*.549*	*.167*	*0*	*30*
	1	*1.10*	*.089*	*3*	*8*
Polyscias murrayii	*2*	*.274*	*.018*	*0*	*7*
	1	*.703*	*.001*	*0*	*0.1*
Planchonella brownlessiana	*2*	*.468*	*.439*	*0*	*94*
	1	*.470*	*.160*	*0*	*34*
Endiandra sankeyana	*1*	*.677*	*.162*	*n.d*	*24*
Ficus watkinsoniana	*2*	*.116*	*.051*	*0*	*44*
	1	*.070*	*.010*	*0*	*14*
Cissus hypoglauca	*2*	*.314*	*.000*	*2*	*0*
	1	*.388*	*.000*	*1*	*0*
Carnavonia sp. 231	*2*	*.232*	*.101*	*1*	*44*
	1	*.460*	*.119*	*0*	*26*
Elaeagnus triflora	*2*	*2.57*	*.024*	*2*	*0.9*
Stenocarpus sinuatus	*2*	*.290*	*.052*	*0*	*18*
Arytera lauterana	*2*	*.401*	*.326*	*0*	*81*
	1	*.838*	*.683*	*0*	*82*
Cardwellia sublimis	*1*	*.489*	*.006*	*0*	*1*
Diploglottis bracteata	*2*	*.864*	*.609*	*4*	*70*

Carnavonia sp.	*2*	*.835*	*.819*	*0*	*98*
Casearia sp.	*2*	*.830*	*.361*	*0*	*44*
Polyosma rhytophloia	*2*	*.131*	*.002*	*1*	*1*
Lomatia fracsinofolia	*1*	*.192*	*.162*	*0*	*43*
Opisthiolepis heterophylla	*2*	*.374*	*.834*	*0*	*223*
	1	*.116*	*.476*	*0*	*410*
Macarangia inamoena	*1*	*.868*	*.003*	*0*	*0.4*
Neolitsea dealbata	*2*	*.300*	*.285*	*4*	*95*
	1	*.201*	*.181*	*0*	*90*
Brackenridgea nitida	*2*	*.474*	*.671*	*0*	*142*
	1	*.410*	*.452*	*0*	*110*
Rhodomyrtis trineura	*2*	*.450*	*.265*	*3*	*59*
	1	*.360*	*n.d*	*1*	*n.d*
Aglaia sapendina	*1*	*.759*	*.839*	*4*	*111*
Scolopia braunii	*2*	*.350*	*.225*	*0*	*62*
Flindersia bourjotiana	*1*	*.389*	*n.d*	*1*	*n.d*

Total phenols in mg/ml gallic acid
* Condensed tannins in mg/ml Eucalyptus regnans kino

Table 2

Fibre fractions and crude protein (% dry weight) of: (1) young foliage less than approximately 3 weeks old and (2) mature foliage between one and 12 months old. L:P is the ratio between lignin and crude protein content of the leaves. TY denotes the group to which the plant item belongs: type I is often low in fibre and higher in crude protein than type II which tends to be higher in fibre and have less crude protein; OL denotes outlying species which belong to neither group (refer to text).

Species	AGE	%PROTEIN	NDF	ADF	LIGN.	CELL.	L:P	TY
F. brayleyana	*2*	*10.63*	*27.96*	*17.33*	*3.01*	*14.52*	*.28*	*I*
	1	*7.81*	*20.28*	*16.21*	*3.76*	*12.61*	*.53*	*I*
S. langii	*2*	*9.44*	*34.63*	*25.88*	*8.98*	*17.73*	*.95*	*I*
	1	*10.63*	*31.13*	*15.76*	*4.66*	*10.64*	*.44*	*I*
E. ruminatus	*2*	*12.81*	*50.92*	*31.63*	*15.87*	*17.74*	*1.24*	*II*
	1	*14.75*	*37.25*	*31.65*	*17.08*	*14.41*	*1.16*	*I*
C. alphandii	*2*	*10.88*	*53.39*	*42.16*	*17.59*	*29.39*	*1.62*	*II*
	1	*12.31*	*49.78*	*43.87*	*12.36*	*28.03*	*1.00*	*II*
Endiandra sp. 62	*2*	*15.13*	*33.56*	*25.11*	*7.29*	*18.62*	*.48*	*I*
L. leefeana	*2*	*15.50*	*57.79*	*44.49*	*21.39*	*22.48*	*1.38*	*II*
	1	*17.50*	*55.20*	*40.41*	*14.83*	*22.67*	*.85*	*II*
C. succirubrum	*2*	*7.88*	*48.96*	*42.60*	*13.43*	*28.25*	*1.70*	*II*
	1	*13.25*	*39.20*	*34.98*	*16.03*	*12.85*	*1.21*	*I*
F. pimentaliana	*2*	*15.00*	*26.59*	*17.75*	*8.47*	*12.03*	*.57*	*I*
A. melanoxylon	*2*	*17.44*	*45.55*	*38.53*	*13.57*	*24.62*	*.78*	*II*
Euodia sp. 305	*2*	*20.31*	*26.41*	*22.58*	*6.11*	*15.27*	*.30*	*I*
	1	*24.38*	*22.88*	*14.65*	*3.00*	*12.19*	*.12*	*I*
C. rigida	*2*	*12.31*	*59.58*	*50.49*	*20.80*	*29.81*	*1.69*	*II*

	1	13.44	54.33	49.13	22.20	22.84	1.65	II
A. petriei	2	15.56	55.80	39.20	23.64	17.39	1.52	II
	1	17.31	31.76	21.73	9.11	13.82	.53	I
A. resa	2	10.88	54.33	41.45	18.05	23.36	1.66	II
	1	12.69	51.69	40.36	29.22	22.24	2.30	OL
P. murrayi	2	16.50	25.77	16.39	7.06	8.62	.43	I
	1	16.88	24.89	22.03	11.76	10.45	.69	I
P. brownlessiana	2	8.13	n.d	39.04	11.94	25.77	1.47	II
	1	7.75	49.97	44.05	9.87	22.84	1.27	II
E. sankeyana	1	10.25	39.58	36.68	5.99	24.94	.58	II
F. watkinsoniana	2	8.38	56.83	36.71	17.23	19.62	2.06	II
	1	7.44	39.05	21.01	4.60	17.34	.62	I
C. hypoglauca	2	8.63	54.65	37.97	20.24	18.16	2.35	II
	1	7.63	41.10	36.20	13.42	21.85	1.76	II
Carnavonia	2	7.69	52.55	38.23	20.96	15.61	2.73	II
sp. 231	1	11.88	68.50	56.57	23.55	35.03	1.98	II
E. triflora	2	21.19	57.66	50.79	27.38	24.50	1.29	OL
S. sinuatus	2	8.81	58.15	49.97	19.34	28.45	2.20	II
A. lauterana	1	12.69	48.64	41.39	13.97	27.46	1.10	II
	1	13.19	47.35	40.41	13.51	24.94	1.02	II
C. sublimis	1	10.63	38.48	25.87	9.22	18.29	.87	I
D. bracteata	2	16.88	60.38	44.78	19.60	26.81	1.16	II
Carnavonia sp.	2	13.38	39.78	32.43	18.34	13.19	1.37	I
Casearia sp.	2	26.94	38.32	27.56	9.30	18.86	.35	OL
P. rhytophloia	2	13.31	29.31	22.48	8.99	12.17	.68	I
L. fracsinofolia	1	8.06	55.00	41.99	14.50	28.64	1.80	II
O. heterophylla	2	11.25	47.52	37.12	10.01	25.72	.89	I
	1	13.75	50.42	26.93	7.24	19.51	.53	II
M. inamoena	1	15.88	46.77	37.98	14.05	23.67	.89	II
N. dealbata	2	11.63	58.48	49.79	21.98	26.99	1.89	II
	1	15.25	24.14	18.69	7.73	10.57	.51	I
B. nitida	2	10.81	57.79	44.28	14.74	27.48	1.36	II
	1	19.38	50.47	37.82	19.45	14.69	1.00	II
R. trineura	2	9.50	59.53	47.74	26.90	21.98	2.83	II
	1	9.68	49.59	42.42	17.24	24.67	1.78	II
A. ferruginia	1	18.00	61.36	44.23	17.49	29.02	.97	II
S. braunii	2	10.63	70.40	54.67	21.30	37.61	2.00	II
F. bourjotiana	1	7.81	39.71	24.84	10.33	15.85	1.32	I

Table 3

Water content (% fresh weight) and leaf toughness of (1) young and (2) mature foliage as defined in Tables 6.1 and 6.2 of favoured food species. Leaves were dried for 48 hours at 500C then 1 hour at 1000C. Leaf toughness is the weight of water plus beaker in grams required to puncture the leaf (average of 8 trials per species).

Species	Leaf age	Water content %	Leaf toughness (g)
Alphitonia petriei	*2*	*78.2*	*1228*
	1	*80.5*	*509*
Carnavonia sp. 231	*2*	*75.8*	*1324*
	1	*80.7*	*519*
Acmena resa	*2*	*75.8*	*1299*
	1	*73.3*	*974*
Polyscias murrayi	*2*	*67.5*	*1012*
	1	*79.1*	*281*
Sloanea langii	*2*	*53.9*	*1669*
	1	*70.9*	*322*
Elaeagnus triflora	*2*	*65.8*	*905*
	1	*72.0*	*881*
Flindersia brayleyana	*2*	*63.7*	*1292*
	1	*70.6*	*983*
Flindersia pimentaliana	*2*	*67.7*	*761*
	1	*71.6*	*502*
Castanospora alphandii	*2*	*64.4*	*1488*
	1	*73.8*	*510*
Opisthiolepis heterophylla	*2*	*61.7*	*1381*
	1	*65.7*	*817*
Endiandra sankeyana	*2*	*45.9*	*1933*
	1	*68.7*	*621*
Ficus watkinsoniana	*2*	*66.8*	*1454*
	1	*71.8*	*817*
Casearia sp.	*2*	*57.9*	*1711*
	1	*62.0*	*1101*
Cryptocarya rigida	*2*	*45.7*	*1047*
	1	*61.3*	*845*
Cardwellia sublimis	*2*	*59.8*	*1462*
	1	*67.3*	*583*
Carnavonia sp.	*2*	*51.9*	*1324*
	1	*69.1*	*709*
Cissus hypoglauca	*2*	*63.7*	*1359*
	1	*73.0*	*663*
Litsea leefeana	*2*	*44.5*	*1139*
	1	*70.2*	*322*
Elaeocarpus ruminatus	*2*	*64.6*	*945*
	1	*71.6*	*887*
Euodia sp. 305	*2*	*71.9*	*872*
	1	*74.9*	*100*
Planchonella brownlessiana	*2*	*59.3*	*1060*
	1	*69.9*	*923*

Table 4

Ten most preferred food items ranked by number of feeding observations

	Leaf age†	No. of Feeding Observations
H. lemuroides		
Flindersia brayleyana	GL	123
Sloanea langii	GL	114
Elaeocarpus ruminatus	OL	106
Sloanea langii	OL	92
Flindersia brayleyana	OL	86
Flindersia pimentaliana	OL	77
Endiandra sp. 62	OL	70
Castanospora alphandii	OL	49
Ceratopetalum succirubrum	OL	42
Litsea leefeana	OL	37
P. herbertensis		
Alphitonia petriei	GL	74
Alphitonia petriei	OL	49
Elaeocarpus ruminatus	OL	13
Elaeocarpus ruminatus	GL	8
Polyscias murrayi	GL	6
Acmena resa	OL	5
Castanospora alphandii	GL	5
Euodia sp. 305	GL	4
Diploglottis bracteata	OL	4
Elaeognus triflora	OL	3
P. archeri		
Endiandra sankeyana	GL	14
Ficus watkinsoniana	OL	11
Litsea leefeana	GL	6
Cryptocarya rigida	GL	5
Cissus hypoglauca	OL	5
Cissus hypoglauca	GL	3
Carnavonia sp. 231	GL	2
Carnovonia sp. 231	OL	2
Euodia sp. 305	OL	1
Opisthiolepis heterophylla	OL	1

† GL = young leaves; OL = mature leaves

Table 5

The nutritional factors affecting the ranking of food items in the diets of the three possum species. *n* is the number of ranked species for which there are nutritional data. The nutritional data for these species were correlated (Spearman rank correlation, r_s) with feeding preferences determined by number of feeding observations.

	r_s	p	n
H. lemuroides			
ADF	0.336	n.s.	22
lignin	0.395	<0.05	22
NDF	0.397	<0.05	22
lignin:protein	0.350	n.s.	22
protein	-0.161	n.s.	22
T.P.	-0.196	n.s.	22
C.T.	0.340	n.s.	18
cellulose	-0.373	n.s.	22
toughness	0.287	n.s.	22
P. herbertensis			
ADF	0.154	n.s.	17
lignin	-0.179	n.s.	19
NDF	0.036	n.s.	19
lignin:protein	-0.247	n.s.	19
protein	0.166	n.s.	19
T.P.	-0.147	n.s.	19
C.T.	0.547	<0.02	16
cellulose	-0.2054	n.s.	17
toughness	0.136	n.s.	17
P. archeri			
ADF	-0.349	n.s.	13
lignin	0.022	n.s.	13
NDF	0.622	<0.02	13
lignin:protein	0.622	<0.02	13
protein	-0.409	n.s.	13
T.P.	0.190	n.s.	13
C.T.	0.173	n.s.	9
cellulose	0.406	n.s.	13
toughness	-0.012	n.s.	18