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ECOLOGY OF GREATER GLIDERS, *PETAUROIDES VOLANS* KERR 1792,  
IN RELATION TO VARIATIONS IN HABITAT QUALITY IN EUCALYPT  
FORESTS IN SOUTH-EAST NEW SOUTH WALES

by

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A thesis submitted for the degree of Doctor of Philosophy of The  
Australian National University from the Department of Forestry.

January 1988



The Greater Glider :-  
*Petauroides volans* Kerr  
(Marsupialia : Pseudocheiridae)

(drawing by Jann E. Williams)

### Originality of Thesis

Except where otherwise acknowledged, this thesis is my own original work.

A handwritten signature in dark ink, appearing to read 'T.W. Norton', with a long horizontal flourish extending to the right.

T.W. Norton



## SUMMARY

L.W. Braithwaite and co-researchers hypothesised that the population density and diversity of the arboreal marsupial fauna of the eucalypt forests near Eden, New South Wales were primarily determined by the concentrations of nitrogen, phosphorus and potassium in the mature foliage of the eucalypts. I investigated this hypothesis in relation to the Greater Glider *Petauroides volans*.

The first main objective of my study was to examine why population densities of *P. volans* are low in eucalypt forests with relatively low concentrations of nutrients in their mature foliage and high in eucalypt forests with relatively high concentrations of nutrients in their mature foliage. Initially, several *a priori* hypotheses were proposed that could account for the observed population densities of *P. volans* in these forests, and these were tested at two forest sites in south-eastern N.S.W. by studying and comparing the ecology of *P. volans* at these sites.

One site of 24.6 ha at Wadbilliga carried four species of eucalypt (*E. dalrympleana*, *E. fastigata*, *E. radiata*, *E. viminalis*). These had high concentrations of N and P in their mature foliage when compared to the range of values known for foliar N and P in this genus. The other site of 50.1 ha was at Morton and consisted of 40.3 ha of two species of eucalypts, *E. gummifera* and *E. piperita*, which formed 'forest type A'. Two smaller areas, termed 'forest types B and C', within the Morton site also supported other eucalypt species, *E. sieberi* at forest type B and *E. consideniana*, *E. pellita* and *E. sieberi* at forest type C. The nutrient concentration in the mature foliage at Morton was generally lower than at Wadbilliga. Basal area and height of the eucalypts, and the relative concentrations of N and P in their mature

foliage suggested an apparent decline in forest site productivity from Wadbilliga through Morton forest types C, B and A. The change in the ratio of *Symphyomyrtus* to *Monocalyptus* eucalypts across these forests also was consistent with the presence of a decline in productivity. Many aspects of the social organisation of *P. volans* were related to this decline.

There was a marked difference in the distribution of resident adult *P. volans* at the two sites. Gliders at Wadbilliga had a relatively even distribution across the site and most of the site was permanently occupied. In contrast, gliders at Morton had an extremely clumped distribution. The majority of the site was unoccupied (forest type A) and resident animals were restricted to forest types B and C which appeared to be the only favourable habitats within the site.

The population density of *P. volans* did not appear to be related to forest site productivity. Based on the entire area of the site, the number of resident adult *P. volans* per hectare was 0.18 at Morton; but on the basis of the area of forest apparently suitable for occupation the population density of gliders was 0.89 animals ha<sup>-1</sup> in forest type B and 1.67 animals ha<sup>-1</sup> in forest type C. This was then higher than the population density of *P. volans* at Wadbilliga (0.88 animals ha<sup>-1</sup>). In contrast, the annual fecundity of the populations of *P. volans* was related to forest site productivity. Resident animals at Wadbilliga and Morton forest type C successfully raised young during each year of the study but those in Morton forest type B did not, although their social cycle was comparable to gliders elsewhere.

Neither Wadbilliga nor Morton appeared to have experienced major disturbances such as wildfire in recent years, and neither predation nor the availability of den sites appeared to influence the distribution of resident gliders. The majority of data on the behaviour and feeding ecology of *P. volans* were consistent with the following observations. The observed distribution and fecundity of *P. volans* in each forest appeared to be related to the availability of high-quality food and this factor was an important determinant of habitat quality. At Morton, for example, the amount of such foods in forest type A was considered to be insufficient to support resident *P. volans*. Although high-quality food was available in forest type B, the amount of this food, at least during the study, was insufficient for successful production of offspring by resident *P. volans*.

The foraging behaviour of *P. volans* at both sites differed little. All gliders attempted to maintain a high intake of new leaf growth in their diet in all seasons so foraging was closely related to the spatial and temporal availability of this food. Female *P. volans* at Wadbilliga and Morton forest type C, for example, spent less time foraging and were able to meet the majority of their annual food requirements from a smaller area of forest compared to females in Morton forest type B. As a consequence, females at Wadbilliga and Morton forest type C also probably expended less energy foraging compared to those in Morton forest type B. These data, combined with those on forest site productivity and eucalypt phenologies, were consistent with the hypothesis that the availability of high-quality food was higher at Wadbilliga and Morton forest type C compared to that at Morton forest type B and particularly Morton forest type A.

*P. volans* consistently foraged for and browsed eucalypt foliage that was high in nitrogen concentration. However, my data were insufficient to implicate foliar nitrogen as the ultimate factor determining browse selection by this species. Clearly, many other foliar constituents, either independent of or in association with nitrogen, may be implicated in browse selection and influence the dietary quality of foliage for *P. volans*.

New data on aspects of the ecology of *P. volans* that are relevant to its management are presented. A polygyny threshold model that may account for all of the known data on the distribution, population fecundity and mating associations (i.e. monogamy or facultative monogamy) exhibited by *P. volans* throughout its range is given. Application of this model may have considerable potential for identifying the high-quality habitat required by *P. volans*.

Finally, areas warranting further research are outlined.

## ACKNOWLEDGEMENTS

This story began in mid-1983. I was sitting at home in Devonport, Tasmania reading the latest edition of *Aust. Wildl. Res.*, which had just arrived. I can remember reading the papers by Braithwaite and Braithwaite *et al.* and thinking 'Wow, this is really interesting, I wonder if it's true (the nutrient hypothesis)' ....

Lots of people helped me bridge the 'gap' between Devonport and Canberra, especially Helen and Mick Statham, Chris Bryant, Penny Gullan, Stuart Davey, Mick Tanton and Wayne Braithwaite. Ta!

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This study is dedicated to Nan, Jann, Trev and Australia, a continent of peace where, *currently*, we can still enjoy, study and learn from the subtleties of our natural environment.

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## CHAPTER 1

### GENERAL INTRODUCTION

#### 1.1 INTRODUCTION

Conservation of fauna is one objective in the multiple-use of native forests in Australia. An essential prerequisite for this is the acquisition of basic knowledge on the causes of the distribution and abundance of forest-dependent fauna. However, as recently as about a decade ago several scientists published warnings that the knowledge of Australia's forest-dependent fauna was minimal, despite this fauna potentially being extremely sensitive to intensive forestry management practices (Tyndale-Biscoe and Calaby 1975; McIlroy 1978). Fortunately this situation is changing and considerable research has been undertaken more recently on the ecology of many segments of this forest-dependent fauna, including the arboreal marsupial species (Friend 1980; Recher *et al.* 1980; Suckling 1982; Braithwaite *et al.* 1984a; Keast *et al.* 1985; Taylor and O'Neill 1986; Norton 1987a,b).

A recent broad-scale study on the arboreal marsupial fauna of the eucalypt forests being harvested for woodpulp at Eden, New South Wales has provided insight into some of the factors which may influence the distribution and abundance of these fauna (Braithwaite 1983; Braithwaite *et al.* 1983; Braithwaite *et al.* 1984b). Braithwaite *et al.* (1983) found gross disparities in the distribution and population density of the Greater Glider *Petauroides volans*, Feathertail Glider *Acrobates pygmaeus*, Sugar Glider *Petaurus breviceps*, Yellow-bellied Glider *Petaurus australis*, Brushtail Possum *Trichosurus vulpecula*, Ringtail Possum *Pseudocheirus peregrinus*, Eastern Pygmy Possum *Cercartetus nanus* and Squirrel Glider

*Petaurus norfolcensis*. In 199 coupes (2890 ha) or 52 per cent of the forest area felled, no animals were found. Sixty-three per cent of all the animals found came from only 9 per cent of the forest area that was managed for wood production (Braithwaite 1983).

The population density of each species of arboreal marsupial was greatest in the same general areas of forest, these being characterised by their flat to undulating topography, their infrequent severe burning, a high degree of forest maturity, high floristic diversity and the occurrence of the eucalypt species *Eucalyptus radiata*, *E. dives* and *E. elata* known as peppermints (Braithwaite 1983). Further analyses led Braithwaite *et al.* (1983) to hypothesise that a gradient in nutrient concentration (i.e. nitrogen, phosphorus, potassium) in mature foliage of the eucalypts was the major determinant of the population density and diversity of arboreal marsupials in the Eden forests. The maximum densities and diversity of arboreal marsupial fauna generally occurred in forest types characterised by eucalypt species with a high concentration of nutrients in their mature foliage.

There were several problems\* associated with the statistical analysis (e.g. the interdependence of many of the habitat variables measured) and interpretation of the data collected in the above study however, and it remained speculative in several areas.

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\*The authors recognised these problems. More recently their original research area has been enlarged to encompass a wider portion of south-east N.S.W. (Considine 1985) thus facilitating a broad-scale examination of some of the hypotheses generated by the earlier research (L.W. Braithwaite, C.S.I.R.O. Division of Wildlife and Rangelands Research, Canberra A.C.T., pers. comm.).

For example, although a statistical correlation between the population density and diversity of arboreal marsupial herbivores (Table 1.1) and foliar nutrients was demonstrated, the correlation may have been a secondary one. In this case these nutrients would vary more or less in the same way as the primary determinants for selection. Further difficulty arises in interpretation when the non-herbivorous species sampled by Braithwaite *et al.* (1983) (Table 1.1) are considered. These species showed a similar correlation to the browsing herbivores, implying that in the case of both feeding categories the relationship may have been secondary (indirect). In this case the relatively high level of nutrients may act as an indicator of the general quality of the trees as habitat.

Knowledge of the form of the correlations between the population density and diversity of arboreal marsupials and the concentration of foliar nutrients in mature eucalypt leaves is important for two main reasons. First, it may provide new insight into some of the biological factors which affect the ecology of these fauna both regionally and possibly elsewhere. This in turn may facilitate the formulation of new hypotheses for testing. Second, such knowledge, even if the correlation is not directly related to easily determined nutrient concentrations but to co-varying parameters, may enable reliable prediction of the location of potential high-quality habitat for arboreal marsupials elsewhere in the general region and possibly more widely in south east Australia. Knowledge of the form of the correlation may also indicate its spatial and/or temporal robustness as well as the means by which such change might occur. This knowledge may have applications for the long-term management of these fauna.

Table 1.1. Feeding categories (following Lee and Cockburn 1985) of the arboreal marsupials sampled by Braithwaite (1983) and Braithwaite *et al.* (1983) during their study at Eden, N.S.W. Note that the Koala is also included. This species was not sampled but is known to occur in the region.

Species	Feeding category
<i>Acrobates pygmaeus</i>	nectarivore
<i>Cercartetus nanus</i>	" (some fruit and insects)
<i>Petaurus breviceps</i>	exudate feeder/insectivore
<i>P. australis</i>	" "
<i>P. norfolcensis</i> (most probably)	" "
<i>Pseudocheirus peregrinus</i>	browsing herbivore
<i>Trichosurus vulpecula</i>	" "
<i>Petauroides volans</i>	" "
<i>Phascogale carolinensis</i>	" "

## 1.2 OBJECTIVES

The purpose of this study was to investigate the correlation originally described by Braithwaite *et al.* (1983). However, from its outset, the study was limited by time and logistic constraints which restricted the investigation to one species of arboreal marsupial, the Greater Glider *Petauroides volans* Kerr 1792 (see Frontispiece; Table 1.1). This species appeared to demonstrate the strongest response to the nutrient gradient proposed by Braithwaite *et al.* (1983) and it is probably the most abundant arboreal, browsing herbivore in the south east region of N.S.W. A comparative approach was adopted for the study, but the lack of data on the comparative ecology of *Petauroides volans* in eucalypt forests with a high and low concentration of nutrients (N,P,K) in the mature foliage necessitated a relatively broad approach. As a consequence, the objectives of the study were limited to the extent that it was not possible to elucidate the specific form of the correlation. Instead, the general nature of the correlation was indicated. This enabled the formulation of more specific hypotheses for testing the form of the correlation at a later stage.

The two main objectives were:

1. To examine why population densities of *Petauroides volans* are low in eucalypt forests with relatively low concentrations of nutrients (N,P,K) in mature foliage of the eucalypts and high in eucalypt forests with relatively high concentrations of nutrients in their mature foliage.
2. To identify further research that potentially could improve our understanding of the ecology of *P. volans* and, hopefully, shed more light on the general ecological relationships between arboreal (marsupial) browsing herbivores and their habitat.

### 1.3 INVESTIGATION

Review of the literature concentrated on the theoretical and observed constraints imposed by the feeding niche occupied by arboreal, browsing herbivores and also on the adaptations exhibited by these species to overcome such constraints. This material is covered in Chapter 2.

Field research initially involved formulating *a priori* hypotheses which could account for the observed distribution and abundance of *P. volans*. Appropriate methods and forest study sites were selected to facilitate the testing of these hypotheses and were followed by field research. Data collected were then analysed and interpreted in relation to the *a priori* hypotheses, the known ecology of *P. volans* and the life histories exhibited by several other mammal species exploiting the arboreal herbivore niche. This material is covered in Chapters 3-6.

A general discussion of the social organisation, behaviour and feeding ecology exhibited by *P. volans* during the field study in relation to the research objectives and the life histories of other mammals exploiting the same niche is presented in Chapter 7. The theoretical and practical implications of the field research are also dealt with in this Chapter, together with areas of study warranting further research.



## CHAPTER 2

### CONSTRAINTS OF THE ARBOREAL MAMMALIAN HERBIVORE NICHE

#### 2.1 INTRODUCTION

This chapter considers some of the general constraints that may impinge on mammals exploiting the arboreal herbivore niche. It also describes some of the apparent adaptations exhibited by herbivores to minimise these constraints.

The topic is broad and diverse and our knowledge is by no means complete. Several aspects of this knowledge have been covered in recent reviews (e.g. Energetics: McNab 1986; Evolutionary ecology: Eisenberg 1981; Smith and Lee 1984; Lee and Cockburn 1985; Digestion: Cork 1981; Hume 1982; Van Soest 1982; Cork 1984; Demment and Van Soest 1985; Foraging theory: Westoby 1974; Pyke 1984; Reproductive physiology: Tyndale-Biscoe and Renfree 1987; Secondary compounds: Swain 1978; Hume 1982; Robbins *et al.* 1987). The following discussion summarises aspects of these reviews and other sources of literature pertinent to my study.

#### 2.2 FOLIAGE AS FOOD

Two characteristics of leaves appear to have influenced markedly the ecology of all mammals that utilise them as food. These are (i) relatively low nutritional value and (ii) significant change in nutritional quality with age. These characteristics impinge on arboreal herbivores in a variety of ways.

##### 2.2.1 Body size constraints

The relatively low nutritional value of leaves (Cork 1981; Hume 1982; Van Soest 1982), coupled with the nature of the substrate being exploited, appears to have been an important extrinsic determinant

of the range of body size of mammals that could successfully exploit the arboreal herbivore niche.

With the exception of rodents (e.g. voles, lemmings, rats), the minimum adult body weight of all mammalian herbivores is about 0.6 kilograms. It is generally assumed that this size constraint is a result of the allometric relationships between the energy requirements, gut capacity and body weight of mammals (Demment and Van Soest 1985). The best data for explaining these allometric relationships are derived from studies on terrestrial mammalian herbivores (Bell 1971; Jarman 1974; Demment and Van Soest 1985). Total metabolic rate is related to the 0.75 power of body weight in eutherians (Kleiber 1961), thus large species appear to be better adapted to utilise low-energy fibrous plant tissues than small species (Hungate *et al.* 1959; Bell 1969; Field 1972; Janis 1976; Sinclair 1977; Krebs 1978; Parra 1978) since their energetic requirements for both basal metabolism and free-existence are considerably lower per unit body weight (Dawson and Hulbert 1970; Gessaman 1973; Nagy 1980; Peters 1983; Peters and Wassenberg 1983; Demment and Van Soest 1985; Nagy 1987). As a consequence, small herbivores would require a faster intake of a given diet and/or a faster release of energy from that diet, to maintain energy equilibrium, when compared to large herbivores. However, since the rate of microbial fermentation of plant fibre appears to be limited (Parra 1978; Hume 1982) small herbivores would need to eat more of a given fibrous diet than larger herbivores, per unit body weight, to maintain energy equilibrium. Several studies show, however, that as food intake increases so does the rate of food passage through the gut (Cork 1981), which, in turn, decreases the digestibility of the plant fibre (Parra 1978) and thus the net dietary energy gain. While small herbivores could compensate for this by increasing food intake even further, there appears to be <sup>an</sup> ~~f~~ upper limit of food intake set by gut capacity (Cork

1981; Hume 1982). Since gut capacity generally decreases as a proportion of body weight as body weight decreases (Parra 1978), small herbivores would be expected to be less capable of meeting their energetic requirements from a fibrous diet than large herbivores.

In contrast, the maximum size constraint imposed on arboreal herbivores is directly related to the ability of the vegetation to carry the weight of the animal without breaking (Fleagle 1978) and the need for efficient foraging, a behaviour that is seriously impaired when an animal becomes too large (Clutton-Brock and Harvey 1977; Eisenberg 1978; Grand 1978). Thus, while terrestrial herbivores may grow to several tonnes in body weight, the upper body weight in arboreal herbivores is about 25 kilograms (Table 2.1).

The restricted range of body size available to arboreal herbivores should influence all the aspects of their ecology dependent on body mass.

#### 2.2.2 Digestive constraints

Leaves have cell walls formed by the structural carbohydrates cellulose, hemicellulose and lignins, and these enclose the cell contents which contain many compounds, including lipids, starch, sugars, soluble proteins, vitamins and amino acids. The cell contents may be almost totally digested by mammals but the structural carbohydrates of the cell walls can only be efficiently degraded with the aid of cellulase enzymes (Moir 1965, 1967; Bauchop 1978) which are not synthesised by mammals. The mammalian herbivores rely on gut micro-organisms which produce cellulases to degrade structural carbohydrates.

Table 2.1 Mean male and female body weight of a range of extant species of arboreal mammalian herbivores. For letters following the species name, interpretation is: A - may not be representative of genus; B - based on one captured female specimen; C - mean value for species.

Species	Mean male body weight (kg)	Mean female body weight (kg)	Source
<i>Nasalis larvatus</i>	24.0	12.0	2
<i>Colobus guereza</i>	14.5	10.0	2
<i>Dendrolagus bennettiansus</i> <sup>A</sup>	13.0	-	3
<i>Phascogalea cinereus</i>	11.8	7.9	3
<i>Indri indri</i>	10.0	10.0	2
<i>Alouatta</i> spp.	7.5	5.7	2
<i>Presbytis obscura</i> <sup>A</sup>	7.4	6.5	2
<i>Simias concolor</i> <sup>B</sup>	-	7.2	2
<i>Bradypus variegatus</i>	3.7	3.5	1
<i>Petauroides volans</i> <sup>C</sup>	1.2		3
<i>Pseudocheirus Archeri</i> <sup>C</sup>	1.19		3
<i>P. herbertensis</i> <sup>C</sup>	1.07		3
<i>Hemibelideus lemuroides</i> <sup>C</sup>	0.97		3
<i>Pseudocheirus peregrinus</i> <sup>C</sup>	0.9		3

Sources: 1. Goffart 1971  
 2. Kavanagh 1983  
 3. Strahan 1983

The nutritional value of leaves as food for herbivores depends primarily on (i) the ability of an animal to degrade efficiently the cell wall fraction and access the cell contents (digestive adaptations), (ii) the proportion of cell wall to cell content fractions in the leaf (nutritional quality) and (iii) the energetic cost of procurement (foraging behaviour). Points (i) and (ii) are considered in further detail below.

### 2.2.3 Digestive adaptations

With the exception of the primate family Colobinae, the marsupial genus *Dendrolagus* and the sloths, all of which have enlarged fore-stomachs (Bauchop and Martucci 1968; Goffart 1971; Bauchop 1978; Cork 1981), arboreal herbivores exhibit to varying degrees an expansion of portions of the hindgut (e.g. caecum, proximal colon) (Milton 1980; Cork 1981; Hume 1982; Hume *et al.* 1984). It is generally assumed that this expansion is to allow for fermentation processes\* (c.f. *Phascolarctos cinereus*, below). The indriids, for example, have simple although capacious stomachs (Hill 1953) but they have greatly elongated caeca and colons which occupy the entire posterior region of the abdomen; the lower intestine and the caecum also exceeds total body length (Hladik 1967). Most soluble nutrients are probably extracted in the stomach and small intestine while the remaining fibrous material is

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\*The literature concerning the mechanisms of these fermentation processes are not relevant in detail to this study. Readers are referred to reviews by Bauchop (1978), Parra (1978), Hume and Warner (1980), Cork (1981), and Hume (1982).

passed into the specialised lower intestine for fermentation by gut micro-organisms (Milton 1980). Development of the caecum in *Petauroides volans* is also relatively extensive and its contents constitute 11-13% of body weight (Cork 1981; Hume 1982; Hume *et al.* 1984).

Although the caecum and proximal colon of *Phascolarctos cinereus* are relatively very large, Cork (1981) in particular has demonstrated that the greater part of the energy assimilated and utilised by this species is derived from cell contents rather than from cell walls (i.e. products of fermentation). Thus, expansion of the caecum and proximal colon in this species appears related to several functions including selective retention of fluid and digesta particles as well as fermentation processes.

The rate of passage of digesta through the gut of those arboreal herbivores which have been studied is remarkably slow. Montgomery and Sunquist (1978) found that the Three-toed Sloth *Bradypus variegatus* defaecates on average once every 8 days and that the estimated 5 per cent and 95 per cent excretion times for a given meal were 2.5 and 50 days, respectively. Passage of food in arboreal marsupial herbivores feeding on *Eucalyptus* leaves is also slow compared to other herbivores of similar or even much larger size (Warner 1981; Cork and Warner 1983; Hume *et al.* 1984) (Table 2.2). Ringtail possums, for example, had a mean retention time (MRT- the average time spent by each digesta fraction within the gut) of 70 hours for solutes and 37 hours for particles (Chilcott and Hume 1984b). The size distribution of digesta particles along the digestive tract suggest that fine particles are selectively retained, with solutes, relative to large particles in the hindgut of *Phascolarctos cinereus*, *Petauroides volans* and *Pseudocheirus peregrinus* but not in *Trichosurus vulpecula* (Table 2.2).

Table 2.2 Digestive adaptations, including rates of passage of digesta, of selected arboreal marsupial herbivores fed on eucalypt foliage. Note that there appears to be a net transfer by  $^{103}\text{Ru}$ -phenanthroline ( $^{103}\text{Ru-P}$ ) from large to small particles of digesta in *Phascolarctos* and *Petauroides volans* thus biasing estimates of retention time towards fine particles (after Cork 1984).

	<i>Phascolarctos cinereus</i>	<i>Trichosurus vulpecula</i>	<i>Petauroides volans</i>	<i>Pseudocheirus peregrinus</i>
Body weight (kg)	5 - 8	2	1	0.7
Gut contents (% body weight):				
Whole gut	20	-	-	-
Site of fermentation (caecum or proximal colon)	10 (C + PC)	8 (C + PC)	10 (C)	- (C)
Coprophagy?	No	No	No	Caecotrophy
Mean retention time (h):				
Solute marker ( $^{51}\text{Cr}$ -EDTA)	213	51	50	70
Particle marker ( $^{103}\text{Ru-P}$ )	100	49	46	37

This characteristic is likely to be an important adaptation to the poorly digestible *Eucalyptus* foliage on which these animals feed (Hume *et al.* 1984; Cork 1986; O'Brien *et al.* 1986). Thus, arboreal herbivores appear to maximise the nutrient assimilation from their generally 'low-quality' diet by limiting the rate of passage of foliage through their digestive tract.

Hume *et al.* (1984) have suggested that the alternative strategy, of increasing leaf intake and reducing passage time, may not be open to arboreal herbivores because of the increased load of secondary compounds that greater intakes would entail (see 2.2.4). Although it is likely that these animals have acquired through natural selection the enzymes required to detoxify and conjugate most leaf secondary compounds, there are significant metabolic costs incurred in these processes (Rhoades and Cates 1976; Hume *et al.* 1984; Richard 1985).

#### 2.2.4 Nutritional quality

The proportion of cell wall to cell content fractions in a leaf affect the nutritional value to a herbivore. Young leaves tend to have many thin-walled cells with considerable cytoplasm while mature leaves have fewer, thick-walled cells with less cytoplasm. Although both young and mature leaves may contain comparable amounts of structural carbohydrates, the nutritional value of young leaves to herbivores is thought to be significantly greater since these leaves contain more cytoplasm and thus more protein than mature leaves (Parra 1978; Demment and Van Soest 1985).

The distinction in nutritional quality between young and mature eucalypt leaves is not clear for arboreal marsupial herbivores. Field observations suggest that a regular and predictable availability of young eucalypt leaves is an important habitat requirement for



*Pseudocheirus peregrinus* (Pahl 1984). On the other hand, proximate analyses of the chemical composition of eucalypt foliage indicate that secondary compounds frequently occur in the cell contents of both 'age classes' but most often in considerably higher concentrations in young leaves (Cork 1984; Cork and Pahl 1984; Table 2.3). Two general types of compounds are recognised; toxic compounds (e.g. alkaloids, cyanogenic glycosides, essential oils) which directly affect the animal's metabolism; and digestion-inhibiting compounds (e.g. tannins as protein-precipitating agents, lignins) (Freeland and Janzen 1974; Hume 1982; Lomdahl 1983; Cork and Pahl 1984). Thus the apparent relative merits of young leaves over mature leaves in terms of their total energy and protein content could be offset by the secondary compounds in the young leaves as those compounds can inhibit digestion and assimilation by herbivores.

The most common secondary compounds associated with eucalypts are essential oils, although other compounds such as polyphenols and cyanogenic glycosides may also occur in relatively high concentrations in some species of eucalypts. Concentration may vary with season (Finnemore *et al.* 1935; Fox and Macauley 1977; Landsberg 1986). Although empirical data on the effect of these oils on the gut micro-organisms of arboreal herbivores are scant, it appears that some gut micro-organisms as in *Phascolarctos cinereus* can tolerate and metabolise essential oils (Freeland and Janzen 1974; Cork 1981).

Tannins are known to complex with the structural carbohydrates of eucalypt leaves and appear to interfere with the digestion of cell walls by arboreal herbivores. Chilcott and Hume (1984a,b) have reported that up to two per cent of dietary nitrogen may escape digestion in *Pseudocheirus peregrinus* because it is locked in indigestible cell walls.

Table 2.3 Ranges in concentration (expressed as % dry matter) of constituents of eucalypt foliage (after Cork 1984).

Constituent	Shoots	(N)	Mature foliage	(N)
Dry matter	35 - 47	(3)	35 - 51	(12)
Organic matter	95 - 97	(3)	94 - 98	(12)
Total nitrogen	1.0 - 2.4	(8)	0.8 - 2.4	(28)
Crude lipid	8 - 15	(5)	8 - 17	(13)
Essential oils	trace - 11	(57)	-	-
Total phenolics	6 - 40	(22)	13 - 25	(9)
Cell-walls (neutral-detergent fibre)	13 - 49	(10)	23 - 56	(20)
Cellulose	7 - 24	(8)	12 - 22	(10)
Lignin	5 - 27	(10)	9 - 27	(20)
Lignin:cell walls	0.3 - 0.6	(10)	0.3 - 0.5	(20)
Gross energy (kJg <sup>-1</sup> )	20 - 23	(5)	20 - 24	(14)

Attempts to relate diet selection by arboreal marsupial herbivores to the nutritional quality (as determined by the composition of selected chemical elements) of available foliage have revealed few consistent trends. Earlier speculation such as that by Troughton (1965) (see Cork 1981) that the dietary selection of *Phascogale cinereus* is inversely related to the concentration of eucalypt essential oils such as cinerole and phellandrene was not supported by more recent quantitative analysis (Southwell 1973; Eberhard *et al.* 1976; Betts 1978; Southwell 1978).

At Lysterfield in Victoria, Cork and Pahl (1984) could find no consistent relationship between the preference of *Pseudocheirus peregrinus* for young and mature foliage and their concentrations of total nitrogen, structural carbohydrates, tannins (condensed or hydrolysable) or total phenolics. Comparable studies for arboreal primates have also produced equivocal results (Hladik 1978; Milton 1979; Milton 1980; Oates *et al.* 1980; Glander 1981). Of the available foliage, new leaves were generally preferred. Leaves lower in structural carbohydrates and higher in nitrogen, compared to their mature counterparts, were frequently selected but total nitrogen concentration was rarely correlated to preferences between plant species. Several studies (McKey 1978; McKey *et al.* 1978; Milton 1979, 1980) have indicated a negative correlation between foliage selection by arboreal primates and the concentration of total phenolics and/or condensed tannins. In contrast, a number of other studies have demonstrated numerous important exceptions to this relationship (Oates *et al.* 1980; Glander 1981).

As indicated in Chapter 1, on a broad-scale, Braithwaite *et al.* (1983) have presented evidence that suggest a relationship between arboreal marsupial herbivores and the concentration of nitrogen, phosphorus and potassium in mature, eucalypt foliage. Other authors

(Freeland and Janzen 1974; Freeland and Winter 1975; Degabriele 1981) have postulated that specific foliar constituents act as limiting factors for arboreal herbivores, thus ultimately affecting their distribution. Degabriele (1983) speculated that nitrogen is a limiting factor in the life of *Phascolarctos cinereus*, although the evidence in support of this was limited.

In summary, there appears to be a general trend for arboreal mammalian herbivores to prefer young leaves over old of the available plant species. However, despite the numerous studies worldwide, the nutritional basis of this selection remains unknown but appears complex. Cork (1984) presents a useful synopsis of this problem. He concluded that the lack of consistent trends may be explained, at least in part, by inadequacies in the current sampling techniques and chemical analyses. Ecological factors not directly related to diet selection may also be implicated, albeit on a temporal basis (Cork 1984).

Clearly, detailed field studies which attempt to relate the ecology of these herbivores to the spatial and temporal availability of their foods may shed more light on this situation. Such was the nature of my study.

## CHAPTER 3

### DESCRIPTION OF REGION AND SITES

#### 3.1 INTRODUCTION

Two forest sites used by L.W. Braithwaite for his survey of the arboreal marsupials and avifauna of the eucalypt forests of the south coast of New South Wales (see Section 1.1) were chosen for my comparative study. The forest site regarded as having a relatively high foliar nutrient status was located in Wadbilliga National Park N.S.W. ( $35^{\circ}20''\text{S}$ ,  $150^{\circ}17''\text{E}$ ) and the forest site considered to have a relatively low foliar nutrient status was situated in Morton National Park N.S.W. ( $36^{\circ}18''\text{S}$ ,  $149^{\circ}33''\text{E}$ ) (Fig. 3.1). The area and shape of both sites were not the same: the Morton site was elongate, encompassing an area of 50.1 ha (Fig. 3.2) while the Wadbilliga site was 24.6 ha in size (Fig. 3.3). Both sites were bisected by firetrails which were used for access.

A preliminary spotlighting survey verified previous observations (L.W. Braithwaite pers. comm.) that the forest site at Wadbilliga supported a relatively high population density of Greater Gliders, whereas the Morton site had a low population density. Few other species of arboreal browsing herbivores were observed at either site during the preliminary survey. Subsequent study showed none of these animals as resident.

#### 3.2 CLIMATE

The study region was recovering from the worst drought since European settlement. This drought commenced in late 1981 and extended until about early May 1983.

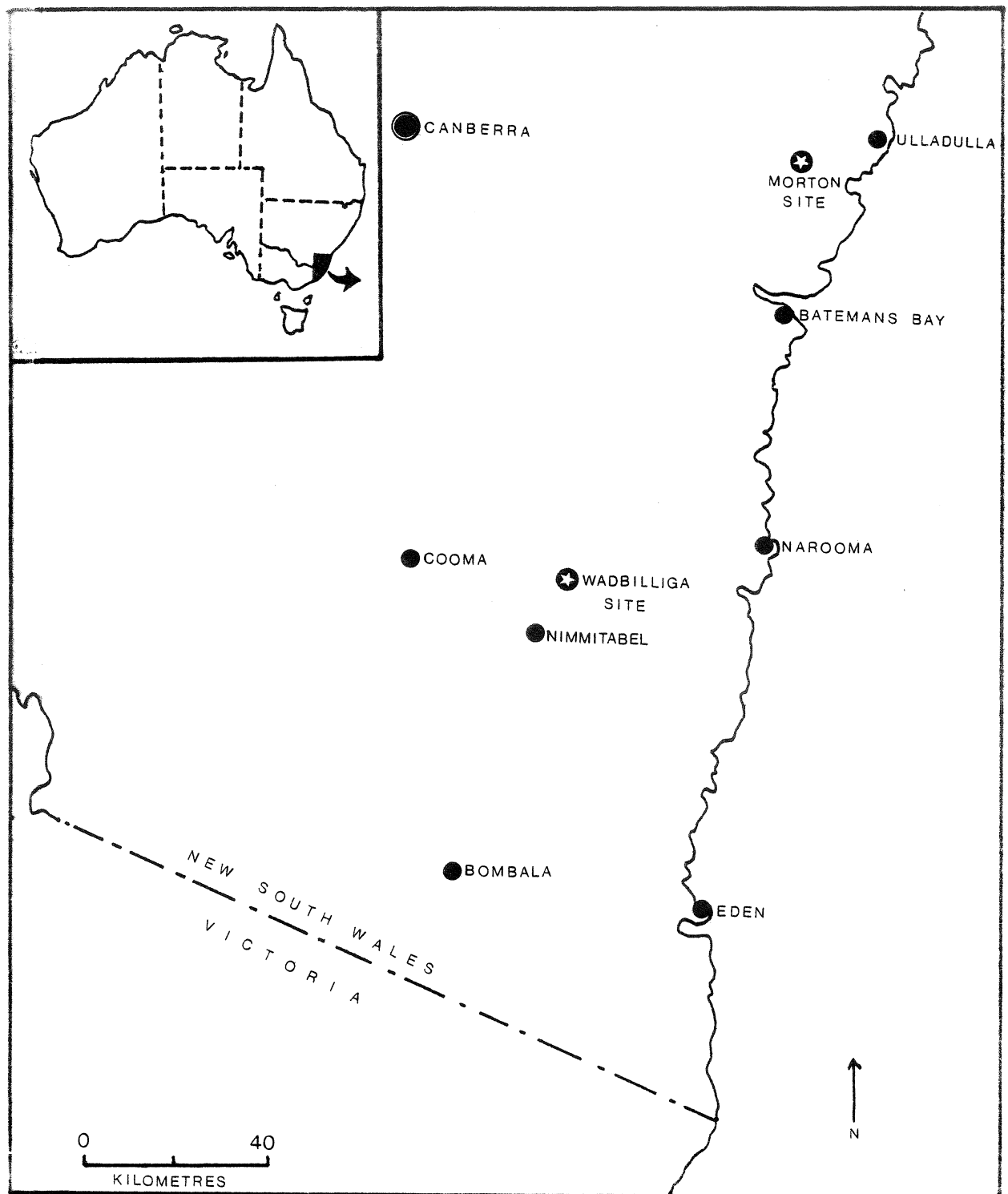


Figure 3.1 Location of study sites in eucalypt forests of south-east New South Wales, Australia. Inset map of Australia shows location of the general study region.

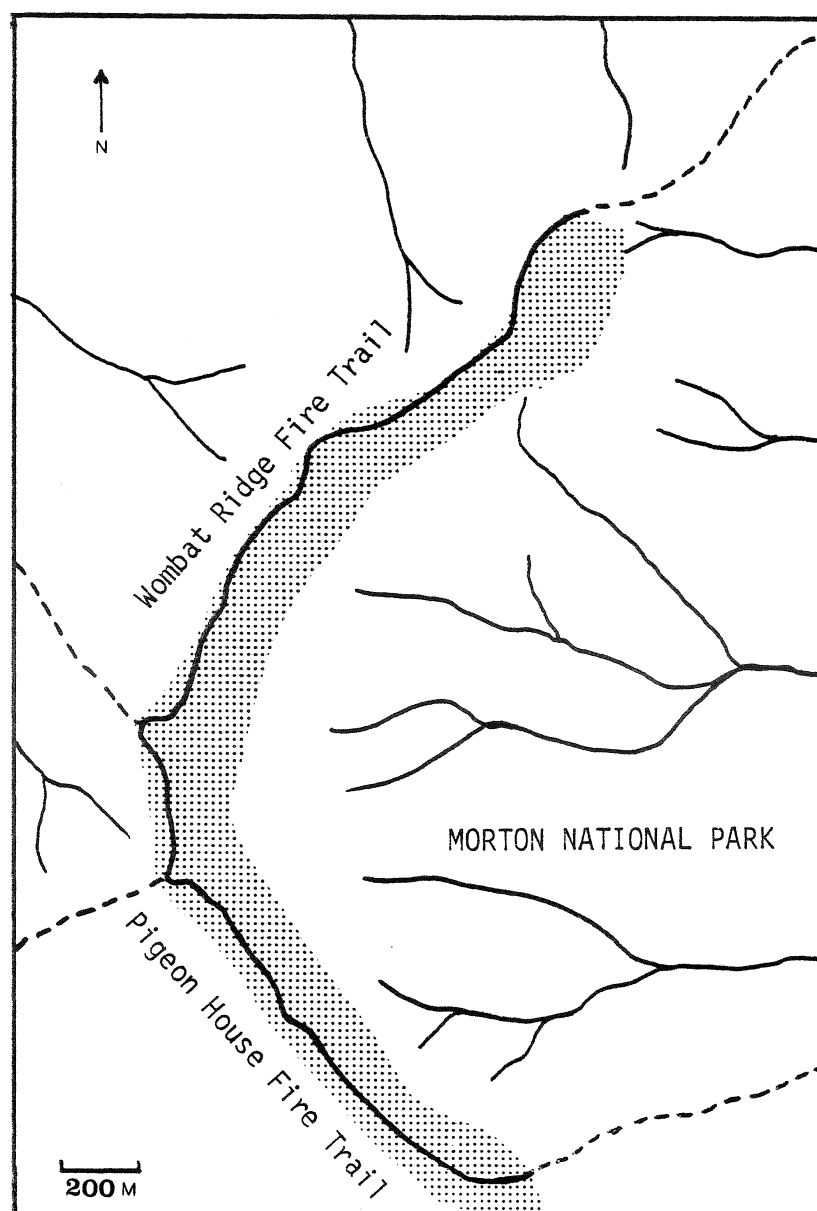


Figure 3.2 Relief map of the Morton region. Study area is shown by shading (Source map: Milton (8927-2-N) 1:25 000 topographic map, CMA, N.S.W.)

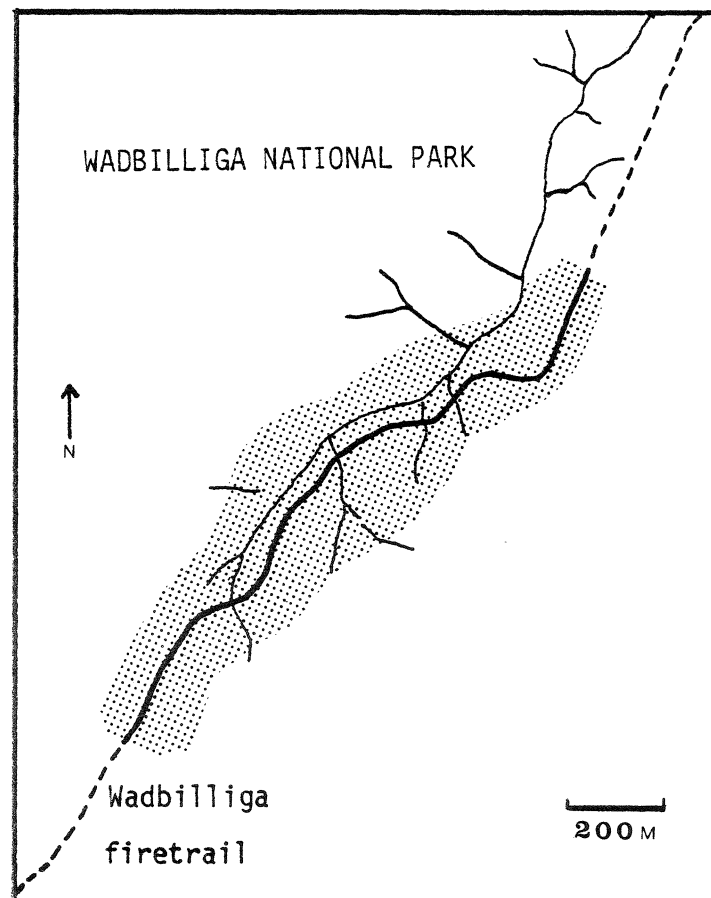


Figure 3.3 Relief map of the Wadbilliga region. Study area is shown by shading (Source map: Yowrie (8825-111-N) 1:25 000 topographic map, CMA, N.S.W.).



Regional climatic data for Wadbilliga and Morton were based on the meteorological records of the Nimmitabel Post Office station and Ulladulla station respectively, and are shown in Figure 3.4. Mean annual rainfall for the Morton region was generally higher compared to the Wadbilliga region while the temperature was characteristically lower at Morton. Temperatures fluctuated seasonally with mean minimum temperatures approaching 0°C in the Wadbilliga region during winter while mean minimum temperatures in the Morton region rarely fell below 7°C during the same period (Fig. 3.4).

### 3.3 GEOLOGY, GEOMORPHOLOGY AND SOILS

The geology of the Morton region and the study site includes siltstones and labile sandstones of Ordovician and Permian origin (Galloway 1978). Through time these sediments have undergone several periods of erosion, deposition, metamorphogenesis and uplifting with the result that the area is now a highly dissected tableland encompassing an altitudinal range of 100-720 m above sea level (Galloway 1978; Budawang Committee 1982). My study site was generally restricted to ridgetops (280-390 m above sea level, Fig. 3.2, Plate A) with underlying gravelly, massive grey-brown soils (Gunn 1978). Several small granite outcrops, probably of Upper Devonian origin, occurred on both the Pigeon House and Wombat Ridge fire trails, within the site.

Runoff of surface water was considerable during and following rainfall and both fire-trails effectively acted as major routes to channel much of the ridgetop water down-slope. Consequently, even following prolonged heavy rainfall, little water percolated below the upper two centimetres of the soil horizon.

A combination of greywacke, shale, phyllite and schist parent materials of Ordovician origin underlay most of the Wadbilliga study

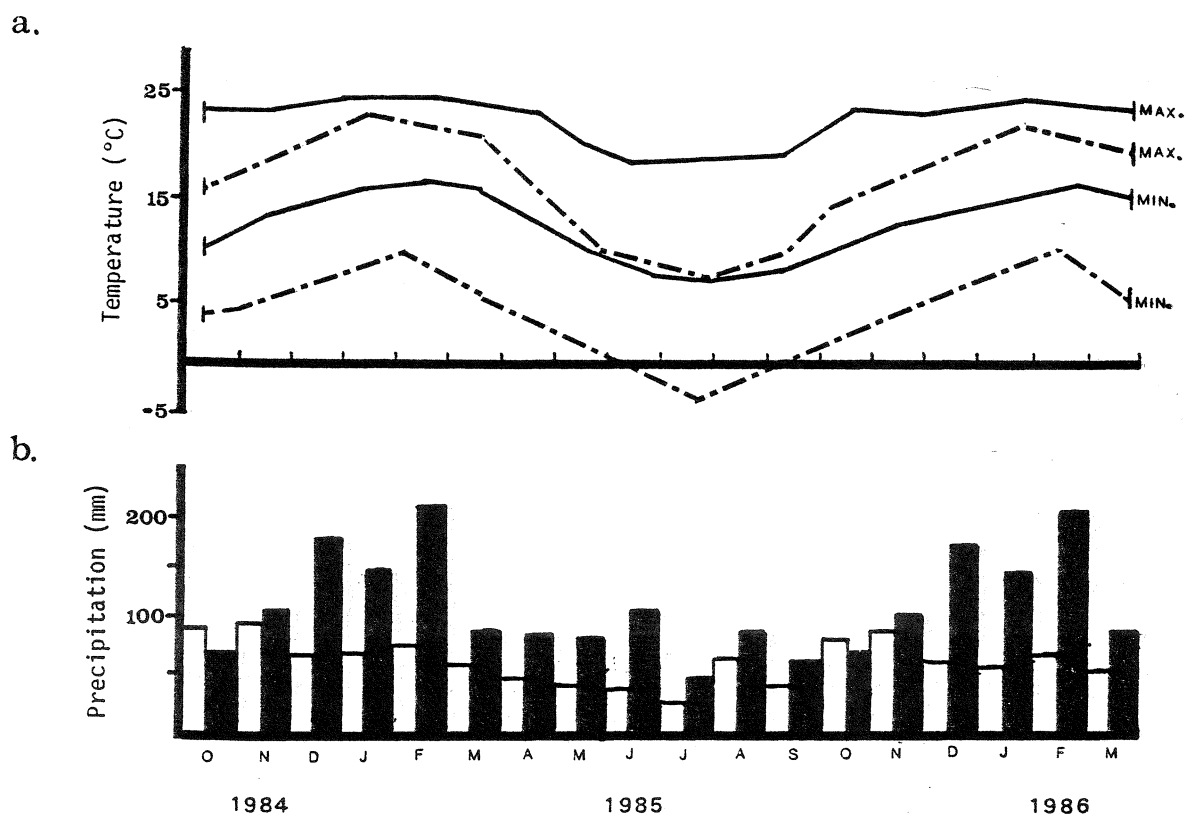


Figure 3.4 Annual climatic data for the Wadbilliga (Nimmitabel station 070067, 36°17'S, 149°17'E; elevation 1056 m; shown by dashed line or open bar) and Morton (Ulladulla station 069031, 35°22'S, 150°29'E; elevation 9.1 m; shown by solid line or solid bar) regions: (a) mean maximum and minimum monthly temperature, (b) mean monthly precipitation. Note that records for Wadbilliga and Morton are based on 87 and 34 years of observations, respectively.

Plate A. Photographs of the Morton forest site showing a portion of forest types A (i) and B (ii). For classification of forest types see Chapter 4.

(i)



(ii)



region, from which characteristically deep brown soils and massive earths have developed (Gunn 1978). Topography of the region (250-1337 m above sea level) varies from deeply dissected mountains and hills, particularly to the south and east, to undulating terrain. The study site was relatively flat and restricted to a moderate-sized gully (930-970 m above sea level, Fig. 3.3, Plate B). A small, possibly ephemeral watercourse flowed through the site. During summer, waterflow was generally restricted to small channels below the ground surface of the watercourse.

### 3.4 VEGETATION

Austin (1978), as part of the survey of the south coast of N.S.W. by the CSIRO Division of Land Use Research, included the Morton site as part of a *Eucalyptus gummifera* group and the Wadbilliga site as part of an *E. fastigata* group in his classification of the region's vegetation. Gradient analysis indicated that altitude, latitude and geology were the major environmental variables associated with variation in forest vegetation. A major latitudinal change was recognised north and south of a line along Currowan Creek and the Clyde River estuary near Batemans Bay (Fig. 3.1) with *E. pellita* and *E. piperita* being restricted to the northern part of the survey region (Austin 1978). As part of the same CSIRO survey, the northern part of the Morton site (i.e. the section on Wombat Ridge fire trail) was included in Land System 33 (*E. gummifera* - *E. sieberi* - *Syncarpia glomulifera* forest type) which represented 45 km<sup>2</sup> or 0.75 per cent of the study region while the southern part of the site was included in Land System 30 (same forest type as above) which represented 100 km<sup>2</sup> or 1.67 per cent of the study region (Gunn *et al.* 1978). However, in terms of the objectives of this study, the above distinction between the northern and southern parts of the Morton site was unwarranted. The



Plate B. Photographs of the Wadbilliga forest site showing height of trees and sparseness of the woody plant species in the understorey.



Wadbilliga study site was included in Land System 13 (*E. radiata* - *E. viminalis* - *E. fastigata* forest type), representing 20 km<sup>2</sup> or 0.33 per cent of the study region (Gunn *et al.* 1978).

L.W. Braithwaite has used a revised classification, which includes several finer subdivisions of M.P. Austin's vegetation analysis of the south coast (Austin 1978) to classify his forest transects (M.P. Austin\* and L.W. Braithwaite\* pers. comm.). Following this classification, the Wadbilliga study site typically falls within the *E. fastigata* group (A type: *E. radiata* - *E. viminalis* - *E. fastigata*, subdivision c. RAD.VIM) while the Morton site falls within the *E. gummifera* group (C type: *E. gummifera* - *E. sieberi* - *Syncarpia glomulifera*, subdivision c. GUM.PIP; C type, subdivision d. SYN.PIP; and C type, subdivision a. GUM.CON which represent my forest types\*\* A, B and C, respectively).

### 3.5 DISTURBANCES

#### 3.5.1 Fire

The frequency and intensity of wildfires during the early history of white settlement are not well recorded. However, it seems probable that the south coast of New South Wales is highly prone to periodic burning, particularly by severe wildfires. Published data for the Morton region shows that major fires burnt this area (and almost certainly the study site) during October-November 1957, February-March 1965, and September-October 1968 (Duggin 1976). Site observations on the composition of forest understorey species, and the depth and type of litter accumulation suggested that the Morton study site had not

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\*C.S.I.R.O. Division of Wildlife and Rangelands Research, Canberra, A.C.T.

\*\*For definition of forest types used in this study see Sub-section 4.2.3

experienced any severe burning for several years and possibly not since the late 1960's.

Data on fires occurring in the Wadbilliga region are less well documented than for Morton. A severe wildfire burnt much of the region (particularly the heath dominated by *Allocasuarina nana* L. Johnson which surrounds the Wadbilliga trigonometric point) and almost certainly the study site between September and December 1968 (Duggin 1976). Since then major fires have occurred in the region (T.W. Norton pers. obs.) but not on the study site (G. Ferguson\* pers. comm.). Site observations suggest that low intensity ground-layer fires have occurred on the site more recently but data on the intensity, frequency and extent of these were not available.

### 3.5.2 Impact of man

Both study regions were almost certainly occupied by Aborigines during the past and since European settlement have experienced numerous impacts including mining (e.g. sluicing for alluvial gold) and land clearance for grazing by domestic stock. Although Morton National Park was only proclaimed in 1967, most of the fire trails around Pigeon House Mountain (e.g. Pigeon House and Wombat Ridge) were constructed during 1959-61 (Budawang Committee 1982). During this study, vehicular access to my Morton site was restricted although some four-wheel drives and off-road motorcycles did frequent the area.

Access to Wadbilliga N.P. and my study site was limited to one trail. Camping was not permitted within the Park and no vehicles were observed stopping within the study site. Vehicles were rarely encountered at night during the sample periods of the study so the effect of vehicular traffic on the behaviour of gliders was probably negligible.

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\*Local farmer at Wadbilliga (see acknowledgements)

## CHAPTER 4

### FOREST SITE ATTRIBUTES AT WADBILLIGA AND MORTON

#### 4.1 INTRODUCTION

This chapter compares the forest sites of Wadbilliga and Morton National Park and attempts to distinguish important site attributes, particularly the distribution and phenology of available plant foods, that may significantly influence the ecology of *P. volans*. It provides the background for Chapters 5 and 6 which consider the relationships between habitat quality and the social organisation, behaviour and feeding ecology of *P. volans*.

#### 4.2 METHODS

##### 4.2.1 Frequency of sampling

The time of sampling, the number of samples, and the frequency of sampling varied with the parameter in question (Table 4.1). For example, climatic data (e.g. temperature, precipitation) were recorded daily, while phenological data were only noted once during a sample period. Some parameters, such as the nutrient status of eucalypt foliage, were only measured once during the study.

##### 4.2.2 Climate

During each sample period, daily minimum and maximum temperatures, and precipitation were recorded using a min-max thermometer and rain-gauge, respectively. Both devices were placed within a central, representative section of each study site. The thermometer was always protected from direct sunlight while the rain-gauge was positioned in the centre of a relatively small opening in the forest canopy (ca. 8 m in diameter). Moon-phase was also noted daily.



Table 4.1 Sampling regime for forest site attributes assessed at Wadbilliga and Morton during the study period March 1984 to August 1986 (D: daily during sample period; M: once during sample period; \*: undertaken over several days of the sample period).

Date of sample period	Site parameters			
	Precipitation and temperature	Floristics and structure	Phenology	Foliage nutrients
Mar - Aug (at least once monthly)		*	*	
1984 Oct	D		M	
Nov	D		M	
Dec	D		M	
Jan	D		M	
Feb	D		M	
Mar	D		M	
1985 Jun	D		M	
Aug	D		M	
Sept			M	
Oct	D		M	
Dec	D	*	M	
Jan	D		M	
Feb	D		M	*
Mar	D		M	

#### 4.2.3 Forest communities

##### 4.2.3.a *Floristics and structure*

Analyses of forest floristics and structure were restricted to tree species and plant nomenclature followed Boland *et al.* (1985) and Costermans (1981). Several one hectare quadrats were surveyed in randomly located sections of each study site that were known to be used by *P. volans* and in other sections that were not used (Chapter 5). Within each quadrat the height and diameter at breast height over bark (DBHOB) within the following sizes classes (cm): 1-9, 10-19, 20-29, 30-39, 40-59, 60-79, 70-99, 100+ were measured for each tree species. The height of trees was measured by Spiegel Relaskop and visual estimation. Colour aerial photographs (1:10 000) were also used to check the floristic/structural assessment of both study sites.

##### 4.2.3b *Phenological data*

During each sampling period at each site the relative abundance of juvenile leaves, buds, flowers, and fruits of each tree species was recorded during daylight, using binoculars. Ten randomly selected individuals of each tree species occurring in each sample quadrat were assessed. Data for each tree species in each quadrat were averaged to give an index of relative abundance for the month of sampling. Indices of relative abundance of phenological categories for each tree species at a study site were obtained by pooling and averaging data from all quadrats where that species was found. All phenological categories were scored according to six arbitrary abundance classes (number of items): 0 (0), 1 (1-100), 2 (101-1000), 3 (1001-10,000), 4 (10,001-100,000), 5 (100,000 +). New leaves were recognised by their size (less than two-thirds mature leaf size), shape, reflectance, position in the crown of the tree, and sometimes texture.

Phenology was also recorded, as above, for tree species occurring in the estimated home range of each individually monitored *P. volans*. In this case, ten individuals (when available) of each tree species found in the animal's home range were monitored. The phenology of individual trees favoured for browsing by *P. volans* were also monitored.

#### 4.2.3c *Nutrient status of eucalypt foliage*

Juvenile and mature foliage of all eucalypt species, except *Eucalyptus consideniana* Maiden, occurring at both study sites were assayed to determine their nitrogen (N) and phosphorus (P) content.

Five samples of foliage from the canopy of each of five randomly selected trees of each eucalypt species in forest areas occupied and not occupied by *P. volans* were shot down with a .222 calibre rifle. Canopy samples of each tree were bulked to give five samples of both juvenile and mature foliage of each eucalypt species. Samples were then packed in black plastic bags and stored in ice until they could be weighed wet and then oven-dried. Following oven drying (which commenced some 6-8 hours after the time the samples were collected) at 80°C for 36 hours, samples were re-weighed to ensure they had reached constant weight and then ground and stored at approximately 20°C in plastic vials in a desiccator until they could be analysed.

Total phosphorus and (ammonium) nitrogen were measured using a Technicon auto-analyser, following micro-Kjeldahl digestion (for full description see Lambert 1976).

## 4.3 RESULTS

### 4.3.1 Climate

Climate data for a 7-10 day period in each month of sampling at each site are shown in Figures 4.1 and 4.2. There were no significant differences between climatic data for the region and for the site, for both Morton and Wadbilliga. Mean monthly maximum temperatures at the Morton site, for example, were similar to the Ulladulla station (Fig. 3.4) during the study period while mean monthly minimum temperatures were often slightly lower at the site (Fig. 4.1).

Precipitation at both study sites was generally consistent with the regional trends (Figs. 4.1, 4.2 and 3.4). Even so, the summer of 1984-1985 was slightly drier than average while the spring-summer period of 1985-1986 was slightly wetter than average for both regions.

The mean monthly temperatures at Wadbilliga were typically lower than those at Morton while precipitation during the sample periods was higher at Wadbilliga. Mean monthly minimum temperatures during the winter of 1985 at Wadbilliga often fell close to or below 0°C while those recorded at Morton never fell below ca. 5°C. During the same period, precipitation and mist commonly occurred on a daily basis at Wadbilliga while precipitation was less frequent at Morton. Mist was encountered rarely at Morton.

### 4.3.2 Forest communities

#### 4.3.2a *Floristics and structure*

The diversity of species of eucalypt varied spatially within the Morton study site (Fig. 4.3 and Plate A, p. 25). Sydney Peppermint *E. piperita* Smith and Red Bloodwood *E. gummifera* (Sol. ex Gaertner) Hochr. occurred throughout the site, and were the sole dominants of the majority (40.3 ha or 80.4%) of the site. This forest area was identified as forest type A. The number of eucalypt species occurring in the

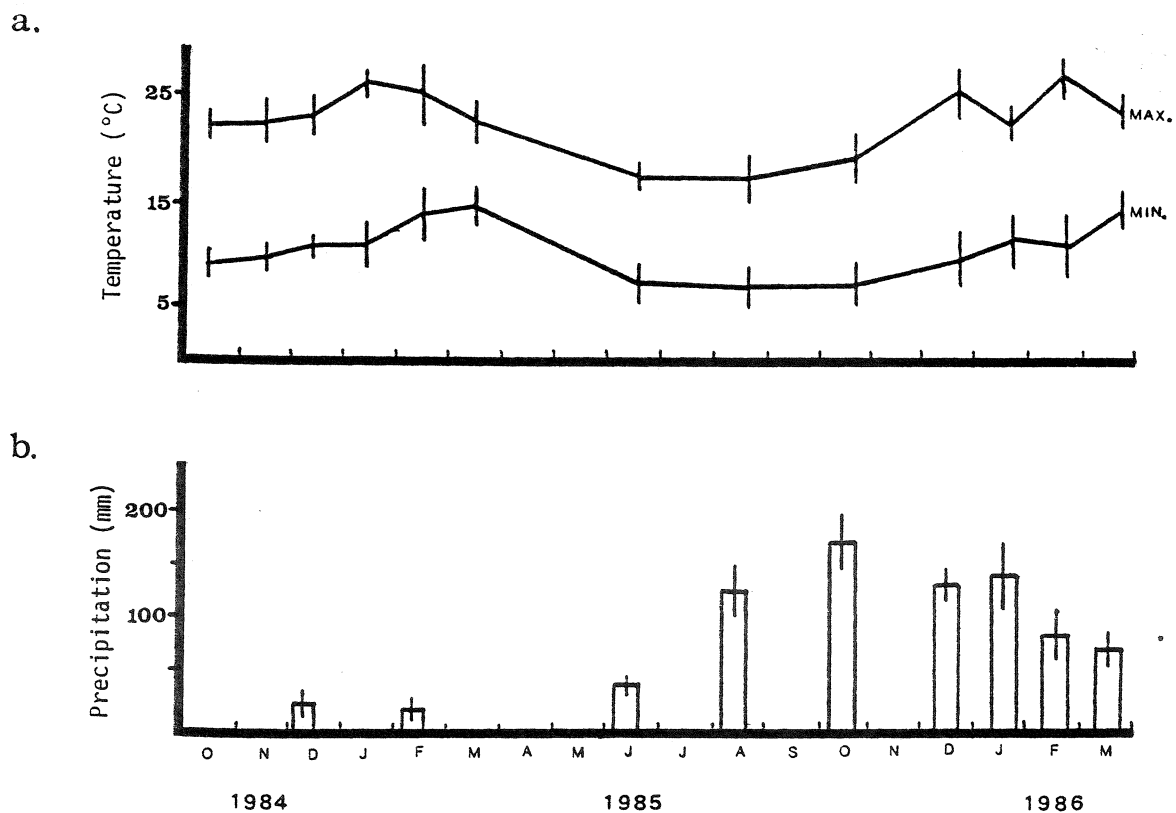
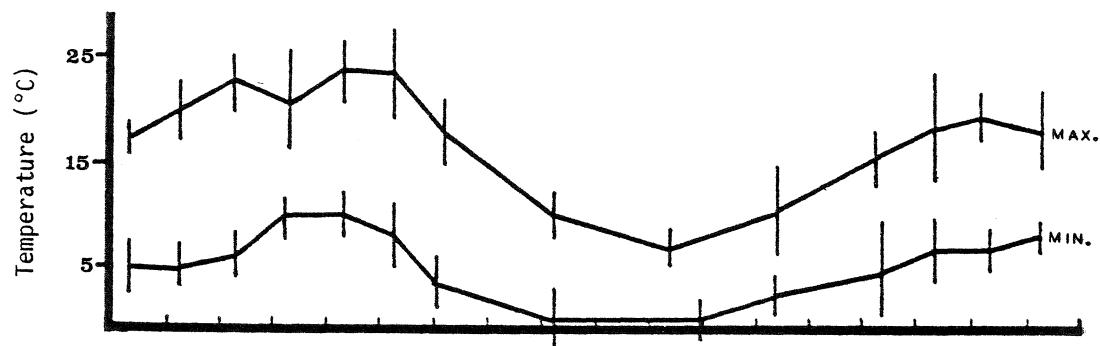


Figure 4.1 Climate data for the Morton site during the period October 1984-March 1986, inclusive; (a) mean maximum and minimum temperatures, (b) mean precipitation. Note that the mean values  $\pm$  standard deviation (vertical bar) are for the 7-10 day sample period of each month the site was visited.

a.



b.

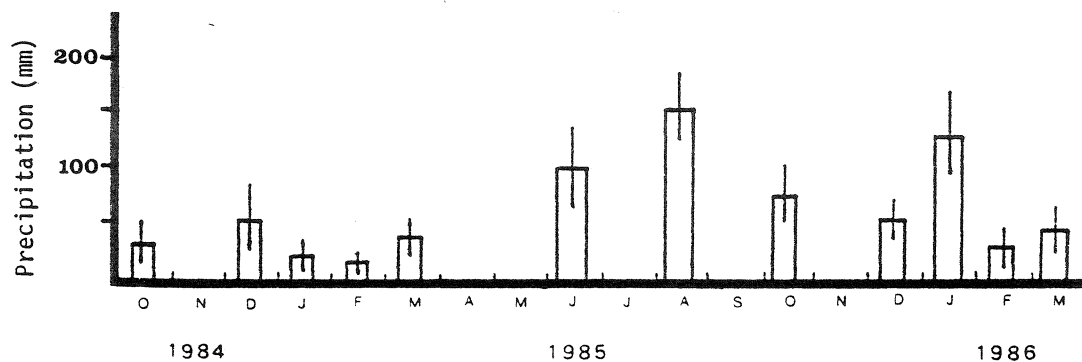


Figure 4.2 Climate data for the Wadbilliga site during the period October 1984-March 1986, inclusive; (a) mean maximum and minimum temperatures, (b) mean precipitation. Note that the mean values  $\pm$  standard deviation (vertical bar) are for the 7-10 day sample period of each month the site was visited.

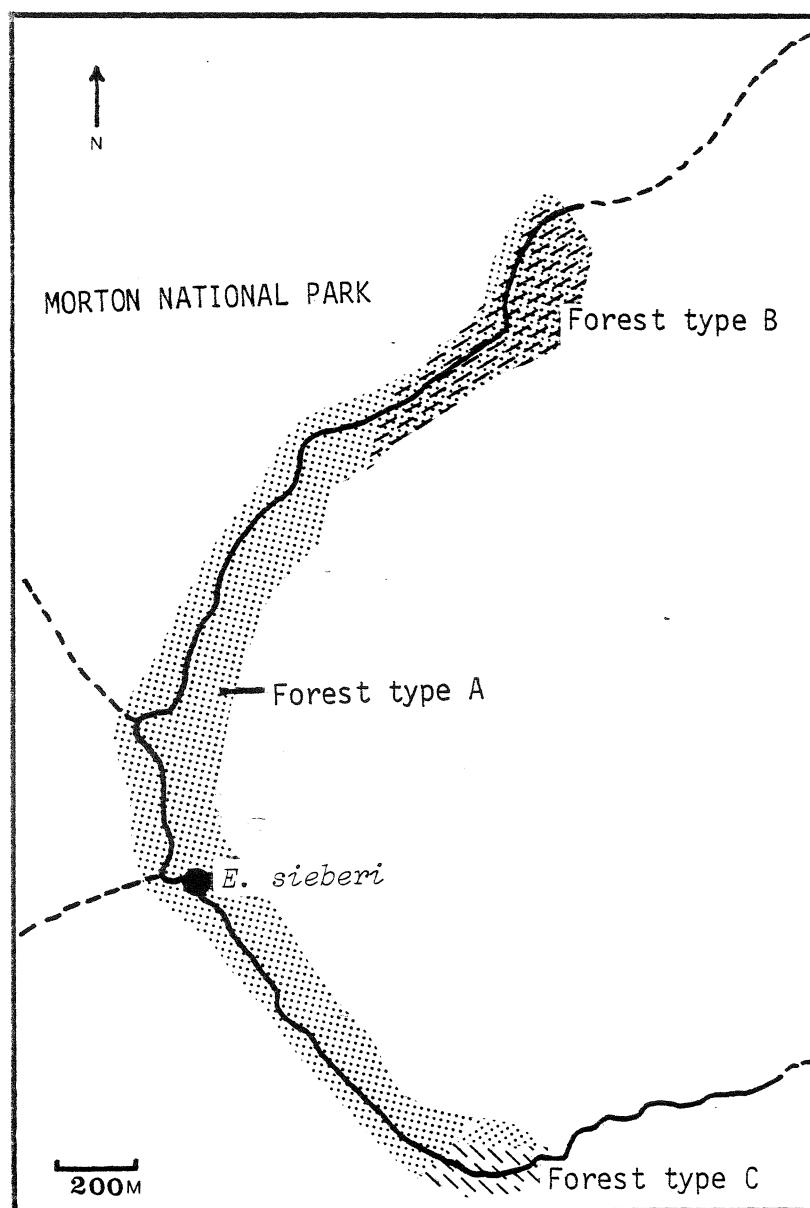


Figure 4.3 Approximate spatial distribution of the eucalypt forest types at the Morton site. See text for full description.

distinct forest areas was three at the northern (forest type B) and five at the southern end (forest type C) of the site. Forest type B had an area of 8.6 ha (17.2%) and was represented by Silvertop Ash *E. sieberi* L. Johnson and Turpentine *Syncarpia glomulifera* (Smith) Niedenzu, as well as *E. piperita* and *E. gummifera*. A smaller (1.2 ha or 2.4%) area of forest (type C) was represented by Large-fruited Red Mahogany *E. pellita* F. Muell., *E. sieberi* and Yertchuk *E. consideniana* Maiden, as well as *E. gummifera* (Fig. 4.3). Several small patches of *E. sieberi* also occurred along both fire-trails within forest type A. The largest of these patches was approximately 0.3 ha and is shown in Figure 4.3. All of these forest types were similar in structure. Tree height ranged from 5-30 m and canopy cover was typically open.

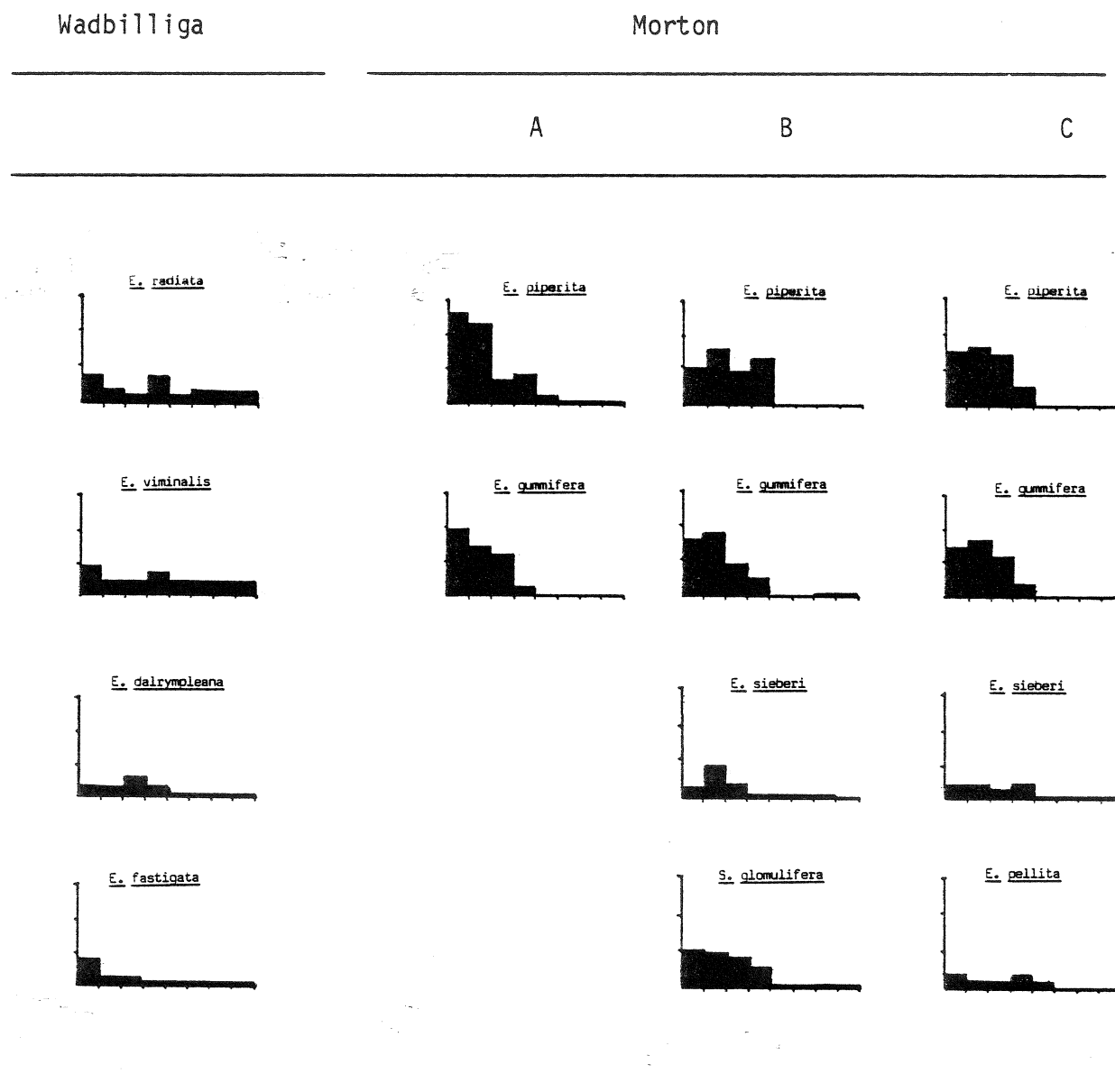
The mean basal area ( $\text{m}^2 \text{ ha}^{-1} \pm \text{SD}$ ) and DBHOB size class frequency of eucalypt species found in each forest type is given in Table 4.2 and Figure 4.4, respectively. Data for *S. glomulifera* are also included. *Eucalyptus piperita* was relatively consistent across all forest types (for example, forest type A mean basal area  $\pm$  S.D., with number of plots in parentheses:  $36.9 \pm 0.8(3)$ , B:  $37.3 \pm 2.0(3)$ , C:  $33.4(1)$ ). The mean basal area and frequency of distribution of DBHOB of *E. sieberi* was also relatively consistent where it occurred in the forest (i.e. forest types B and C; Table 4.2, Figure 4.4). The occurrence of *S. glomulifera* in forest type B appeared to correlate with a decline in the relative abundance of *E. gummifera*. *Eucalyptus pellita* and *E. consideniana* made relatively small contributions to the total mean basal area of forest type C. Dense pockets of woody understorey species occurred throughout the site, particularly in forest type B.

The Wadbilliga study site was dominated by Narrow-leaved Peppermint *E. radiata* Sieber ex DC. subsp. *radiata* and Manna Gum *E. viminalis* Labill.: Mountain Gum *E. dalrympleana* Maiden and Brown



Table 4.2 Mean basal area ( $\text{m}^2 \text{ ha}^{-1} \pm \text{SD}$ ) for *Eucalyptus* spp. and *Syncarpia glomulifera* at body study sites (asterisk indicates total basal area of eucalypts). Number of quadrats sampled was three at Wadbilliga and Morton forest types A and B, and one at Morton forest type C.

	Morton			Wadbilliga
	Type A	Type B	Type C	
<i>E. consideniana</i>	-	-	0.7	-
<i>E. gummifera</i>	31.2 $\pm$ 7.7	24.1 $\pm$ 1.7	30.2	-
<i>E. pellita</i>	-	-	3.7	-
<i>E. piperita</i>	36.9 $\pm$ 0.8	37.3 $\pm$ 2.0	33.4	-
<i>E. sieberi</i>	-	11.8 $\pm$ 1.1	13.1	-
<i>S. glomulifera</i>	-	28.3 $\pm$ 4.2	-	-
<i>E. dalrympleana</i>	-	-	-	3.8 $\pm$ 0.1
<i>E. fastigata</i>	-	-	-	8.7 $\pm$ 0.6
<i>E. radiata</i>	-	-	-	39.0 $\pm$ 4.1
<i>E. viminalis</i>	-	-	-	33.4 $\pm$ 5.6
Total mean basal area	68.1	101.5 (73.2)*	81.1	84.9



DBHOB size classes (cm): 1 (1-9), 2 (10-19), 3 (20-29), 4 (30-39), 5 (40-59), 6 (60-79), 7 (80-99), 8 (100 +).

Figure 4.4 Diameter at breast height over bark (DBHOB) size class frequencies of *Eucalyptus* spp. and *Syncarpia glomulifera* representing forest types at both study sites. (Note: ordinate represents stems  $\text{ha}^{-1}$  and divisions are 0, 100, 200, 300; abscissa represents DBHOB size classes and divisions are 0, 1, 2, 3 ---- 8).

Barrel *E. fastigata* Deane and Maiden were much less common (see Plate B, p. 27). *E. dalrympleana* was relatively evenly distributed throughout the site while *E. fastigata* was found predominantly on less well-drained areas in the eastern half of the site. Also, *E. radiata* tended to favour relatively better-drained soils than the other species, irrespective of site aspect. Some trees of this species were noticeably stunted on the periphery of the site. Despite these differences, the whole study site was classified as one floristic unit.

Structurally, the majority of the site was relatively uniform. Trees ranged in height from 5-40 m and the forest canopy was open. *Eucalyptus radiata* ( $39.0 \pm 4.1 \text{ m}^2 \text{ ha}^{-1}$ , no. of plots = 3) and *E. viminalis* ( $33.4 \pm 5.6 \text{ m}^2 \text{ ha}^{-1}$ , no. of plots = 3) contributed most significantly to the total mean basal area of the Wadbilliga study site (Table 4.2). The frequency classes of DBHOB for all species, except *E. radiata*, were biased towards larger diameter individuals (Fig. 4.4). The understorey of this site was relatively sparse and the ground layer was often dominated by Cyperaceae spp.

Total mean basal area of eucalypts ranged from  $84.9 \text{ m}^2 \text{ ha}^{-1}$  at Wadbilliga to  $68.1 \text{ m}^2 \text{ ha}^{-1}$  for forest type A at Morton (Table 4.2). The Morton site had total mean basal areas of  $73.1 \text{ m}^2 \text{ ha}^{-1}$  for forest type B and  $81.1 \text{ m}^2 \text{ ha}^{-1}$  for forest type C. The decrease in total mean basal area of eucalypts across these forests was assumed to reflect a corresponding decrease in site productivity (Carron 1968; R.G. Florence pers. comm.\*; S.M. Davey\* pers. comm.; R.P. Kavanagh\*\* pers. comm.).

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\*\*Wood Technology and Forest Research, Forestry Commission of N.S.W., Beecroft, Sydney.

#### 4.3.2b *Nutrient status of eucalypt foliage*

Determination of the nitrogen and phosphorus concentrations in juvenile and mature foliage of eucalypt trees growing at both sites were undertaken:

- i. to compare the concentrations of foliar nutrients of the eucalypt species growing within each forest type;
- ii. to assess if these foliar nutrient values fell within the range of values cited in the current literature (particularly Braithwaite *et al.* 1983);
- iii. to confirm that the Wadbilliga site warranted the title 'relatively high foliar nutrient status' and that the Morton site had a 'relatively low foliar nutrient status'; and
- iv. to provide a crude estimate of the nutrient intake of individually monitored *P. volans* (see Sub-section 6.3.3).

The amount of variation in the concentration of foliar nutrients (N and P) between samples of the same tree species was relatively high (but not significantly different) for all eucalypts at both study sites. The mean nutrient concentration of N and P either for juvenile leaves or for mature leaves of *E. gummiifera* and *E. piperita* did not differ significantly across all forest types at Morton (Tables 4.3 and 4.4).

The mean concentration (expressed as % dry weight  $\pm$  S.D.) of nitrogen and phosphorus in juvenile eucalypt foliage did not differ significantly from the mean concentration of N and P in mature foliage of the same species (Student's t-test,  $P > 0.05$ ; Table 4.5) (Table 4.3). Unlike phosphorus, however, the mean concentration of nitrogen tends to

e 4.3 Mean foliar nutrient concentrations (expressed as percentage of oven-dry weight) of nitrogen and phosphorus in juvenile (J) and mature (M) leaves of eucalypt species at Morton and Wadbilliga N.P., N.S.W. Standard deviations are shown in parentheses.

	Species	Subgenus <sup>a</sup>	Section <sup>b</sup>	Series <sup>c</sup>	No. of Samples	Nitrogen		Phosphorus	
						J	M	J	M
on:									
st type A	<i>Eucalyptus gummifera</i>	C	CA	F	5	0.93 (0.07)	0.71 (0.26)	0.041 (0.12)	0.0 (0.0)
	<i>E. piperita</i>	M	A	T	5	0.96 (0.27)	0.70 (0.23)	0.046 (0.021)	0.0 (0.0)
st type B	<i>E. gummifera</i>	C	CA	F	5	0.88 (0.06)	0.68 (0.11)	0.032 (0.011)	0.0 (0.0)
	<i>E. piperita</i>	M	A	T	5	-	0.74 (0.09)	-	0.0 (0.0)
	<i>E. sieberi</i>	M	A	K	5	0.95 (0.24)	0.82 (0.32)	0.059 (0.022)	0.0 (0.0)
	<i>E. consideriana</i>	M	A	K	-	Not sampled			
st type C	<i>E. gummifera</i>	C	CA	F	5	0.91 (0.14)	0.71 (0.08)	0.027 (0.007)	0.0 (0.0)
	<i>E. pellita</i>	S	E	C	5	1.32 (0.13)	0.94 (0.26)	0.073 (0.014)	0.0 (0.0)
	<i>E. piperita</i>	M	A	T	5	0.92 (0.18)	0.71 (0.21)	0.048 (0.015)	0.0 (0.0)
	<i>E. sieberi</i>	M	A	K	5	0.97 (0.13)	0.86 (0.14)	0.049 (0.023)	0.0 (0.0)
Wadbilliga:									
	<i>E. dalrympleana</i>	S	P	I	5	1.55 (0.15)	1.39 (0.06)	0.079 (0.031)	0.0 (0.0)
	<i>E. fastigata</i>	M	A	K	5	0.92 (0.06)	0.77 (0.35)	0.074 (0.008)	0.0 (0.0)
	<i>E. radiata</i>	M	A	T	5	1.88 (0.17)	1.46 (0.31)	0.054 (0.026)	0.0 (0.0)
	<i>E. viminalis</i>	S	P	I	5	1.93 (0.29)	1.41 (0.27)	0.081 (0.010)	0.0 (0.0)

Corymbia, M: Monocalyptus, S: Symphyomyrtus; b. A: Renantheria, CA: Rufaria, E: Transversaria, P: Maidenaria; Salignae, F: Gummiferae, I: Viminalis, K: Obliquae, T: Piperitae

Table 4.4 Analysis of variance across forest types A, B and C at Morton of the nutrient concentration of nitrogen (N) and phosphorus (P) for juvenile leaves and mature leaves of *Eucalyptus gummifera* and *E. piperita* (bold type) sampled. The values shown are the sample variance ratio ( $F_S$ ) (Sokal and Rohlf 1969, p. 185). Note that for all analyses: n for each area = 5; no. of areas = 3; df (among areas) = 2; df (within areas) = 12; N.S. = not significant ( $F_{.05[2,12]} = 3.87$ ).

	N		P	
Juvenile leaves	0.52	N.S.	0.68	N.S.
	-		-	
Mature leaves	0.41	N.S.	0.83	N.S.
	<b>0.64</b>	<b>N.S.</b>	<b>0.70</b>	<b>N.S.</b>

Table 4.5 Student's t-test analyses (Sokal and Rohlf 1969) comparing the concentration of nitrogen (N) and phosphorus (P) in the juvenile and mature foliage of the same species of eucalypt for Morton and Wadbilliga. The values shown are the t-statistic. Note that for the analyses shown:  $n = 5$ ;  $df = 8$ ;  $t_{0.05[8]} = 2.31$ . No significance levels are shown as all t-statistic values were less than 2.31 (i.e. not significant).

Site	Forest type	Eucalypt species	N	P
Morton	A	<i>E. gummifera</i>	1.28	0.62
		<i>E. piperita</i>	0.84	0.41
	B	<i>E. gummifera</i>	1.24	0.38
		<i>E. piperita</i>	-	-
		<i>E. sieberi</i>	0.71	0.68
	C	<i>E. gummifera</i>	2.03	-0.86
		<i>E. pellita</i>	2.22	-0.49
		<i>E. piperita</i>	1.99	0.94
		<i>E. sieberi</i>	1.16	0.74
	Wadbilliga	<i>E. dalrympleana</i>	2.11	-1.85
		<i>E. fastigata</i>	1.76	1.61
		<i>E. radiata</i>	2.28	-1.66
		<i>E. viminalis</i>	2.29	1.28

be higher in juvenile leaves than in mature leaves of the same eucalypt species (e.g. *E. pellita*: juvenile foliage  $N = 1.22 \pm 0.13$ ,  $n = 5$ ; mature foliage  $N = 0.94 \pm 0.26$ ;  $n = 5$ ) (Table 4.3).

With the exception of *E. fastigata*, all eucalypt species at Wadbilliga had higher concentrations of N and P for both juvenile and mature foliage than the eucalypts sampled at Morton.

#### 4.4 DISCUSSION

The floristic and structural composition of both sites most probably reflects local and regional climatic and edaphic factors (Florence 1963, 1964; Austin 1978; Turner *et al.* 1978), although the latter factors were not quantified during this study. Both study sites were located on massive, relatively well-drained soils. Mean annual precipitation was lower at Morton compared to Wadbilliga while the climate was characteristically milder at Morton compared to Wadbilliga.

The composition of *Eucalyptus* subgenera at either site probably (indirectly) reflects their relative differences in soil fertility since *Symphyomyrtus* species, on the south coast of N.S.W. at least, predominate on relatively more fertile soils while the poorest soils support only species (usually a mixture) from the subgenus *Monocalyptus* (Florence 1981; Lambert and Turner 1983). At Wadbilliga, the ratio of *Symphyomyrtus* to *Monocalyptus* subgenera was equal (2 spp. of each) while at Morton only one *Symphyomyrtus* species was present; *E. pellita*, which had a limited distribution and small mean basal area. Overall, the site potential at Wadbilliga appeared substantially higher than that at Morton (cf. Gunn 1978) and this difference was reflected by the floristics and vegetation structure of each site.



The division of the Morton study site into forest types A, B, and C may reflect subtle changes in soil fertility and drainage. For example, forest type A was typically restricted to the higher (ridgetop) areas of the site and was dominated by *E. gummifera* and *E. piperita*, two eucalypt species commonly associated with poor, well-drained soils (Beadle *et al.* 1972; Boland *et al.* 1985). In contrast, forest types B and C supported species (i.e. *Syncarpia glomulifera* and *E. pellita*, respectively) known to favour relatively more fertile soils (Boland *et al.* 1985; J. Turner\* pers. comm.). Further, forest types B and C were located lower on the ridgetop than most of forest type A (Fig. 4.3) and, as a consequence, probably received more water from upslope compared to forest type A; particularly water channelled along both fire trails. Thus forest types B and C appeared to reflect more productive micro-site conditions than forest type A. This hypothesis was also supported by the decrease in total mean basal area of eucalypts from forest type C through forest type B to forest type A (Table 4.2). *Syncarpia glomulifera* was not browsed by *Petauroides volans* during the study (Chapter 6).

Overall, mean concentrations (as % dry matter) of N and P for both juvenile and mature foliage of eucalypts from both study sites generally fell within the range of values cited in the literature (Table 4.6). Two exceptions, however, were *E. piperita* and *E. pellita*. *E. piperita*, had a mean concentration (as % dry matter) of N and P for mature foliage (N = 0.716, P = 0.035, mean for all forest types) considerably lower than the range of mean values given (N = 1.02-1.05, P = 0.045-0.046, as % dry matter) for trees of the same species sampled in Kioloa State Forest (Mak 1982). Comparative data from other sources on the mean concentrations of N and P in the juvenile foliage of the eucalypt species sampled in my study were not available (Table 4.6).

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\*Chief, Wood Technology and Forest Research, Forestry Commission of N.S.W., Beecroft, Sydney

Table 4.6 Range of mean nitrogen (N) and phosphorus (P) concentrations (expressed as % oven-dry weight) recorded from other forest localities within south eastern Australia for mature foliage of the eucalypt species sampled during this study. All of the studies cited below used similar nutrient assay techniques.

Eucalypt species	N	P	Source
<i>E. consideniiana</i>	0.79-0.90	0.040-0.052	1,2,3
<i>E. dalrympleana</i>	1.17-1.46	0.049-0.089	1,2
<i>E. fastigata</i>	0.89	0.065	1
<i>E. gummifera</i>	0.69-0.96	0.033-0.038	1,2,3
<i>E. pellita</i>	1.29-1.39	0.044-0.060	3,4
<i>E. piperita</i>	1.02-1.22	0.043-0.046	3,4
<i>E. radiata</i>	1.05-1.54	0.067-0.069	1,2
<i>E. sieberi</i>	0.79-1.11	0.042-0.050	1,2,3
<i>E. viminalis</i>	1.28-1.33	0.075-0.076	1,2

Source: 1: Braithwaite *et al.* (1983)

2: Lambert and Turner (1983)

3: Mak (1982)

4: L.W. Braithwaite (unpubl. data)

The mean foliar concentrations of N and P for the eucalypt species sampled confirmed that Morton and Wadbilliga warranted the titles 'relatively low foliar nutrient status' and 'relatively high foliar nutrient status', respectively. The significance of these data are considered more fully in Chapters 5-7.

#### 4.5 SUMMARY

The forest sites at Wadbilliga and Morton were compared in an attempt to distinguish important site attributes which may influence the ecology of *P. volans*. Mean annual precipitation was lower at Morton compared to Wadbilliga while the climate was characteristically milder at Morton compared to Wadbilliga. The floristics and vegetation structure at either site appeared to reflect their relative differences in soil fertility; forest site potential at Wadbilliga appeared to be substantially higher than that at Morton. Within the Morton site, three forest types (A, B and C) were identified on the basis of several parameters including structure, eucalypt species diversity and total mean basal area of eucalypts. Of these forest types, B and C appeared to reflect more productive micro-site conditions than A. The mean foliar concentrations of nitrogen and phosphorus for the eucalypt species sampled confirmed that Morton and Wadbilliga warranted the titles 'relatively low foliar nutrient status' and 'relatively high foliar nutrient status', respectively.

## CHAPTER 5

SOCIAL ORGANISATION OF *P. VOLANS* AT WADBILLIGA AND MORTON

## 5.1 INTRODUCTION

This chapter describes and compares the social organisation exhibited by populations of *P. volans* at Wadbilliga and Morton. In the first instance, data were collected to test three *a priori* hypotheses that were generated to account for the observed population density of *P. volans* at Wadbilliga (relatively high foliar nutrient status) and Morton (relatively low foliar nutrient status), as determined by a preliminary spotlighting survey (Chapter 3, Section 3.1). These hypotheses were:

- i. The population density of *P. volans* at Morton is low, compared to Wadbilliga, because there are few areas of forest (i.e. trees with a relatively high concentration of foliar nutrients) which appear able to support resident animals.
- ii. The population density of adult male and female *P. volans* at Morton is low because these animals maintain larger home ranges than their respective counterparts at Wadbilliga.
- iii. The population density of *P. volans* at Morton is low, compared to Wadbilliga, because the majority of gliders encountered are transients dispersing to more favourable habitat.

Differences between Wadbilliga and Morton in the availability of suitable denning sites for gliders and in predation pressure were also assessed as these parameters were other potential explanations for the observed variation in population density.

Data collected on other aspects of the social organisation of *P. volans* were considered in relation to forest productivity and other data given in the literature.

## 5.2 METHODS

The forest study sites were described in Chapter 4.

### 5.2.1 Assessment of *P. volans* populations and individuals

The initial assessment of the distribution and population density of *P. volans*, and the capture and tagging (see below) of individuals was undertaken at both study sites between March and August 1984 (Table 5.1). After August 1984, populations and individuals of *P. volans* were monitored (see below) on a regular basis until the completion of the study during late August 1986.

### 5.2.2 Distribution and population density

The size and spatial distribution of glider populations was assessed using spotlights (both red and white light) along predetermined transects during all sample months of the study (Table 5.1).

From these data, population density was calculated by dividing the number of gliders known to be alive (KTBA) by the sample area plus a perimeter buffer zone of thirty metres. The sample area was determined from measurements taken on the ground and from aerial photographs. The buffer zone was included to compensate for any over-estimation of population density caused by sampling gliders which may have had part of their home range outside the intended sample area. This was considered possible as my knowledge of the home range of individual animals varied. The buffer zone was omitted when the sample area abutted stunted forest or other vegetation types (e.g. heath) considered unfavourable for occupation by gliders.

Table 5.1 Sampling regime for *P. volans* parameters assessed at Wadbilliga and Morton during the study period March 1984 to August 1986 (D: daily during sample period; M: once during the sample period; \*: undertaken over several days of the sample period).

Date of sample period	<i>P. volans</i> parameters		
	Capture and tagging of animals	Monitoring populations	Monitoring individuals
Mar-Aug	*	*	
1984 Oct		M	D
Nov		M	D
Dec		M	D
Jan		M	D
Feb		M	D
Mar		M	D
1985 Jun		M	D
Aug		M	D
Sept		M	-
Oct		M	D
Dec		M	D
Jan		M	D
1986 Feb		M	D
Mar		M	D
Apr		M	D
Jul		M	-
Aug		M	-

### 5.2.3 Capture, measurement and tagging of animals

All animals were captured by shooting down the branch on which they were perched. Animals were captured by hand after they had glided to the ground, and then placed in a hessian bag for immediate assessment. Captured individuals were weighed, measured (e.g. body length, pes length; see Table 5.1) using calipers and a ruler, and then released at the base of the tree in which they had been perched. Reproductive condition and general body condition (i.e. ectoparasite load, condition of pelage, number and position of wounds and scars, condition of molars) were also noted. Gliders with a body weight heavier than 1000 g were classified as adults and those with a body weight less than 1000 g were recorded as immatures (juveniles) (after Smith 1969). The weighing scales (Salter GEO, Sydney) were checked regularly for accuracy.

Captured gliders were ear-tagged with fingerling fish tags (Salt Lake Stamp Co., U.S.A.) and tail-tagged with plastic ear-tags, designed for use on cattle (Spackman Rural Supplies, Queanbeyan, N.S.W.), labelled with individually recognisable patterns made with Scotchlite reflective tape (3M Australia Pty Ltd, Mt Waverley, Victoria).

Many of the remaining animals of each population were identified by their distinctive pelage colouration (which varies greatly in this species), or body marks, or were distinguished by their distribution within the study area, their sex and by their association with other gliders. Dependent juveniles were identified by their association with a particular female. If the identification of untagged individuals was in doubt these data were not recorded.

### 5.2.4 Calculation of home range

To aid comparability with recently published literature, the home range of resident adult gliders (i.e. those adult gliders present

on the site during the majority of the study period) was determined using the modified minimum area method of Harvey and Barbour (1965) as adapted by Henry (1984), and Kehl and Borsboom (1984). All-night observation of gliders (following the methods outlined in Chapter 6, 6.2.1a) on nine nights spread over nine months of the study period was the minimum criterion necessary for home range estimation.

#### 5.2.5 Den tree selection and den use

Tree hollows that were regularly used (i.e. at least twice during the study period) by gliders for shelter during daylight were called dens. Trees with these hollows were called den trees. Den use and den tree selection was recorded throughout the study by noting the number of times a glider sheltered in a particular den, and the species, height and DBHOB of the den tree, respectively. The aspect, and height of the den above the ground was also recorded. Dens used more than five times during the study were called primary dens.

#### 5.2.6 Analysis of data

Whenever possible, data were analysed using parametric tests. These tests were preferred to non-parametric statistics because they are more powerful and enable more reliable interpretations of the data to be drawn, compared to the latter techniques (R.B. Cunningham, Statistical Advisor to the Faculty of Science, ANU, Canberra; pers. comm.).

All statistical analyses were performed with a programmable Hewlett-Packard calculator or on the A.N.U. Univac computer network using Fortran. All analyses, whether parametric or non-parametric, follow those outlined by Sokal and Rohlf (1969), Seber (1973), Alvey *et al.* (1982), Dobson (1983) and Norušis (1983) and are explained whenever used in the text. For example, one and two-way analysis of variance tests follow those outlined by Sokal and Rohlf (1969) in



Chapters 8-11 of their text. Assumptions of these analyses were tested (e.g. homogeneity of variances - Bartlett's test) using internal programs within *Genstat* or *SPSS*, or following that detailed by Sokal and Rohlf (1969, Chapter 13) and Norušis (1983). Critical values for statistical analyses were derived from Rohlf and Sokal (1969), Forestry and Timber Bureau (1975) or statistical packages (e.g. *Genstat*), when applicable.

### 5.3 RESULTS

Data are from 1271 hours of night observations during the period October 1984 - August 1986, inclusive.

#### 5.3 Wadbilliga

##### 5.3.1a *Population distribution and structure*

Resident adult *P. volans* at Wadbilliga were distributed relatively evenly throughout the site and most of the site (18.3 ha or 74%) was occupied permanently during the study period (see 5.3.1b). Areas avoided by resident adults did not generally differ in floristics from other areas of the site but were less structurally diverse and had relatively smaller trees on relatively drier microsites (Chapter 4). As a consequence, these areas provided fewer suitable food resources and possibly fewer tree hollows as potential dens for gliders, compared to adjacent forest. A full discussion of this appears in Section 5.4.

Eighteen resident adult gliders (9 of each sex), four non-resident adults and ten dependent juveniles, one of which subsequently became a resident adult, were identified during the study (Fig. 5.1). Of the eighteen resident adults, ten were captured, measured, ear-tagged and released (Table 5.2).

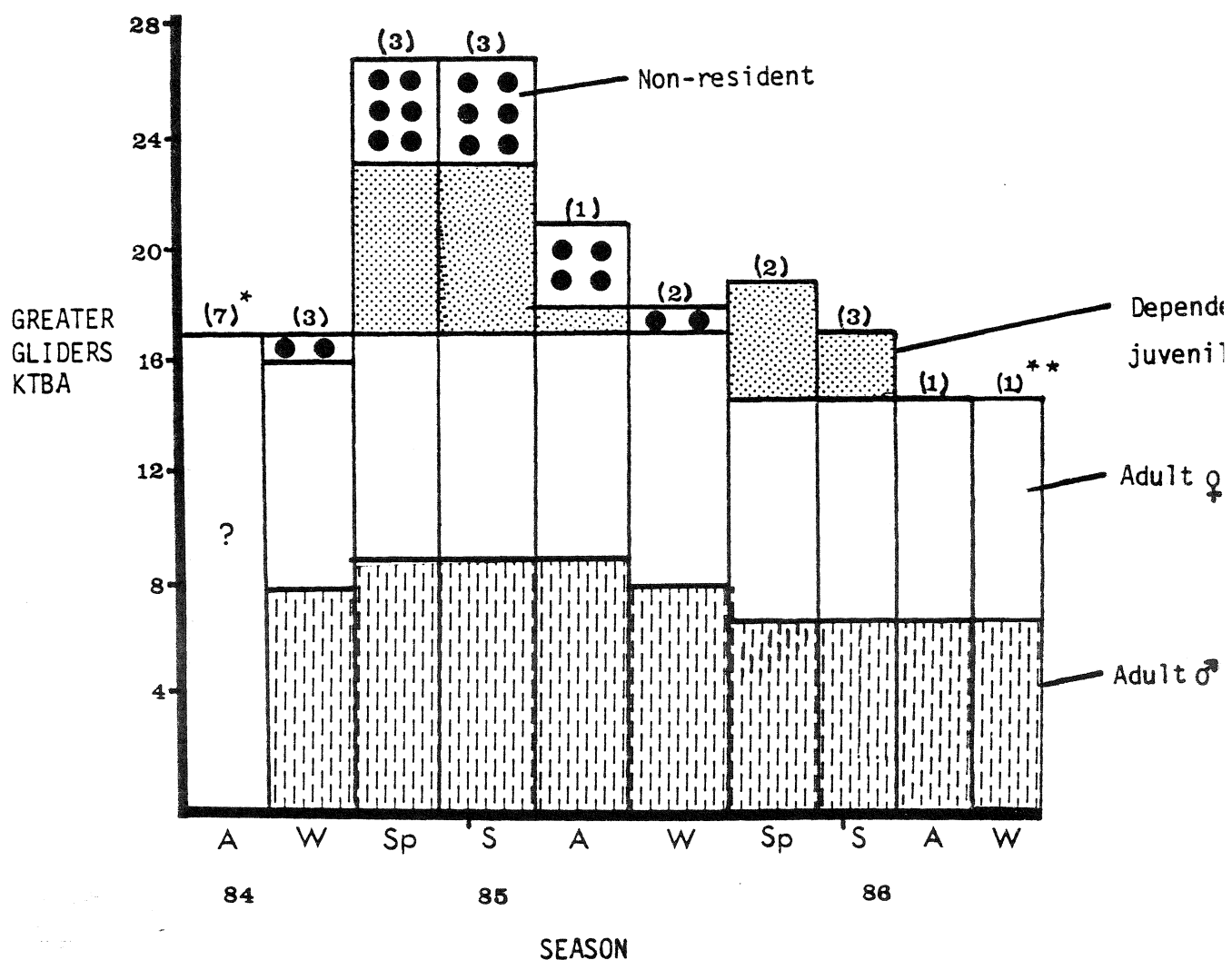


Figure 5.1 Seasonal population structure of *P. volans* known-to-be-alive (KTBA) at Wadbilliga N.P. between February 1984 and September 1986 (+population structure uncertain; ++may underestimate total population due to low sample size and problems associated with KTBA estimate). Numerals shown in parentheses represent number of sample periods during season.

**Table 5.2** Sex and number, tag, body weight and external body measurements, if known, of resident adult\* *Petauroides volans* at Wadbilliga and Morton N.P. during the study. Data given are for gliders captured between March and November 1984. All pouch young were small and did not bias female body weight significantly (M: male; F: female).

Site	Sex/No.	Tag	Weight (g)	Head-vent length (cm)	Head length (cm)	Head width (cm)	Ear (cm)	Pes (cm)	Tail (cm)	Comments
Wadbilliga										
	Male 1	Green	1360	39.1	6.53	3.28	2.57	3.74	55.2	
	M2	Red	1400	43.0	7.7	3.15	2.55	5.0	50.0	
	M3	Unmarked (UM)	-	-	-	-	-	-	-	
	M4	Blue/Red	1130	31.1	6.05	2.86	3.94	4.4	45.1	
	M5	UM	-	-	-	-	-	-	-	
	M6	Blue	1360	31.2	5.96	2.90	3.25	4.2	41.0	
	M7	UM	-	-	-	-	-	-	-	
	M8	Silver/Red	1250	31.7	6.42	3.22	3.27	4.43	47.8	
	M9	UM	-	-	-	-	-	-	-	
Mean $\pm$ S.D.			1300 $\pm$ 110	36 $\pm$ 6	6.5 $\pm$ 0.7	3.1 $\pm$ 0.2	3.1 $\pm$ 0.6	4.4 $\pm$ 0.5	47.8 $\pm$ 5.3	
	Female 1	UM	-	-	-	-	-	-	-	
	F2	Blue/Yellow	1660	39.2	6.62	3.02	3.44	4.58	51.8	
	F3	Silver/Green	1390	42.6	7.2	3.11	3.09	4.27	50.6	Pouch young ( $\delta$ )
	F4	Yellow	1265	45.4	7.78	4.39	2.68	4.2	50.4	Pouch young ( $\phi$ )
	F5	Silver	1280	36.1	5.73	3.15	2.91	3.89	43.1	
	F6	Yellow/Blue	1630	37.1	6.56	2.99	3.01	4.54	45.1	Pouch young ( $\delta$ )
	F7	UM	-	-	-	-	-	-	-	Pouch young ( $\phi$ )
	F8	UM	-	-	-	-	-	-	-	
	F9	UM	-	-	-	-	-	-	-	
Mean $\pm$ S.D.			1445 $\pm$ 189	40.1 $\pm$ 3.9	6.8 $\pm$ 0.8	3.3 $\pm$ 0.6	3.0 $\pm$ 0.3	4.3 $\pm$ 0.3	48.2 $\pm$ 3.8	
Morton										
	Male 1	Orange	1220	32.8	6.27	3.18	3.3	4.2	47.3	
	M2	Yellow	1430	40.0	7.25	4.27	3.34	4.9	52.1	
	M3	Silver	1560	32.9	6.61	3.75	3.83	4.1	49.7	
	M4	UM	-	-	-	-	-	-	-	
	Juvenile	Blue/Orange	820	26.8	6.73	3.08	2.75	4.7	45.5	
Mean $\pm$ S.D.			1403 $\pm$ 172	35.2 $\pm$ 4.1	6.7 $\pm$ 0.5	3.7 $\pm$ 0.5	3.5 $\pm$ 0.3	4.4 $\pm$ 0.4	49.7 $\pm$ 2.4	
	Female 1	Green	1425	37.2	6.97	3.52	3.8	4.2	53.1	
	F2	Red	1460	42.1	7.18	4.33	3.4	4.8	52.5	
	F3	Blue	1520	37.9	7.15	3.91	3.97	4.5	52.2	
	F4	Red/Silver	1400	43.2	7.09	3.25	2.85	4.9	50.3	
	F5	UM (White head)	-	-	-	-	-	-	-	
	F6	UM	-	-	-	-	-	-	-	
Mean $\pm$ S.D.			1451 $\pm$ 52	40.1 $\pm$ 3.0	7.1 $\pm$ 0.1	3.8 $\pm$ 0.5	3.5 $\pm$ 0.5	4.6 $\pm$ 0.3	52.0 $\pm$ 1.2	

\*Data for one juvenile male (Blue/Orange tag) are also given but are not included in mean calculations; (?) sex not known; UM : animal without tag.

The total number of *P. volans* recorded on the site varied considerably from a maximum of twenty-seven during spring and summer 1985 to fifteen during autumn and winter 1986. This variation was due primarily to fluctuations in the number of non-resident adults and dependent juveniles that were seen. In contrast, the total population of resident adult *P. volans* was relatively stable ranging from 17 in spring 1984 to 15 in autumn and winter 1986 (Fig. 5.1). Many of these animals were present throughout the study and only a few individuals disappeared from or were 'recruited' to this pool. During the study the sex ratio of resident adult *P. volans* was close to parity; in winter 1986 the ratio was 1:1.14. On average ( $n = 8$ , autumn 1984 excluded due to uncertainty about the structure of the population), sixteen adults (8 males, 8 females), one juvenile and 0.5 non-residents were present on the site during each season between winter 1984 and winter 1986. Since non-resident *P. volans* are typically excluded from the home range of resident adults and dependent juveniles overlap the home range of their mothers, the estimation of population density may best be based on the number of resident adult *P. volans*. This was 0.88 animals  $\text{ha}^{-1}$  (calculated for the area of the site permanently occupied).

Captured male *P. volans* ( $\bar{x}$  body weight (g)  $\pm$  S.D. =  $1300 \pm 110$ ,  $n = 5$ ) were similar in body weight (Student's t-test:  $t = 1.48$ ,  $df = 8$ ,  $P > 0.05$ ) to captured adult females ( $\bar{x} = 1445 \pm 189$ ,  $n = 5$ ; Table 5.2). Assuming that all resident adults conform to these mean weights this gave a biomass of  $1200 \text{ g ha}^{-1}$  for the area of the site occupied by resident adult *P. volans*.

A pair of Powerful Owls frequented the study site during September 1985, and may have been present earlier. With only 2 one-night spotlighting surveys to assess the total population of *P. volans* on the site between March and September 1985, the impact of these birds on the glider population could not be determined. However, several *P. volans* were not seen again after the owls appeared: four non-resident adult *P. volans* (3 males, 1 unknown sex) were sighted during the capture of individual gliders but were not seen again after August 1985. Two resident males (M) (M8, M9) also disappeared during the winter of 1985 while one resident female (F) (F5) disappeared during late August-early September 1985 (Table 7.3). No carcasses of *P. volans* were found during this period. The Powerful Owls were not seen, or heard calling, after October 1985.

#### 5.3.1b *Use of home range and dens*

A minimum of about 15 nights of observations (usually one sighting per night per month) was required to estimate the home range of each of the less intensively monitored resident adult *P. volans* at Wadbilliga (Fig. 5.2). The home ranges of *P. volans* observed on less than 15 nights were not calculated.

With the exception of one male (M1), all resident adult *P. volans*\* appeared to be monogamous. The home ranges of monogamous adults varied from 0.8 ha (F2) to 1.9 ha (M3, M6, F5) (Table 5.3). The home range of M1 was 1.6 ha. The mean home ranges of intensively-monitored and less-monitored individuals of the same sex were comparable (Table 5.3). Similarly, the mean home range of monogamous males ( $1.8 \pm$

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\*resident adult males not associated with females are not considered in this discussion (see 5.3.1c).

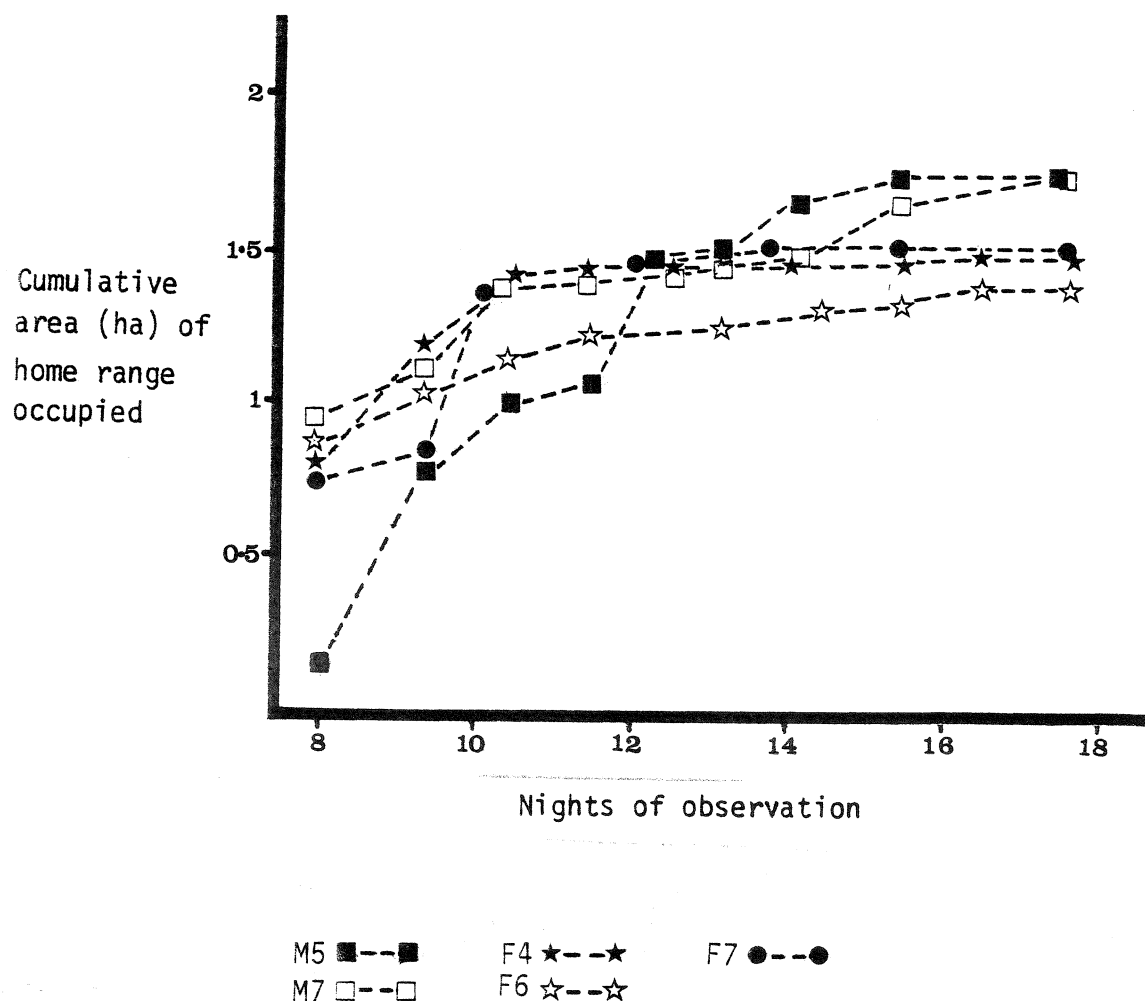


Figure 5.2 Cumulative area of home range occupied by less-intensively monitored resident adult male and female *P. volans* at Wadbilliga. Resident gliders were defined as those living on the site for a minimum of 9 months. One or two loci were typically obtained each night of observation. Generally, only one night of observation occurred in each sample month.

Table 5.3 Period on site, number of nights observed, number of loci used in home range calculation and home range estimates for resident adult *P. volans* at Wadbilliga N.P. Asterisk denotes bigamous male, all other resident adults were considered to be monogamous. Note the home ranges of animals with less than 15 loci were not calculated.

Glider	Period on site (months)	Nights seen	No. of loci	Home Range (ha)
Male 1*	23	32	219	1.6
M2	20	28	305	1.7
M3	15	17	276	1.9
Mean home range for intensively-monitored monogamous males				1.8 $\pm$ 0.1
M4	19	14	14	-
M5	22	20	22	1.7
M6	21	16	16	1.9
M7	22	30	33	1.7
M8	19	14	14	-
M9	11	06	06	-
Mean $\pm$ S.D. for other males				1.8 $\pm$ 0.1
Female 1	23	29	312	1.5
F2	20	31	402	0.8
F3	20	31	257	1.8
Mean $\pm$ S.D. for intensively-monitored females				1.4 $\pm$ 0.5
F4	22	30	30	1.4
F5	15	18	28	1.9
F6	21	33	33	1.6
F7	23	32	32	1.5
F8	11	17	17	1.5
F9	20	29	35	1.4
Mean $\pm$ S.D. for other females				1.5 $\pm$ 0.2

0.11 ha,  $n = 5$ ) was not significantly different (Student's  $t$ -test:  $df = 12$ ,  $t = 2.0$ ,  $0.05 < P < 0.1$ ) from the mean home range of resident females ( $1.5 \pm 0.31$  ha,  $n = 9$ ). (Table 5.3).

The spatial and probable breeding relationships between resident adult gliders are shown in Figure 5.3. Both sexes were relatively sedentary and remained within predictable home ranges while present on the site. The home range of males partially or completely overlapped that of their female partner (or partners in the case of M1) but never the home range of adjacent resident males. Similarly, the home range of adjacent resident adult females did not overlap except when one dependent female juvenile (F8) used part of the home range of its mother (F2) after becoming independent (Fig. 5.3).

The proportion of home range visited during nightly activities by intensively-monitored resident adult male and female *P. volans*, expressed on a seasonal basis, was between 65 and 85 per cent (Fig. 5.4). There was no significant difference in the percentage area of home range used by females during each season (one-way ANOVA:  $F_{3,35} = 1.32$ ;  $P > 0.25$ ). Females typically visited more than 60 per cent of the area of their home range but rarely more than about 75 per cent on any night, throughout the year. One-way analysis of variance indicated that there was a significant difference in home range use by male *P. volans* on a seasonal basis ( $F_{3,17} = 3.92$ ;  $P < 0.05$ ), and a GT2-method test (Sokal and Rohlf 1969, p. 248) showed that significant differences ( $df = 20$ ;  $m$  (studentised maximum modulus) = 3.17;  $P < 0.05$ ) occurred between the home range used in summer and all other seasons (Fig. 5.4). Sample sizes for the above analyses are given in Figure 5.4. During the summer, males also regularly frequented a larger proportion of their home range that overlapped with that of their female partner(s), compared to other seasons. With the exception of summer, male *P. volans* exhibited a similar pattern of



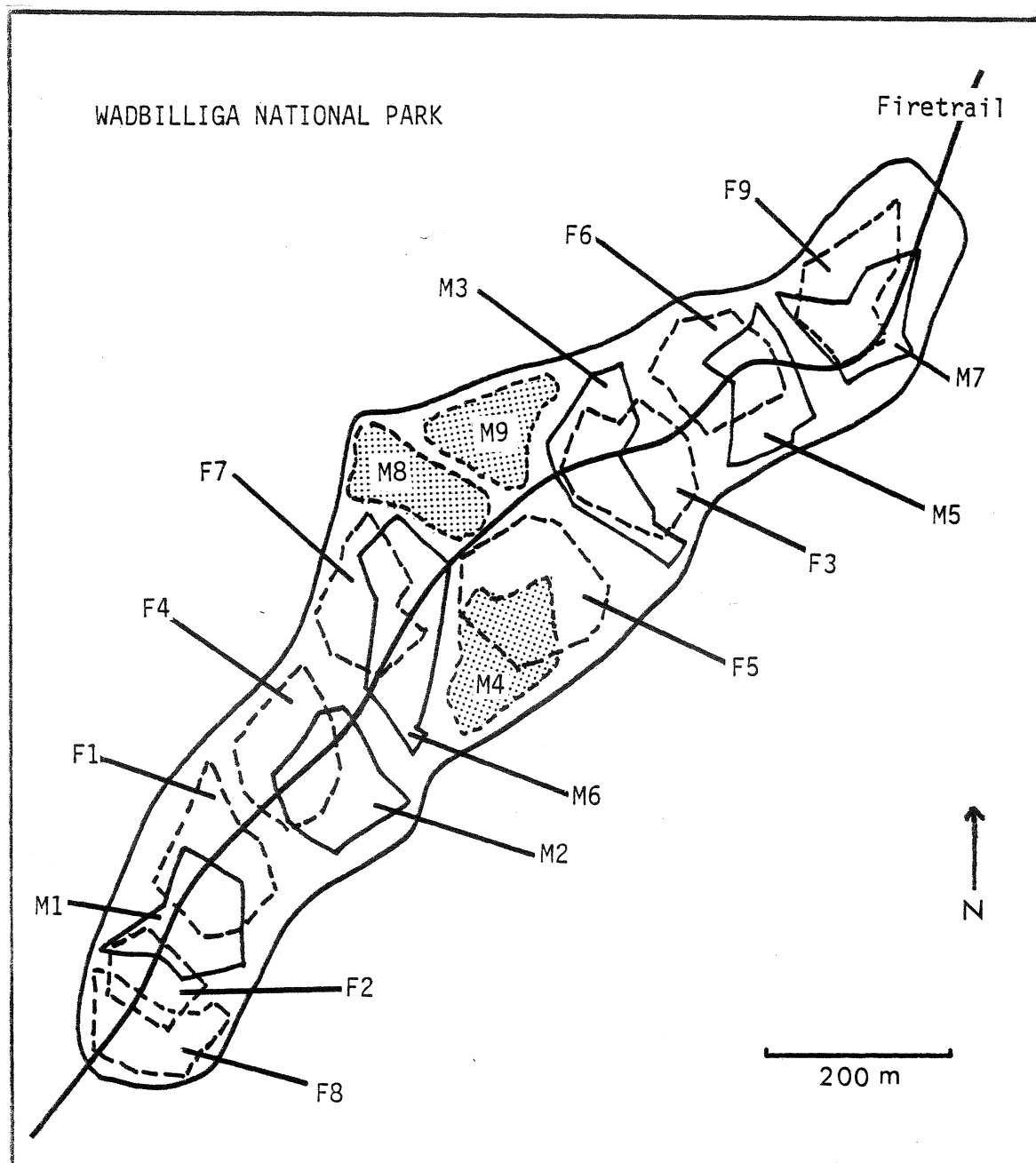


Figure 5.3 Approximate spatial arrangement of the home range of resident male (solid line) and female (dashed line) *P. volans* at Wadbilliga. Numbering of individual animals follows that given in Table 5.2. Home ranges with stippling indicate non-resident animals.

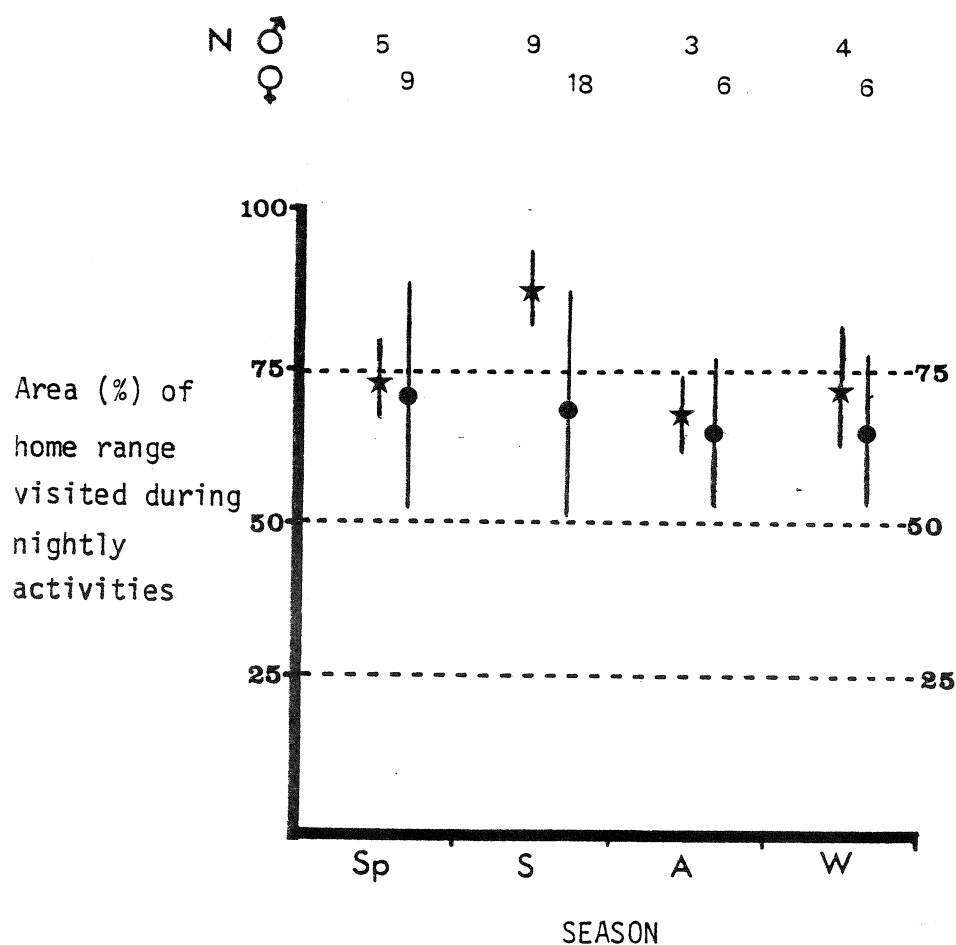


Figure 5.4 Mean percentage area of estimated home range visited by resident adult male (star) and female (circle) *P. volans* at Wadbilliga during nightly activities, expressed on a seasonal basis (vertical bar represents standard deviation, N = sample size). Note that M1 (see Table 5.3) was excluded from the calculations.

home range use to that of resident females. Male *P. volans*, however, usually appeared to visit slightly more of their home range on any one night compared to females, although the difference was not significant. The increase in ranging by male *P. volans* occurred during the season with the shortest mean night-length (hours) and appeared to be related to defence of females and/or resources (see below), mating, and probably the dispersal of newly-independent young. Changes in use of home range by resident female *P. volans* was more related to spatio-temporal variability in the availability of food resources and is discussed in Chapter 6, Sections 6.2 and 6.3.

Of nineteen tree hollows regularly used as dens by intensively monitored male and female *P. volans*, 8 were located in *Eucalyptus viminalis*, 5 in *E. dalrympleana*, 4 in *E. radiata*, and 2 in *E. fastigata*. All of these trees ('den trees') were alive. The smallest diameter at breast height over bark (DBHOB) of a den tree was 0.68 m and the largest was 1.73 m. The mean DBHOB ( $\pm$  S.D.) of all den trees was  $1.05 \pm 0.4$  m. The height above ground of dens ranged from 4.2 m to 22.7 m with a mean height ( $M \pm$  S.D.) of  $14.2 \pm 5.8$  m. There was no significant difference in the aspect (i.e. whether located in the N.W., N.E., S.W. or S.E. quadrant) of tree hollows used as dens by gliders (one-way ANOVA:  $F_{3,15} = 1.32$ ;  $P > 0.25$ ).

The number of trees used as dens by individual intensively-monitored *P. volans* was small and ranged from 2 (F2, F4) to 5 (F3). These den trees invariably contained one hollow that was suitable for denning. The mean number of dens ( $\text{no. ha}^{-1} \pm$  S.D.) used by male\* ( $2.1 \pm 0.5$ ) and female ( $2.4 \pm 0.4$ ) gliders was not significantly different (Student's t-test:  $df = 17$ ,  $t = 1.31$ ,  $P > 0.05$ ).

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\*these data do not include dens shared with female partners

Most *P. volans* regularly visited and used their den trees during each season of the study. The exception was F2 which used one of its two den trees in 82 per cent of all observations ( $n = 28$ ).

It was difficult to ascertain whether or not *P. volans* preferred certain eucalypt species as den trees. Species and individual trees may have different morphologies which lead to differences in the formation and occurrence of hollows. As a result, the expected frequency of use of den trees by gliders may not be directly related to the abundance of each tree species. At Wadbilliga, the frequency of occurrence of eucalypt species in the forest differed significantly (Chi-square test:  $df = 3$ ,  $\chi^2 = 22.85$ ,  $P < 0.001$ ) from the frequency of occurrence of species used as den trees, and this was also the case within the home range of each glider (Table 5.4). However, it was not possible to determine if these differences were due to *P. volans* selecting den trees other than at random.

The population density of *P. volans* at Wadbilliga was 0.88 gliders  $ha^{-1}$  and the mean number of den trees per hectare used by resident adults never exceeded 2.4. On this basis, the occurrence of at least 2.1 den trees  $ha^{-1}$  of forest at Wadbilliga should ensure the retention of this population density of gliders. With 17.3 trees per hectare at Wadbilliga of a size suitable for den trees (i.e.  $DBH_{OB} > 0.70$  m), even allowing for the possibility that not all of these trees had suitable unoccupied hollows, the population density of *P. volans* at Wadbilliga appeared not to be limited by the availability of den trees.

#### 5.3.1c Mating association, social cycle and population fecundity

The mating association of *P. volans* was facultative monogamy (*sensu* Kleiman 1977, 1981). Six resident adult males appeared to be monogamous and one was bigamous. Two males (M8, M9) were not associated with females (Table 5.5). One adult male from outside the site and one

Table 5.4 Chi-square analyses (Sokal and Rohlf 1969) comparing the frequency of occurrence of eucalypt species (Chapter 4) within the home range of individual, intensively-monitored male and female *P. volans* at Wadbilliga with the frequency of occurrence of eucalypt species used as den trees by these animals. Numbering of animals follows that given in Table 5.2; Ed = *Eucalyptus dalrympleana*, Ef = *E. fastigata*, Er = *E. radiata*, Ev = *E. viminalis*; \* =  $P < 0.05$ .

Glider	Eucalypt spp.	Observed frequency	Expected frequency	df	Statistic ( $\chi^2$ )	Significance level
M1	Ed	0	1.5814	2	6.10	*
	Er	1	0.1696			
	Ev	2	1.2489			
M2	Ed	1	0.1164	3	9.12	*
	Ef	0	0.3694			
	Er	0	1.3793			
	Ev	2	1.1349			
M3	Ed	0	0.0656	3	8.68	*
	Ef	1	0.1044			
	Er	0	0.9187			
	Ev	1	0.9113			
F1	Ed	0	0.8757	2	7.32	*
	Er	2	0.4108			
	Ev	1	1.7135			
F2	Ed	1	0.1802	1	4.10	*
	Ev	1	1.8198			
F3	Ed	1	0.1240	3	10.92	*
	Ef	1	0.1732			
	Er	1	1.8452			
	Ev	1	1.8575			

newly-independent female were recruited to the resident adult 'pool'. One male lost its partner for reasons unknown in spring 1985/6 (Table 5.6).

Despite the apparently strong bond between monogamous pairs of male and female gliders, some males pursued other females during the breeding season, albeit infrequently. The stimulus(i) for these forays may be related to visual and olfactory cues such as the proximity of another female glider and of her partner. For example, in March 1986 one male (M5 in Fig. 5.3) pursued and attempted to mate with a female (F9) from a home range adjacent to that of his mate. After a pursuit of 51 minutes the male returned to his normal home range. During the pursuit the female resisted mating by moving her position within the tree canopy but did not attempt to move to another part of her home range. The foray by the male glider did not extend more than some 45 metres from the boundary of its established home range. The male (M7) occupying this area was not seen during this period. Four other pursuits (i.e. M6  $\longrightarrow$  F3 (twice), M5  $\longrightarrow$  F3, M5  $\longrightarrow$  F9) under similar circumstances were observed during the 1985 and 1986 breeding seasons. No fights were observed and only one of these pursuits appeared to terminate with successful mating (i.e. M5  $\longrightarrow$  F9 in March 1986).

One male (M1 in Fig. 5.3) changed from a monogamous to a bigamous association during the study. This situation arose when the male normally associated with female F2, which occupied an area adjacent to M1, disappeared in March 1984. As the closest established male, M1 appears to have adjusted its home range to facilitate mating with F2. This male then maintained contact with F2 for the remainder of the study although their respective home ranges only partially overlapped. Further, the offspring of this pair was a female (F8) which subsequently remained within part of her mother's home range (see Fig. 5.3). Concurrently, the bigamous male glider also successfully mated, and sired a young glider (unknown sex) with its original female partner (F1).

Table 5.5 Mating association of resident adult *P. volans* at Wadbilliga during the study (F8 remained on the site when she became independent of her mother, F2; M4 became single when F5 disappeared - probably taken by a Powerful Owl).

Season	1984		1985				1986		
	W	Sp	S	A	W	Sp	S	A	W
Bigamous association	1 M1,F1,F2	1	1	1	1	1	1	1	1
Monogamous pairs	6 M2-F4, M6-F7 M4-F5, M7-F9 M5-F6, M3-F3	6	6	6	6	5	5	5	5
Not associated with opposite sex	1 M8	2	2	2	2	2 F8,M4	2	2	2
Recruitments	0	1 M9	0	0	1 F8	0	0	0	0
Disappearances	0	0	0	0	1 M9	2 M8,F5	0	0	0

The annual social cycle (*sensu* Henry 1985) of *P. volans* is given in Figure 5.5. All matings between gliders over two social cycles (i.e. February 1984–September 1986) were observed between February 10th and May 6th although 66 per cent of all copulations ( $n = 12$ ) were observed in March and April. Males shared dens with associated females between February 10th and September 28th. During this period the bigamous male (M1) shared the dens of both associated females (F1 and F2) although most time was spent with F1. Breeding males were solitary between September 28th and February 10th (Fig. 5.5).

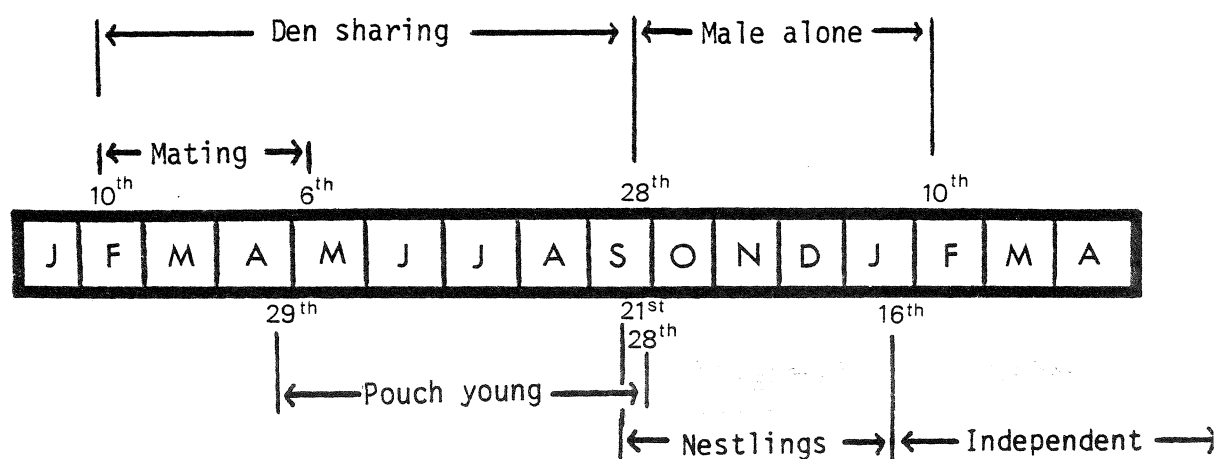
Female *P. volans* carried pouch young between April 29th and September 28th and maintained nestlings between September 21st and January 16th during the study. With the exception of F8, which remained within part of its mother's home range on becoming independent after March 14th 1985, all juveniles were independent by January 16th of the year following their conception (Fig. 5.5). Juveniles dispersed from the site during a 5–6 week period after January 16th, by which time they were about 11 months old.

Female *P. volans* are monovular and polyoestrus and annual fecundity of individuals never exceeds one. Annual population fecundity at Wadbilliga varied from 75 per cent in the 1984/5 breeding season to 57 per cent in the following breeding season (Table 5.6). In the 1984/5 season six of the eight resident female *P. volans* raised young (3 males, 1 female, 2 unknown sex). In the following season three of these females again raised young along with F9, which had failed to raise offspring in the 1984/5 season (Table 5.6).

No information on the mortality of small young is available. Two females (F2, F5) which were captured and inspected in the 1984/5 breeding season were not carrying young in the pouch although F2 was



Adult male / female



Mother / young

Figure 5.5 Annual social cycle (*sensu* Henry 1985) of resident adult *P. volans* at Wadbilliga. Dates shown encompass interactions observed between associated males and females (above month line), and mother and young (below month line) for two social cycles between February 1984 and September 1986. Total duration of interactions shown underestimates true duration by no more than 28 days.

Table 5.6 Annual population fecundity of resident adult *P. volans* at Wadbilliga during the study. Numbering of females follows that given in Table 5.2. Juveniles of unknown sex are shown by question mark. F8 omitted from 1985/6 breeding population due to the extended period of dependency on its mother (F2).

Female	Offspring for breeding season	
	1984/5	1985/6
F1	—————> ?	—————> ?
F2	—————> ♀ (F8)	—————> ?
F3	—————> ♂	—————> ?
F4	—————> ♀	
F5		Disappeared
F6	—————> ♂	
F7	—————> ?	
F9		—————> ♀
Annual population fecundity	75%	57%

(known female body weights (g) during 1984/5 breeding season: F2 - 1660, F3 - 1390, F4 - 1265, F5 - 1280, F6 - 1630)

observed later with a young in the pouch. Two of the three females which failed to raise young in the 1985/6 season were observed mating with their partners. Thus at least 29 percent of mated females failed to raise young in the 1985/6 season and some mated females also probably failed to raise young in the previous year.

#### 5.3.1d *Communication and social interactions*

A detailed description of the communication, social behaviours and interactions between adults, and adults and young are not directly relevant to the objectives of this study and will be considered elsewhere. As a summary, both male and female *P. volans* regularly mark parts of their home range with scent (from the cloacal region) and urine. For intensively-monitored individuals, the mean number of markings per night ( $\pm$  S.D.) ranged from  $10.3 \pm 3.2$  ( $n = 6$ ) in winter to  $17.0 \pm 3.4$  ( $n = 9$ ) in spring, and  $12.1 \pm 2.9$  ( $n = 6$ ) in winter to  $14.2 \pm 5.4$  ( $n = 18$ ) in summer for males and females, respectively.

Juvenile young apparently dispersed from the study site soon after becoming independent of their mothers. Only one agonistic encounter (between F9 and its daughter) was observed at this time.

Non-resident *P. volans* were generally restricted to the periphery of the general area occupied by resident *P. volans* (see Fig. 5.3). In some instances, non-residents were observed traversing this area but their movements (frequently gliding) were usually swift and distant. For example, during November 1984 one non-resident *P. volans* was sighted three times in approximately 40 minutes in separate parts of the site. During this period it had moved at least 470 metres and encroached on the home range of several gliders. Resident male

*P. volans* were not observed pursuing gliders that entered their home range and since transient gliders spent little time in occupied forest areas it is assumed that olfactory cues play a significant role in maintaining the established home range boundaries of resident adults.

### 5.3.2 Morton

#### 5.3.2a *Population distribution and structure*

In contrast to the resident *P. volans* at Wadbilliga, the adult gliders observed at Morton had a clumped distribution which mirrored the distribution of a diversity of *Eucalyptus* spp. and *Syncarpia glomulifera* in a given area (see Chapter 4, Sub-section 4.3.2). Eight resident adult gliders (3 males, 5 females) and three non-resident adults were identified within forest type B during the study (Fig. 5.6). A total of five individual *P. volans* (1 male, 1 female, 1 dependent juvenile male that subsequently dispersed, 1 dependent juvenile female that later became a resident, 1 non-resident male) were observed at forest type C during the study while no *P. volans* were seen in forest type A (i.e. a forest stand dominated by *E. gummifera* and *E. piperita*). Thus, the average seasonal population of resident adult *P. volans* was 3 males and 4 females in forest type B and 1 male and 1 female in forest type C.

Nearly eight hectares or 91.9 per cent of forest type B was occupied by resident adult *P. volans*, giving a population density of 0.89 animals ha<sup>-1</sup> during the study. Resident adult *P. volans* occupied 100 per cent of forest type C which gave a population density of 1.67 animals ha<sup>-1</sup>. The calculations of population density are based on the area of forest in each forest type that was occupied by the mean seasonal number of resident *P. volans* (for full discussion see Section 5.4).

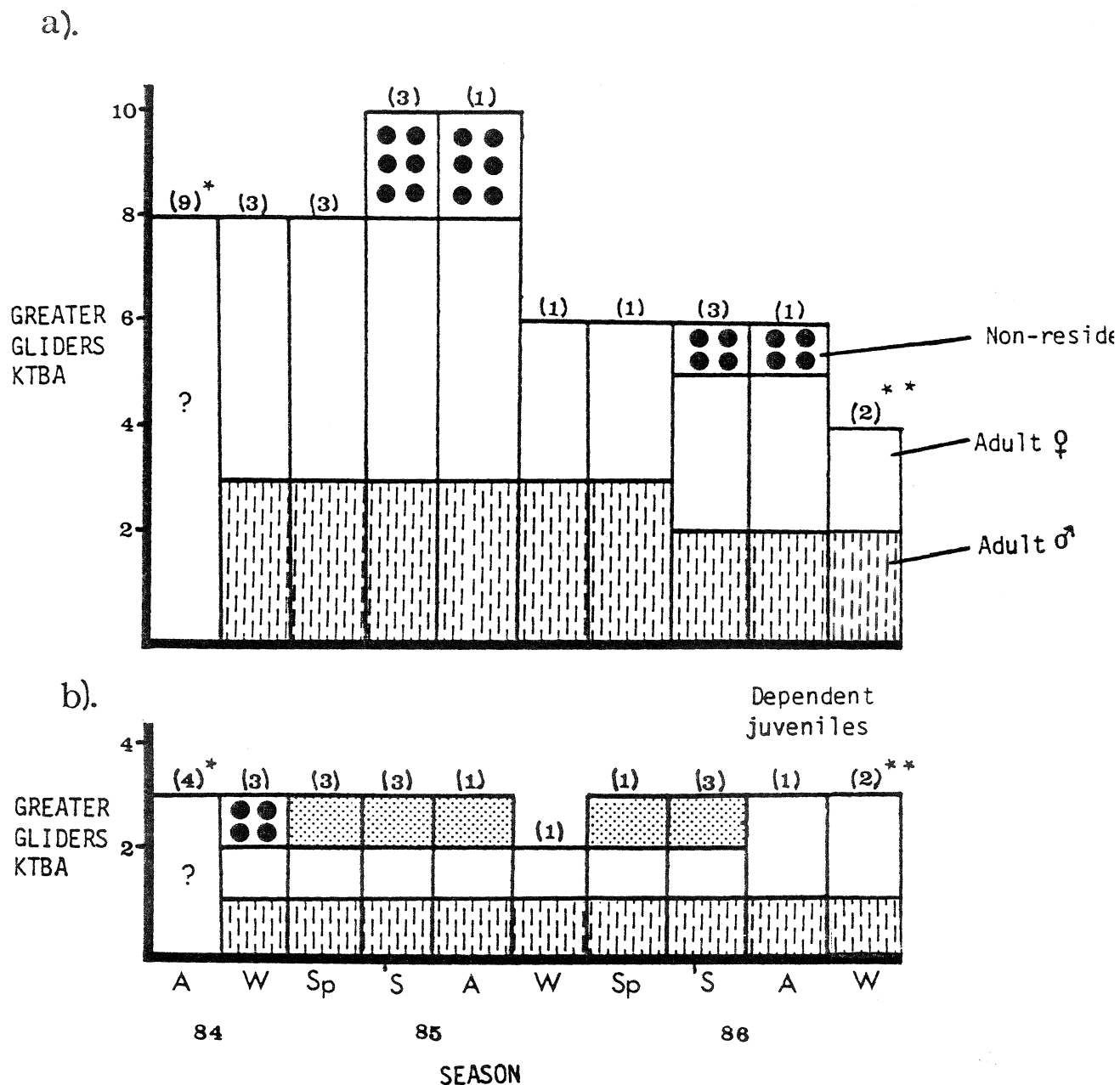


Figure 5.6 Seasonal population structure of *P. volans* known-to-be-alive (KTBA) in forest type B (a), and forest type C (b) at Morton N.P. (+population structure not known; ++may underestimate total population due to low sample size and problems associated with KTBA estimate). Numerals shown in parentheses represent number of sample periods during season. See text for full explanation.

Of the sixteen individuals observed at Morton, eight *P. volans* were captured, measured, ear-tagged and released (Table 5.2).

The total number of *P. volans* seen in forest type B ranged from a maximum of ten in spring and summer 1985 to four in winter 1986 (Fig. 5.6). Similarly, the number of resident adult *P. volans* varied from a maximum of eight (3 males, 5 females) in winter 1984 to four (2 males, 2 females) in winter 1986. Thus only two male gliders (M1, M3; see Tables 5.2 and 5.7, and Fig. 5.6 for numbering of individuals) and two females occupied part of forest type B for the duration of the study. The sex ratio of residents was female-biased (1:1.67) between winter 1984 and autumn 1985 but moved to parity (1:1) in winter and spring 1985. No juveniles were raised by any resident females (Fig. 5.6).

Only one pair of *P. volans* (M4, F6) was resident within forest type C and was present for the duration of the study (Fig. 5.6). The fecundity of this pair of gliders and the status of this mating association is considered later (5.3.2c). A non-resident male *P. volans* was sighted during winter 1984 and may have been present in the preceding season.

Since the adult *P. volans* resident in forest type C were not captured, their body weights cannot be compared with those *P. volans* resident in forest type B. The mean body weight (g)  $\pm$  S.D. of adult male ( $1403 \pm 172$ ,  $n = 3$ ) and female ( $1451 \pm 52$ ,  $n = 4$ ) *P. volans* captured in forest type B were not significantly different (Student's t-test:  $df = 5$ ,  $t = 0.54$ ,  $P > 0.05$ ; Table 5.2). Assuming that all resident adults conform to these mean weights this gave a biomass of  $1164.3 \text{ g ha}^{-1}$  for forest type B and  $2378.3 \text{ g ha}^{-1}$  for forest type C.

Table 5.7      Period on site, number of nights observed, number of loci used for home range calculation and home range estimates for resident adult male (M) and female (F) *P. volans* in forest type B (a), and forest type C (b) at Morton during the study (asterisk denotes intensively-studied gliders). All gliders in forest type B were considered to be monogamous. M4 in forest type C became bigamous in 1986.

Glider		Period on site (months)	Nights seen	No. of loci	Home range (ha)
<hr/>					
a)	M1*	22	31	261	1.3
	M2*	19	19	215	1.4
	M3	22	34	34	1.4
Mean $\pm$ S.D. for males					1.4 $\pm$ 0.1
<hr/>					
	F1*	22	30	483	1.5
	F2*	21	32	263	1.5
	F3	12	17	17	1.3
	F4	12	15	16	1.5
	F5	22	22	26	1.6
Mean $\pm$ S.D. for females					1.5 $\pm$ 0.1
<hr/>					
b)	M4*	23	30	224	1.4
	F6*	23	28	290	0.9
<hr/>					

During the study three resident *P. volans* (M2, F3, F4 and F5 in Fig. 5.7) disappeared from forest type B. The reason for this was unknown (see Section 5.4). The only predators regularly seen or heard on the site were the Lace Monitor *Varanus varius* (Shaw), the Barn Owl *Tyto alba* (Scopoli) and the Boobook Owl *Ninox novaeseelandiae* (Latham). However, it is doubtful whether *P. volans* would have been taken by these animals.

#### 5.3.2b *Use of home range and dens*

A minimum of about 12 nights of observations was required to estimate reasonably the home range of each less-intensively monitored resident adult *P. volans*. All resident gliders were observed regularly and all of their home ranges were calculated. With the exception of M4, all resident *P. volans* at Morton were monogamous. The home ranges of animals varied from 0.9 ha (F6) to 1.6 ha (F5) (Table 5.7). Within forest type B the home range of intensively-monitored gliders and less-monitored individuals did not differ significantly (Student's t-test:  $df = 6$ ,  $t = -0.74$ ,  $P > 0.05$ ), nor was the mean home range for each sex (males  $1.4 \pm 0.1$  ha, females  $1.5 \pm 0.1$  ha) significantly different (Student's t-test:  $df = 6$ ,  $t = -1.63$ ,  $P > 0.05$ ).

Both resident adult Greater Gliders (M4, F6) within forest type C were intensively monitored. The home range of M4 (1.4 ha) overlapped that of F6 and was similar in size to the home ranges of resident adult males in forest type B. M4 occasionally ranged into portions of forest type A which were adjacent to forest type C. In contrast, F6 had a much smaller home range than all female gliders resident in forest type B (Table 5.7).

The spatial and probable breeding relationships between resident adult *P. volans* in both forest types B and C are shown in Figure 5.7. Most gliders were relatively sedentary and generally remained within



predictable home ranges while present on the site. Within forest type B, the home range of males never completely overlapped that of their partner or appeared to overlap other males. However, in the case of M2 and M3, part of their respective home ranges abutted. In contrast, the home ranges of females partially overlapped in two <sup>instances</sup> although these gliders were rarely observed in proximity.

The proportion of home range visited during nightly activities by intensively-monitored resident adult male and female *P. volans* was between 70 per cent and 85 per cent (Fig. 5.8). Home range use by M1 and M2 in forest type B and M4 in forest type C was similar, hence all data for males were pooled. There was no significant difference in the percentage area of home range used by male *P. volans* during each season (one-way ANOVA:  $F_{3,31} = 1.34$ ;  $P > 0.25$ ). Resident female *P. volans* in forest type B and F6 in forest type C routinely visited about 70 to 85 per cent of their respective home ranges each night and this pattern did not vary significantly between seasons (one-way ANOVAS, Forest type B:  $F_{3,21} = 0.80$ ,  $P > 0.25$ ; Forest type C:  $F_{3,9} = 0.67$ ,  $P > 0.05$ ) (Fig. 5.8). Thus, irrespective of forest type, resident adult male and female *P. volans* typically visited between about 70 and 85 per cent of their respective home ranges on any one night of the year, although males appeared to visit proportionally slightly more of their home range on any one night, compared to females.

Sixteen tree hollows were regularly used as dens by intensively-monitored male and female *P. volans* in forest type B. Eight dens were located in *Eucalyptus piperita*, 5 in *Syncarpia glomulifera*, and 3 in *E. gummifera*. No *E. sieberi* were used as den trees. In forest type C, F6 and M4 used 5 den trees, 4 of which were *E. piperita* and 1

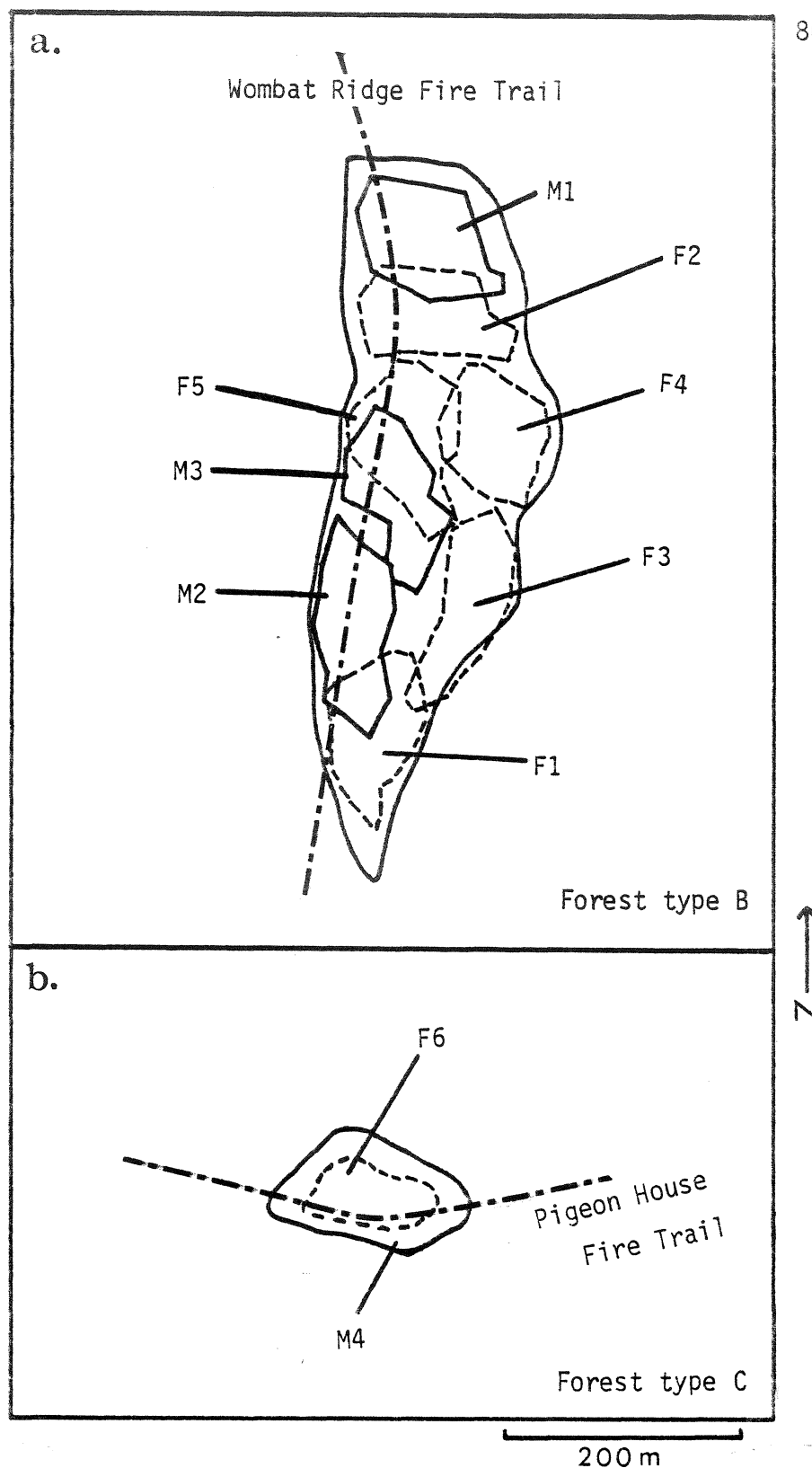


Figure 5.7 Approximate spatial arrangement of the home range of resident male (solid line) and female (dashed line) *P. volans* in in forest type B (a) and forest type C (b) at Morton. Numbering of individual animals follows that given in Table 5.2.

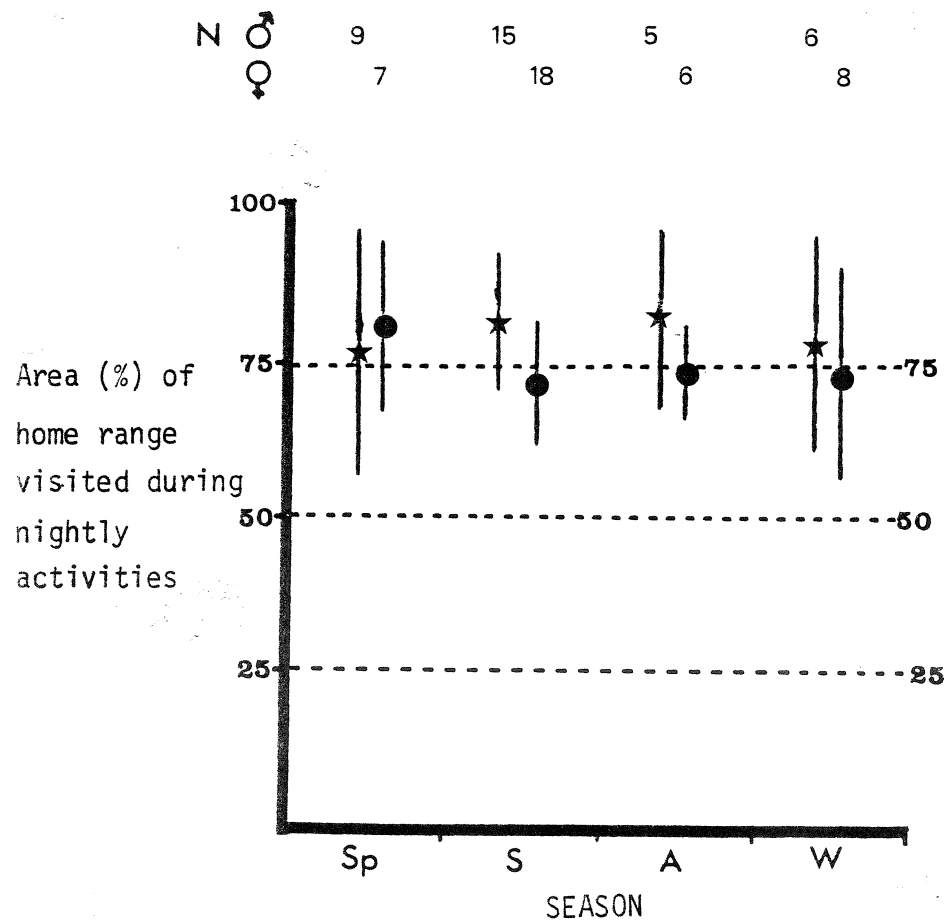


Figure 5.8 Mean percentage area of estimated home range visited by resident adult male (star) and female (circle) *P. volans* in forest types B and C at Morton during nightly activities, expressed on a seasonal basis (vertical bar represents standard deviation, N = sample size). Note that data for males, and females in both forest types were pooled since their home range use in each season was not significantly different (see text).

in *E. pellita*. *E. sieberi*, *E. gummifera* and *E. consideniana* were not used as den trees. Suitable hollows in dead trees and in live trees were used by *P. volans*.

There was no significant difference between the DBHOB of trees used by *P. volans* for denning in forest types B and C, or the height above ground of dens in each forest type (Student's t-tests: DBHOB:  $df = 19$ ,  $t = 1.25$ ,  $P > 0.2$ ; Height:  $df = 19$ ,  $t = 0.94$ ,  $P > 0.2$ ). The DBHOB of den trees ranged from 0.51 m to 1.43 m and the mean DBHOB ( $\pm$  S.D.) was  $0.86 \pm 0.3$  m. The height above ground of dens ranged from 3.7 m to 15.4 m with a mean height ( $\pm$  S.D.) of  $9.7 \pm 4.0$  m. One-way analysis of variance showed no significant difference in the aspect of tree hollows used as dens by *P. volans* ( $F_{3,17} = 0.98$ ,  $P > 0.25$ ).

The frequency of occurrence of the tree species in the forest differed significantly from the frequency of occurrence of species used as den trees by resident *P. volans* in forest type C but not in forest type B (Table 5.8).

The number of trees used as dens by intensively-monitored *P. volans* in both forest types was similar and ranged from 2 (F6 in forest type C) to 4 (e.g. M2, F2). As found at Wadbilliga, *P. volans* invariably used one hollow per den tree. The mean number of dens ( $\text{no. ha}^{-1} \pm$  S.D.) used by male (excluding dens shared with their female partner) and female gliders was  $2.7 \pm 0.5$  and  $2.3 \pm 0.4$ , respectively and did not differ significantly (Student's t-test:  $df = 4$ ,  $t = 2.17$ ,  $P > 0.05$ ). Most gliders regularly visited and used their den trees during each season of the study.

Table 5.8 Chi-square analyses (Sokal and Rohlf 1969) comparing the frequency of occurrence of eucalypt species (Chapter 4) at Morton forest types B and C to the frequency of occurrence of eucalypt species used as den trees by intensively-monitored *P. volans*. Numbering of animals follows that given in Table 5.2; NS = not significant; \* =  $P < 0.05$ .

Tree spp.	Observed frequency	Expected frequency	df	Statistic ( $\chi^2$ )	Significance level
Forest type B					
<i>E. gummifera</i>	3	3.7990	3	2.81	NS
<i>E. piperita</i>	8	5.8798			
<i>E. sieberi</i>	0	1.8128			
<i>Syncarpia glomulifera</i>	5	4.4611			
Forest type C					
<i>E. consideniana</i>	0	0.1432	4	10.73	*
<i>E. gummifera</i>	0	0.8476			
<i>E. pellita</i>	1	1.8619			
<i>E. piperita</i>	4	0.1281			
<i>E. sieberi</i>	0	2.0192			

With a population density of *P. volans* at Morton of 0.89 gliders ha<sup>-1</sup> in forest type B and 1.67 gliders ha<sup>-1</sup> at C, and a maximum mean number of 2.7 den trees per hectare used by resident adult *P. volans*, the occurrence of at least 2.4 den trees ha<sup>-1</sup> in forest type B and 4.5 den trees ha<sup>-1</sup> in forest type C should ensure retention of this density of gliders in both forest types. The number of trees ha<sup>-1</sup> of a size likely to contain suitable hollows for dens (i.e. DBHOB >0.55 m) was 34.2, 42.0 and 21.7 for forest types A, B and C respectively. Hence, even allowing for the possibility that not all of these trees had suitable unoccupied hollows, it appeared unlikely that the population density and distribution of *P. volans* at Morton was limited by the availability of dens.

### 5.3.2c *Mating association, social cycle and population fecundity*

The observed mating association of *P. volans* at Morton varied between forest types. It was monogamy in forest type B and facultative monogamy (*sensu* Kleiman 1977, 1981) in forest type C. Three resident adult males and females (i.e. M1-F2, M2-F1, M3-F5; in Fig. 5.7) in forest type B, and 2 adults (M4, F6) in forest type C were consistently associated throughout most of the study. One resident female (F3) apparently was not associated with any male resident in forest type B although it was infrequently associated with at least one non-resident male *P. volans*. One female *P. volans* (F4 in Fig. 5.7) resident in forest type B was not known to be associated with any male (resident or transient).

Only one pair of *P. volans*, M4 and F6 in forest type C, successfully raised young during the study. This pair raised one young during both breeding seasons covered by the study (i.e. a male in 1984/5, a female in 1985/6; see Table 5.2). The juvenile male disappeared, presumably dispersed, from forest type C after mid-March 1985. In

contrast, the newly-independent juvenile female (F7) remained associated (home ranges partially overlapped) with its parents (see Fig. 5.7) and was still present within a similar area during August 1986. Hence M4 probably formed a bigamous association between F6, and their daughter once she reached sexual maturity.

The annual social cycle of *P. volans* at Morton was similar to that for Wadbilliga (see Fig. 5.5) with some exceptions which appear closely related to the significantly reduced population fecundity of this site relative to that at Wadbilliga. Five matings were observed (60% of these in March) between February and May over the two social cycles covered by the study. Paired resident adult *P. volans* shared dens between February and August and males were usually solitary between mid-August and mid-February.

The social cycle and activities of females known to have been mated were similar although females resident in forest type B failed to raise young during both breeding seasons of the study. No data are available on the mortality rates of small young. Four females (F1, F2, F3, F4) captured for tagging during early June 1984 were not carrying pouch young. Of these females, F1 and F2 were probably associated with resident males (Fig. 5.7).

The annual fecundity of the populations of *P. volans* at Morton was the same for both breeding seasons. That is, zero for forest type B (3 resident pairs) and 100 percent for forest type C (1 resident pair).

#### 5.3.2d *Communication and social interactions*

Resident male and female *P. volans* regularly marked parts of their home range with scent and/or urine. For intensively-monitored individuals (Table 5.6) in occupied forest types B and C, the mean number of scent markings per night ( $\pm$  S.D.; expressed on a seasonal basis) was in the range  $12.1 \pm 4.4$  ( $n = 18$ , females in summer) to  $18.7 \pm 5.2$  ( $n = 15$ , males in summer).

Twenty-one agonistic encounters between resident adults were observed during the study but the majority of these ( $n = 15$ ) were restricted to females with overlapping home ranges in forest type B (Fig. 5.7), all of which were initiated when females were feeding in the same area at the same time. This invariably occurred in winter or early spring (Fig. 5.8). Female antagonists rarely fought ( $n = 3$ ), usually one female would retreat after a confrontation of several minutes duration and move to an adjacent feeding area (see Sub-section 6.3.3).

Agonistic encounters between males in forest type B ( $n = 6$ ) invariably occurred when non-residents entered the home range of resident male *P. volans* for several minutes duration.

Four of the six incursions by non-residents occurred before the breeding season and appeared to be directed more towards the resident male than to his mate which often was not nearby. Resident male *P. volans* responded by chasing the intruder from the area. No fights were observed.

No agonistic encounters between adult and juvenile *P. volans* were observed.



## 5.4 DISCUSSION

### 5.4.1 Social organisation in relation to forest productivity

A summary of the social organisation of resident adult *P. volans* at Morton and Wadbilliga is shown in Table 5.9. Data on the social organisation of *P. volans* at Glengarry North, south east Victoria (adapted from Henry 1984, 1985) are also included for comparison. In Chapter 4 I showed that the productivity of forest sites, as measured by the concentrations of foliar nutrients and the total mean basal area of eucalypt species present in each forest, increased from Morton forest type A, through forest types B and C to the Wadbilliga site. The change in the ratio of *Symphyomyrtus* to *Monocalyptus* eucalypts across these forests also was consistent with the presence of a gradient in productivity. The social organisation of *P. volans* appeared to respond to this gradient in forest site productivity. This response is considered below.

#### 5.4.1a Population distribution and structure

In contrast to the resident *P. volans* at Wadbilliga which were relatively evenly distributed throughout the site, the resident adult *P. volans* at Morton had a clumped distribution and only 19.6% of the total site was occupied. Resident *P. volans* were absent from forest type A (40.3 ha) but occupied forest types B (8.6 ha) and C (1.2 ha). Wadbilliga and Morton were selected originally for study on the basis that they had a relatively high (Wadbilliga) and relatively low (Morton) population density of *P. volans* but this initial assessment was misleading. If the density of populations of gliders at Morton was based on the entire area of the site then the number of resident adult *P. volans* per hectare was 0.18. However, if the density of gliders was based on the area of forest apparently suitable for occupation then the population density of *P. volans* in forest type B (0.89 animals ha<sup>-1</sup>) and forest type C (1.67 animals ha<sup>-1</sup>) was actually higher than the density of *P. volans* at Wadbilliga (0.88 animals ha<sup>-1</sup>; Table 5.9).

Table 5.9 Summary of the social organisation of resident adult *Petauroideus volans* at Morton, Wadbilliga and Glengarry North, south east Victoria. Data for Glengarry North are adapted from Henry (1984, 1985) and data for the forest site parameters assessed in this study are given in Chapter 4. +: statistic shown is mean  $\pm$  S.D., number of animals is given in parentheses; ++: statistic shown is mean  $\pm$  S.D., number of females is given in parentheses.

Parameter	Morton forest types			Wadbilliga	Glengarry North
	A	B	C		
Area of site (ha)	40.3	8.6	1.2	24.6	116
Proportion of site occupied by gliders (%)	0	92	100	74	36
Population density of gliders (animals ha <sup>-1</sup> )	-	0.89	1.67	0.88	0.48
Effect of the availability of den trees and predation on the population density of gliders	not limiting (NL)	NL	NL	NL	NL
Biomass of gliders (g ha <sup>-1</sup> )	-	1164.3	2378.3	1200	645
Sex ratio (males:females)	-	1:1.33	1:1	1:1-1:1.14	1:1.5
Gliders without a regular partner	-	2 females	0	2 males	2 females
Mating association	-	monogamous	facultative monogamy	facultative monogamy	facultative monogamy
Mean annual population fecundity (%) <sup>+</sup>	-	0 (4)	100 (1)	66 $\pm$ 12.7 (8)	50 in 1982 (12)
Females known to be mated but not breeding (%)	-	>50	0	>29 in 1985/6	probably <50 in 1982/3
Mean home range (ha) <sup>+</sup> : Bigamous males	-	-	1.4 (1)	1.6 (1)	2.1 $\pm$ 0.66 (4)
Monogamous males	-	1.4 $\pm$ 0.1 (3)	-	1.8 $\pm$ 0.11 (5)	1.4 $\pm$ 0.19 (2)
Females	-	1.5 $\pm$ 0.1 (4)	0.9 (1)	1.5 $\pm$ 0.33 (8)	1.3 $\pm$ 0.46 (9)
Occurrence of overlap of female home ranges	-	relatively high	-	extremely low	relatively low
No. of agonistic behaviours observed between females	-	15	-	0	3
Average no. of <i>P. volans</i> resident during the study period <sup>++</sup>	0	7 $\pm$ 2.0 (4)	2 (1)	16 $\pm$ 0.1 (8)	20 $\pm$ 1.9 (12)

All of the above estimates of population density for *P. volans* fall within the range of values cited in the literature for other areas of Australia (Table 5.10). The population density of *P. volans* for the Morton site as a whole ( $0.18 \text{ animals ha}^{-1}$ ) was similar to the population density of *P. volans* studied at Armidale ( $0.24 \text{ animals ha}^{-1}$ ) by Griffith (1973). The estimate of Griffith (1973) also included forest not occupied by gliders. The population density of *P. volans* at Wadbilliga and Morton forest types B and C were higher than that ( $0.56 \text{ animals ha}^{-1}$ ) at Glengarry North, south east Victoria (Henry 1985), which is the only long-term study of the social organisation of *P. volans* published. Unlike my study, Henry (1985) included non-residents and dependent juveniles in his estimation of the population density of *P. volans*. If these animals are excluded, the population density of *P. volans* at Glengarry North was  $0.48 \text{ animals ha}^{-1}$  (Table 5.9).

My data emphasise the point illustrated by Braithwaite (1983) and raised by Henry (1985, p. 194), that the distribution of *P. volans* may be extremely clumped. It then becomes important to define carefully the habitat of populations of *P. volans* when estimating their density. My data also show that an estimate of population density, when considered alone, may not adequately reflect the actual productivity or quality of the habitat occupied by *P. volans*.

All of the populations of resident adult *P. volans* that were monitored during this study were similar in that they were relatively stable and very few individuals were lost or recruited. Each population did contain a few non-resident adults which appeared to immigrate and emigrate at random, possibly seeking access to favourable habitat and/or partners (see 5.4.1c).

Table 5.10 Data on aspects of the population ecology of *Petauroides volans*; method of home range calculation: 1. 'Minimum area method' (Hayne 1949), 2. 'Modified minimum home range method' (Harvey and Barbour 1965); \*: estimate of population density based on the mean total number of sightings in a four hectare sample plot.

Location	Habitat	Length of study (months)	Size of study area (ha)	Sample size	Sex ratio	Population density (ha <sup>-1</sup> )	Home range (ha)	Method of home range calculation	Source
Buccleuch S.F. near Tumut, NSW	Wet sclerophyll forest	9 (over 5 yrs)	2226 (consisted of several forestry coupes)	790	1:1.56	1.16 - 2.55	-	-	Tyndale-Biscoe and Smith (1969)
Styx River S.F. near Armidale, NSW	Dry and wet sclerophyll forest	6	165 (a road transect 33 km in length)	-	1:2.23	0.25	-	-	Griffith (1973)
Eucalypt forests being harvested for woodpulp at Eden, N.S.W.	Dry and wet sclerophyll forest	18	5606	373	-	0-60 (animals per 100/ha)			
Wongi S.F. near Maryborough in SE Queensland	Coastal woodland	58	30	13-19	-	1.6 - 2.3	♂ 2.6 ♀ 2.5	1 & 2	Kehl and Borsboom (1984)
Coolangubra S.F. near Bombala, NSW	Wet sclerophyll	-	100	84	-	0.5 - 1.3	-	-	Kavanagh (1984; pers. comm.)
Bondi S.F. near Bombala, N.S.W.	Riparian eucalypt forest corridors retained within a pine plantation	4 (over 2 years)	Varied	-	-	0.08 - 1.36	-	-	Shields (1985)
Kioloa S.F. near Batemans Bay, NSW	Wet and dry sclerophyll forest with patches of temperate rainforest	60+	8000	-	-	0.0 - 2.25*	-	-	(Davey pers. com)

No data are available on the distance dispersed by newly-independent young; on the long-distance movements of non-established adults; or on the ability of these gliders to colonise favourable but unoccupied forests. The success rate for the establishment of permanent territories by non-residents was very low (e.g. one adult male (M9) at Wadbilliga) in this study, which is a similar situation to that reported for *P. volans* at Glengarry North (Henry 1984).

The main predator of *P. volans* is the Powerful Owl *Ninox strenua* (Seebeck 1976; Tilley 1982). These owls may range over an area in excess of 800ha (Seebeck 1976) and a pair of owls may kill one glider per night (Fleay 1968). Hence, owls may have a significant influence on populations of *P. volans*. A pair of owls were present at Wadbilliga during part of the study. Some *P. volans*, including one resident female, were probably taken by these birds but they had a minimal effect on the density of the resident population. Henry (1985) reported that several *N. strenua* were resident at Glengarry North but probably only one *P. volans* was taken. In contrast, during approximately the same period as this study, the resident population of *P. volans* at Waratah Creek, Coolangubra State Forest, N.S.W. (some 65 km SSE of Wadbilliga) was reduced to about eight per cent of its original density due to predation by Powerful Owls (R.P. Kavanagh pers. comm.).

Non-resident *P. volans* and newly-independent young may be more susceptible to predation, particularly by *N. strenua*, than resident *P. volans* (see also Tyndale-Biscoe and Smith 1969). These transient animals often move in forest areas unfamiliar to them and so may have less access to the protection afforded by suitable dens. Non-residents and newly-independent young *P. volans* also range further than resident adults, and so are more likely to be exposed to predation.

#### 5.4.1b *Use of home range and dens*

The range of sizes of the home range of resident *P. volans* monitored in this study followed that cited in the literature (Tables 5.9, 5.10). There was no consistent relationship between size of home range and forest productivity. For example, the mean home range of monogamous males in the relatively poor forest types B and the relatively rich forest type C at Morton, and Glengarry North were the same (1.4 ha; Table 5.9). The mean size of the home range of males at Morton was significantly smaller (Student's t-test:  $df = 8$ ,  $t = -5.72$ ,  $P > 0.001$ ) than that of males in the relatively richer forest at Wadbilliga (Table 5.9). In contrast, the mean size of the home range of females at Morton, Wadbilliga and Glengarry North was similar. Monogamous males in each forest did, however, usually have a larger home range than their resident females.

Most den trees used by intensively-monitored *P. volans* during this study contained only one hollow that was used as a den, so the mean number of den trees ( $ha^{-1}$ ) was generally synonymous with the mean number of dens ( $ha^{-1}$ ) used by gliders. *P. volans* used 2.1-2.7 dens per hectare, irrespective of site productivity. This figure can be compared to that for *P. volans* at Wongi State Forest, south east Queensland (i.e. 3.7 den trees  $ha^{-1}$ ; data adapted from Kehl and Borsboom 1984). In contrast to the 2-4 dens regularly used by resident gliders during my study, Kehl and Borsboom (1984) found that gliders (average home range of 2.6 ha) used 3 or 4 different dens per month although each glider tended to use two particular dens (which they termed 'primary dens') at a greater frequency than its other den sites. One adult male, for example, had 18 known dens but only used three dens for 42 per cent of all observations.

The frequency of occurrence of eucalypt species in the forest differed significantly from that of den trees at Morton forest type C and Wadbilliga. It was not known if these differences were due to selection of specific tree species for den sites by *P. volans* or whether different tree species differed in their rate of formation of hollows. An initial attempt to assess the availability of suitable hollows for *P. volans* at each site proved too unreliable to allow calculation of the availability of hollows on the basis of species of tree. Overall, *P. volans* at both sites tended to inhabit dens in the tallest and largest (DBH0B) trees, which was expected since these trees were the ones most likely to contain hollows large enough for gliders (Inions 1985). In comparison, Kehl and Borsboom (1984) found that 48 per cent of dens used by *P. volans* were sited in hollow *E. umbra* that were significantly taller and significantly larger in diameter than the average for this species. *E. umbra* was the most common tree species on their site (22%); it also contained 44 per cent of all hollows. *E. umbra* was also the tree most utilised for feeding and took up 55 per cent of the feeding time of *P. volans*. There was no indication that tree species or type of hollow (trunk or limb) influenced the selection of 'primary dens' (Kehl and Borsboom 1984).

The aspect of tree hollows used as dens did not influence den selection by *P. volans* in my study. One female glider at Wadbilliga frequently used a den which had an entrance facing almost directly skyward and visited it during periods of heavy rainfall. Similar observations of den use by *P. volans* have been recorded for animals in Kioloa State Forest, south east N.S.W. (Robinson 1984). The results of Robinson's study and studies on den selection by other arboreal marsupials (for a review see Inions 1985) indicate that several factors, relating both to the hollow itself (e.g. temperature patterns; Calder 1979) and to the surrounding habitat (e.g. location of food resources), can influence den selection (McCoub and Noble 1981; Saunders *et al.* 1982).

The population density of *P. volans* at Wadbilliga and Morton did not appear to be limited by the availability of den trees. Henry (1985) also concluded that the availability of den trees was not limiting the density of *P. volans* at Glengarry North. Similarly, the availability of den trees (26 trees ha<sup>-1</sup> contained hollows) did not appear to be limiting the population density of *P. volans* at Wongi State Forest, although Kehl and Borsboom (1984) did not state this.

#### 5.4.1c *Mating association, social cycle and population fecundity*

Wittenberger (1979) postulated that mammalian reproduction, which characteristically involves a relatively greater commitment of time and energy by the female than the male, has led to a preponderance of promiscuous mating associations. Bigamy or polygyny are primarily related to the density of resources which are critical to the survival of individuals of a species. For example, these associations are most likely to occur when males are able to defend access to more than one female (mate defence: defence of females by bigamous or polygynous males) or can monopolise access to desirable resources and hence the females that are dependent on those resources (resource defence: defence of resources by bigamous or polygynous males) (Emlen and Oring 1977; Wittenberger 1979). It is assumed that the size of the home range of breeding females is set by the minimum area necessary to supply food and shelter, and to raise offspring. However, bigamy or polygyny can also arise when females do not require the direct assistance of males to raise offspring.

In my study, a bigamous mating association was only observed in forests with a relatively high site productivity and occurred when the home range of a male overlapped that of two females. The bigamous male *P. volans* (M1) at Wadbilliga had no involvement in raising his offspring and maintained exclusive access to both of his partners during the mating season. For example, M1 lived close to both of his partners



during this period thus ensuring exclusive access to them during oestrus. The home range of M1 only overlapped about 60 per cent of the home range of each of his partners. However, no other resident or transient males attempted to approach this forest area or the partners of M1. Bigamy in this case appeared to be dependent primarily on the amount of critical resources present other than shelter sites since the availability of den trees did not seem to be limiting the population density of *P. volans*. However, it was not clear if mate defence and/or resource defence by M1 or other factors were maintaining this mating association.

In contrast to M1, the majority of the resident *P. volans* at Wadbilliga were monogamous. As the availability of den trees did not appear to be limiting the distribution and density of resident gliders, theory (outlined above) would suggest that the occurrence of both bigamous and monogamous mating associations may be related to heterogeneity in the distribution of other critical resources (i.e. non-shelter resources) across the site. The resource most likely to be limiting the distribution, density and possibly the mating association adopted by *P. volans* was the presence or absence of suitable concentrations of high-quality food. The role of quality and quantity of food in the diet of arboreal herbivores has been dealt with in Chapter 2. At Morton, the occurrence of high-quality food also appeared to be a major factor determining the distribution, mating association and probably the fecundity of the discrete populations of *P. volans* each year. This aspect is examined in more detail in the next chapter.

The social cycle of *P. volans* at Wadbilliga and Morton was similar and followed a similar pattern to that of resident *P. volans* studied at Glengarry North (Henry 1984). The mean annual fecundity of these populations, however, was different and appeared to be related to site productivity (Table 5.9). For example, none of the resident females

in the relatively low productivity forest (type B) at Morton successfully raised young during the study. In contrast, the mean annual population fecundity of *P. volans* in the relatively high productivity forest (type C) at Morton was 100 percent. In the relatively high productivity forest at Wadbilliga, however, not all resident and paired adult females raised young each year; the annual fecundity of the population of gliders was 66 per cent which was similar to that of the population of *P. volans* at Glengarry North (Table 5.9). The body weight of resident adult female *P. volans* at Wadbilliga and Morton was similar (Table 5.2), so body weight alone was not a reliable predictor of the annual fecundity of females.

Hocking (1981) studied populations of *T. vulpecula* inhabiting eucalypt forests of different post-fire ages (0-60 plus years) in southern Tasmania. He found differences in fecundity and the proportion of juveniles between populations. Animal condition, juvenile survival, fecundity and population growth rate increased from one to 4-6 year old forest. The fecundity and growth rate of populations declined continuously in forests aged greater than 4-6 years. Variation in reproductive success between populations was attributed to nutritional (qualitative and quantitative) differences between sites. Clout (1977) reported a similar situation for *T. vulpecula* inhabiting young and old pine plantations in New Zealand. An attempt to quantify the 'successional age' of forests at Morton and Wadbilliga was not made in my study. However, qualitatively, forest types A, B and C at Morton, for example, appeared to be of comparable age. Thus differences in the presence/absence or fecundity of resident populations in each forest type at Morton were not considered to be directly attributable to successional age *per se*.

The study region encompassing Morton and Wadbilliga was recovering from the worst drought since European settlement (Chapter 3,

Section 3.2). The short- and long-term impact of this drought on the reproductive condition of resident *P. volans* at both sites is unknown. It is possible, for example, that the drought may have affected animals by influencing the amount of high-quality food available to them in each forest (see Chapter 6). However, as the annual population fecundity of *P. volans* within each forest was comparable throughout the duration of the study, the longer-term effect of the drought was considered minimal.

With the exception of the population studied by Griffith (1973) at Armidale, all populations of *P. volans* studied have been characterised by sex ratios biased to females (Table 5.10). The discrete populations of *P. volans* monitored in this study also followed this pattern (Table 5.9). Although the sex ratio of Morton forest type C was unity it changed to 1 male:2 females late in the study. Tyndale-Biscoe and Smith (1969a) suggested that the biased sex ratio of *P. volans* appeared to be a consequence of a higher mortality among weanling males compared to females since newly-independent juvenile males may be forced to disperse by adult males which are intolerant of their presence. This hypothesis was supported in part by the observed recruitment of newly-independent juveniles in Morton forest type C and at Wadbilliga during this study. At Morton forest type C, for example, the juvenile offspring raised in 1984 was male and was apparently dispersed from the site on becoming independent. In contrast, a female sibling was raised in 1985 and she subsequently remained on the site. Several studies on other arboreal marsupials (e.g. Dunnet 1964; Tyndale Biscoe 1973; Hocking 1981; Green 1984: all of whom studied *Trichosurus vulpecula*; Pahl 1985: *Pseudocheirus peregrinus*) have shown or inferred that resident adult males were intolerant of their newly-independent male offspring and induced them to disperse. It has been suggested that in stable populations of long-lived mammal species such as *P. volans*, young males are dispersed because it is to the advantage of resident

adult males to eliminate potential sources of breeding competition (Smith and Lee 1984; Henry 1985). Alternatively, the avoidance of inbreeding may offer another explanation for this phenomenon (Wittenberger 1979).

Many species of mammals and birds exhibit sex differences in natal and breeding dispersal. In mammals, male-biased dispersal is most common and *P. volans* fits this pattern. In birds however, the predominant dispersing sex is female. Pusey (1987) has recently reviewed the relative importance of intrasexual competition and inbreeding avoidance in producing sex-biased dispersal in birds and mammals. She considered it difficult to distinguish the relative importance of these two hypotheses in most cases. Cockburn *et al.* (1985) have demonstrated that competition for resources can be excluded as a cause of male-biased dispersal in, at least, some species of *Antechinus*. These authors concluded that males and mothers of the species benefit from this dispersal by the avoidance of close inbreeding. Dispersal in other mammalian species such as squirrels (e.g. *Spermophilus beeldingi*) and primates is also best explained by the inbreeding avoidance hypothesis (Pusey 1987). Determination of the relative importance of these two hypotheses in *P. volans* would require experimental manipulation (see Dobson 1982). From the observations at Morton forest type C, it seems clear that the dispersal of the juvenile male was not related to intra- or intersexual competition for the available food resources.

At Glengarry North, Henry (1984) observed that some resident adult females did not have partners and did not reproduce. Several gliders, of either sex, without regular partners were also observed during this study. None of these gliders reproduced. The reason for their single status is unknown (for a full discussion see Chapter 7,

Section 7.2). The presence of two resident females without partners at Morton forest type B meant there were only three resident females which potentially could raise young at this site during the study.

#### 5.4.1d *Communication and social interactions*

Scent-marking, by cloacal dragging and with urine, was the principal means of remote communication by *P. volans* and served to demarcate the home range of individuals. Secretions from the para-cloacal gland of females also appeared to communicate their reproductive status to male gliders. These observations agree with those of Henry (1984) for *P. volans* at Glengarry North. Biggins (1984) considered cloacal dragging to be a common method of scentmarking by arboreal marsupials. Several of these species (e.g. Sugar Glider, Brushtail Possum) also use urine for a communicative function (Biggins 1984), as do many other mammalian species (Stoddart 1976).

In general, *P. volans* apparently attempted to minimise the occurrence of aggressive intraspecific behaviours, hence minimising the possibility of physical injury and conserving energy expenditure. The only agonistic behaviours observed during this study occurred at Morton forest type B and were between resident females in the region where their home ranges overlapped. In contrast, the home ranges of resident females at Wadbilliga did not overlap or abut and no agonistic behaviours were observed. Henry (1984) also observed some agonistic interaction between resident female *P. volans* at Glengarry North in the region where their home ranges overlapped.

#### 5.4.2 *A priori* hypotheses

- i. The population density of *P. volans* at Morton is low, compared to Wadbilliga, because there are few areas of forest (i.e. trees with a relatively high concentration of foliar nutrients) which appear able to support resident animals.

Data collected were **consistent** with this hypothesis. The population density of *P. volans* at Morton was low (0.18 resident animals ha<sup>-1</sup>) compared to Wadbilliga (0.88 resident animals ha<sup>-1</sup>). Only one-fifth (forest types B and C) of the total area of forest at Morton appeared able to support resident *P. volans* in contrast to three-quarters of the total area of forest at Wadbilliga which supported gliders. Forests supporting resident gliders were, in general, dominated by eucalypts with relatively high concentrations of foliar nutrients.

- ii. The population density of adult male and female *P. volans* at Morton is low because these animals maintain larger home ranges than their respective counterparts at Wadbilliga.

This hypothesis was **rejected**. The mean size of the home range of male *P. volans* at Morton was significantly smaller than that of males at Wadbilliga. The mean size of the home range of female *P. volans* at Morton and Wadbilliga was comparable.

- iii. The population density of *P. volans* at Morton is low, compared to Wadbilliga, because the majority of gliders encountered are transients dispersing to more favourable habitat.

The hypothesis was **rejected**. By far the majority of *P. volans* observed at Morton and Wadbilliga was resident.

#### 5.4.3 Conclusion

Data collected on the social organisation of *P. volans* at Wadbilliga and Morton rejected the hypotheses that variations in home range size and residential status of adult gliders could account for the observed population density of gliders in these forests. Similarly, the availability of suitable denning sites and predation pressure did not appear to account for the observed population density. As hypothesis

i. (Section 5.4.2) was supported, it was postulated that the observed population density of gliders at Wadbilliga and Morton may be due to the presence or absence of suitable concentrations of high-quality food within these two sites. Further, the availability of such food may also influence the distribution, mating association and probably the annual fecundity of populations of *P. volans*.

## CHAPTER 6

### BEHAVIOUR AND FEEDING ECOLOGY OF *P. VOLANS* AT WADBILLIGA AND MORTON

#### 6.1 INTRODUCTION

This chapter investigates the postulate that the availability of high-quality food may be a significant factor in determining the distribution, mating association and probably annual fecundity of populations of *P. volans*. The behaviour and feeding ecology of resident populations of *P. volans* at Wadbilliga and Morton are examined, particularly in relation to the spatial and temporal availability of food resources in their respective habitats.

#### 6.2 METHODS

The forest study sites were described in Chapter 4. The frequency of sampling of *P. volans* follows that outlined in Chapter 5, Section 5.2.

##### 6.2.1 Behaviour and feeding ecology

##### 6.2.1a *Types and quantification of behaviour*

The behaviour of gliders was classified into five groups: G (Grooming), F (Feeding), S (Stationary), M (Moving), and O (Other - e.g. mating).

Whenever possible, the behaviour of selected tagged *P. volans* was recorded at five minute intervals throughout the night (i.e. from time of first emergence from the den to time of last return to the den). The first behaviour exhibited by each glider at each five minute check was recorded as the behaviour of that animal for the preceeding five minutes. The location of the glider at each five minute check was



also noted following the classification described in 6.2.1b, below. Sometimes it was possible to monitor two gliders concurrently.

Daily, seasonal and annual activity budgets for gliders were obtained by summing and averaging, for the appropriate time period, the frequency of each behavioural class recorded. These data were expressed as percentages of total activity.

#### 6.2.1b *Feeding heights and sites*

The feeding height and site of feeding by individually monitored *P. volans* were classified in terms of tree position (trunk, branch base, mid-branch, outer-branch), and actual and relative height (below the canopy, lower canopy, upper canopy) (Fig. 6.1). These data were recorded for each five minute period during the intensive all night sampling regime described in 6.2.1a.

#### 6.2.1c *Food selection and diet composition*

The feeding behaviour and food selection of *P. volans* were noted during the spotlighting of transects to assess population size and distribution (Chapter 5, Sub-section 5.2.2) and during the intensive monitoring periods. During the latter periods, the species of tree browsed and the material eaten (i.e. young leaf, mature leaf, petiole, buds, flowers, other) were recorded (when clearly observed) for each five minute period that feeding behaviour was observed.

The composition of the diet of individually monitored *P. volans* was quantified as the proportion of feeding time spent on different food materials.

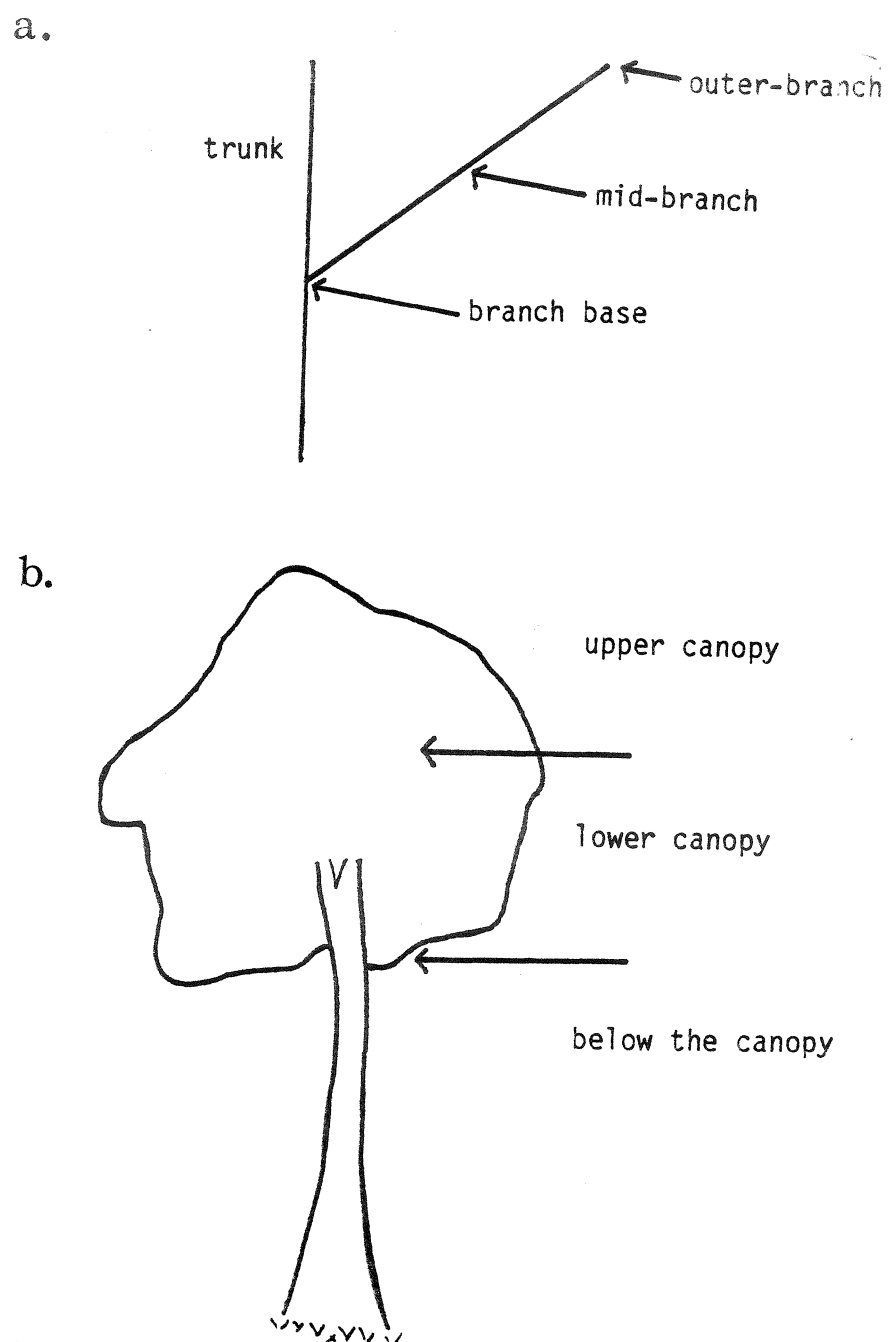


Figure 6.1 The feeding height and site classification used during the monitoring of individually tagged *P. volans* (a: position in tree, b: relative height in tree).

#### 6.2.1d *Foraging areas*

The foraging area of each intensively-monitored *P. volans* was defined as that area (ha) which encompassed 95 per cent of its observed annual feeding activities. This area was determined using the same method of calculation outlined for the estimation of home range size (Chapter 5, Sub-section 5.2.4). The mean foraging area of an individual glider was determined by averaging the size of this area obtained for each year of the study. The mean foraging area of all intensively monitored gliders in a forest type represents the average size of all foraging areas determined during the study.

#### 6.2.1e *Estimated nightly range of movement*

It was not possible to estimate the movements of *P. volans* in three-dimensions. Hence the estimate of nightly ranging described below represents the minimum distance traversed by intensively monitored gliders during their nightly activities. The nightly ranging of individual gliders was estimated by summing the linear distance (i.e. the distance measured on a horizontal plane between the centre of the base of the tree the glider moved from to the centre of the base of the tree the glider moved to) between the trees each glider traversed during its nightly activity period. An average of these data was then taken to provide a mean value for the time period or animals in question (e.g. mean distance travelled by males at Morton forest type B during winter).

#### 6.2.2 Analysis of data

Methods used for the analysis of data are detailed in Chapter 5, Sub-section 5.2.6.

### 6.3 RESULTS

Data are from 1271 hours of night observations during the period October 1984-August 1986, inclusive.

### 6.3.1 Behaviour: activity budgets

#### 6.3.1a *Effects of climate and lunar cycle*

*P. volans* is nocturnal. Intensive monitoring of gliders leaves the observer with the impression that activity is often suppressed when heavy rain falls for several hours during the night and/or when there is a clear full moon shining for several hours. However, a comparison of the length of the period of nightly activity of *P. volans* during these wet or moonlit periods with that observed on nights without rainfall outside of the full-moon phase showed no significant differences (Mann-Whitney test:  $n_1 = 43$ ,  $n_2 = 35$ ,  $t = 0.94$ ,  $P > 0.05$ ). Data for the activity (mean percentage time of nightly activity period spent Stationary, Moving, Feeding, Grooming or Other) of intensively-monitored *P. volans* were analysed. Mean values for both sexes were combined for each site and grouped into those recorded during prolonged periods of heavy rainfall or when the full moon shone for several hours, and were compared with data from rainless, dark nights. There were no significant differences (Mann-Whitney test:  $P > 0.05$ ) for gliders at Wadbilliga or at Morton (Table 6.1). All subsequent analyses of the activity of intensively-monitored *P. volans* were based on observations recorded during all climatic conditions and phases of the lunar cycle.

#### 6.3.1b *Effect of presence of an observer*

The activity of intensively-monitored *P. volans* showed no significant difference between near the start of the study in October, November and December 1984 and near the end in October and December 1985. Mean values for activity periods were combined for both sexes at each site and compared: the Mann-Whitney test gave  $n_1 = 18$ ,  $n_2 = 12$ ,  $U = 116.5$ ,  $P > 0.2$  for Wadbilliga and  $n_1 = 18$ ,  $n_2 = 12$ ,  $U = 108$ ,  $P > 0.3$  for Morton. The time of emergence of *P. volans* from dens did not differ significantly between the start and end of the study at either

Table 6.1 Comparison of the percentage time (min) of nightly activity period spent Stationary, Moving, Feeding and Grooming and Other by intensively-monitored resident adult male and female *P. volans* at Morton and Wadbilliga under heavy rainfall and/or when the full moon shone for several hours and rainless, dark nights. Statistical analysis used was the Mann-Whitney test (following Sokal and Rohlf 1969, p. 433). Statistics shown are t values. For all analyses:  $n_1 = 43$ ,  $n_2 = 35$ ; NS = non-significant ( $P > 0.05$ ).

Activity	Morton	Wadbilliga	Significance level
Stationary	1.73	1.70	NS
Moving	1.66	1.59	NS
Feeding	1.43	1.28	NS
Grooming and Other	1.11	1.15	NS

Wadbilliga or Morton. Emergence was measured as minutes after sunset, and data for both sexes were combined for the Mann-Whitney test ( $n_1 = 18$ ,  $n_2 = 12$ ,  $U = 120.5$ ,  $P > 0.2$ ). These analyses confirmed that my presence within the home range of an intensively-monitored glider did not affect its behaviour during monitoring, either on a nightly or long-term basis.

### 6.3.1c *Activity patterns*

The most notable aspect of the activity patterns of intensively-monitored *P. volans* was the similarities rather than the differences between sexes, between the location of their forest site or between their season of monitoring.

The length of the period of activity (i.e. from first emergence from the den until final return to the den) of *P. volans* was relatively constant during each year of the study. For example, the length of the activity period of all males (number of observations = 78) during each season of the study ranged between 7.1 h (71.7% of night-length during spring) and 8.9 h (63.1% of night-length during winter) with a mean (hours  $\pm$  S.D.) of  $7.9 \pm 0.7$ . The activity period of females ( $n = 78$ ) during each season at Wadbilliga and Morton ranged between 7.0 h (70.1% of night-length during summer) and 9.1 h (65.2% of night-length during winter), with a mean  $\pm$  S.D. of  $7.7 \pm 0.6$ .

The time of emergence (minutes after sunset) from dens by gliders did not differ significantly between seasons for either sex (one-way ANOVAS:  $F_{3,74}$  (males) = 1.43,  $P > 0.05$ ;  $F_{3,74}$  (females) = 2.21,  $P > 0.05$ ), between forest sites for either sex (Student's *t*-tests:  $df = 154$ ;  $t$  (males) = 1.26,  $P > 0.05$ ;  $t$  (females) = 0.93,  $P > 0.05$ ), or between sexes when data from both Wadbilliga and Morton were combined (Student's *t*-test:  $df = 154$ ,  $t = 1.17$ ,  $P > 0.05$ ). Fifty per cent of all emergences

( $n = 156$ ) were recorded within 72 min of sunset while 90 per cent of all emergences occurred within 104 minutes of sunset. The earliest recorded emergence was 21 min after sunset (F6 at Morton during spring 1985; Fig. 5.7) and the latest emergence occurred 134 min after sunset (F3 at Wadbilliga during autumn 1985; Fig. 5.3). The length of the period of activity following emergence was relatively constant, irrespective of night-length, so gliders returned to their dens earlier (before sunrise) in winter when, for example, mean night-length at Wadbilliga was about 14 h, than in summer when mean night-length was about 9.7 h.

The amount of time intensively-monitored *P. volans* spent grooming or engaged in 'other' behavioural activities was small and relatively constant during each season of the study. When these behavioural categories were combined they typically accounted for less than 5 per cent of the total time for all nightly activity of gliders.

The time *P. volans* spent feeding was also relatively constant, irrespective of sex, forest site or season. The time spent feeding ranged from 1.8 h (25.2% of total activity time) for F3 at Wadbilliga during summer 1985 to 3.2 h (37.1% of total time spent active) for F2 at Morton during autumn 1985. The mean time (hours  $\pm$  S.D.) for all observations ( $n = 156$ ) of feeding by all *P. volans* was  $2.3 \pm 0.4$ , about 29 per cent of the total time spent in activities during any night. On average, about one-third of the total activity period of *P. volans* during each night of the year was taken up in feeding, grooming and 'other' behaviour.

The other two-thirds of its nightly emergence period involved various moving and stationary behavioural activities. All *P. volans* spent significantly more of their time stationary rather than moving (Student's *t*-test,  $df = 154$ ,  $t = 27.68$ ,  $P < 0.001$ ). On a nightly and on a

seasonal basis, the amount of time spent moving each night by intensively-monitored male and female *P. volans* at Wadbilliga and Morton ranged between 12.3 per cent and 24.1 per cent of the total emergence time, with a mean ( $\pm$  S.D.) of  $18.5 \pm 4.4$ . On any one night, male *P. volans* appeared to spend slightly more time moving than did female *P. volans* in the same forest sites, but the difference was not significant (Student's t-test:  $df = 154$ ,  $t = 1.48$ ,  $P > 0.05$ ). All gliders appeared to spend slightly more time moving during their nightly activities in winter and spring than in summer and early autumn, but again the difference was not significant (one-way ANOVA:  $F_{3,74} = 2.04$ ,  $P > 0.05$ ).

The percentage of the nightly emergence period spent stationary by male and female *P. volans* ranged from 39.7 per cent to 58.3 per cent, with a mean ( $\pm$  S.D.) of  $48.3 \pm 6.8$ . Females F1 and F2 in Morton forest type B appeared to spend slightly more time moving and slightly less time stationary during each season than female F6 in Morton forest type C and all females at Wadbilliga (see 6.3.1e). Again, the differences proved to be non-significant (Student's t-tests:  $df = 76$ ,  $t$  (moving) = 1.38,  $P > 0.05$ ;  $t$  (stationary) = 1.49,  $P > 0.05$ ).

The intensively-monitored *P. volans* spent a minimum of about 40 per cent of their respective nightly emergent periods stationary or inactive while at least 12 per cent of their nightly activity periods was spent moving.

*P. volans* often used the same trees, and frequently the same limbs of trees when dispersing from or re-entering their dens. With the exception of these periods, gliders showed no significant trends in their temporal pattern or sequence of tree use during their nightly activities. The method of travel used by gliders was determined by the distance between the tree crowns they traversed. Whenever



possible, *P. volans* walked or jumped between tree crowns. When the crowns were more than about 15 m apart, gliders volplaned. Gliders were never observed on the ground.

#### 6.3.1d *Foraging areas*

Male and female *P. volans* at both Wadbilliga and Morton used some areas of their home range more intensively and for different observed frequencies of behavioural activities than other areas. This was very noticeable for observations on feeding by intensively-monitored *P. volans*. Males in particular fed within portions of their home range which were considerably smaller than the total area of forest encompassed by their nightly travels. An important practical point arising from this in relation to management is that the use of home range size to define the minimum area of forest required by each glider to sustain its annual food requirements is misleading. To reduce the effect of this potential problem, the foraging area (i.e. the area encompassing 95 per cent of all annual feeding observations) of each glider was calculated.

The mean size (hectares) of the foraging areas of male and female *P. volans* at both sites is shown in Table 6.2. Although the sizes of the home range and of the foraging area of male gliders were not significantly different (GT2-method,  $P > 0.05$ ), the area of the home range which contained the remaining 5 per cent of their annual feeding activities differed significantly (GT2-method,  $P < 0.05$ ) between sites (Table 6.2). Male *P. volans* at Wadbilliga used a forest area, on average, about 40 per cent (0.52 ha) larger than was required to meet most of their annual food requirements. In contrast, males in forest type B at Morton used an area only slightly larger (about 10% or 0.13 ha) than that required to sustain most of their annual food requirements.

Table 6.2 Analyses of foraging area in relation to home range size of intensively-monitored male and female *P. volans* at Wadbilliga and Morton (A: mean size (ha  $\pm$  S.D.) of home range; B: mean size of foraging areas (encompassing 95% of annual observations of feeding); C: mean size of home range which contained the remaining 5 per cent of annual observations of feeding; values sharing the same superscripts across rows are not significantly different, GT2-method (Sokal and Rohlf 1969),  $P > 0.05$ ).

	Morton		Wadbilliga
	Forest type B	Forest type C	
Males A	1.35 $\pm$ 0.07	1.4	1.73 $\pm$ 0.15
B <sup>+</sup>	1.22 $\pm$ 0.02 <sup>a</sup>	1.07 $\pm$ 0.09 <sup>a</sup>	1.21 $\pm$ 0.06 <sup>a</sup>
C <sup>++</sup>	0.13 $\pm$ 0.05 <sup>a</sup>	0.33 $\pm$ 0.09 <sup>b</sup>	0.52 $\pm$ 0.11 <sup>b</sup>
No. of observations	4	2	6
No. of animals	2	1	3
Females A	1.5 $\pm$ 0.1	0.9	1.4 $\pm$ 0.5
B <sup>+</sup>	1.33 $\pm$ 0.04 <sup>a</sup>	0.76 $\pm$ 0.02 <sup>b</sup>	1.14 $\pm$ 0.3 <sup>ab</sup>
C <sup>++</sup>	0.17 $\pm$ 0.09 <sup>a</sup>	0.14 $\pm$ 0.02 <sup>a</sup>	0.26 $\pm$ 0.18 <sup>a</sup>
No. of observations	4	2	6
No. of animals	2	1	3

Statistics (studentised maximum modulus values, following Sokal and Rohlf 1969, p. 248) for GT2-method analyses: Note that for all analyses  $k = 3$ ;  $df = 9$ ; B = gliders from Morton forest type B; C = gliders from Morton forest type C; W = gliders from Wadbilliga, \* =  $P < 0.05$ ; NS = not significant.

	B vs C	B vs W	C vs W		B vs C	B vs W	C vs W
Males: +	2.13NS	1.64NS	2.18NS	Females: +	3.48*	2.26NS	2.06NS
++	3.35*	3.95*	2.07NS	++	1.37NS	1.41NS	1.33NS

The mean size of the foraging areas of female *P. volans* at Wadbilliga was 1.14 hectares and was intermediate between, but not significantly different from, the values for females in Morton forest type C (0.76 ha) and Morton forest type B (1.33 ha) (Table 6.2). The latter two values were significantly different (GT2-method,  $P < 0.05$ , Table 6.2). In contrast to most male *P. volans*, however, female gliders typically used a considerably smaller area of forest, not significantly different between sites, above that required to meet most of their annual food requirements (Table 6.2).

The smaller 'excess' area of forest used by male *P. volans* at the Morton forest type B site with a relatively low nutrient content in the foliage contrasted markedly with the large excess area of forest retained by males at the Wadbilliga site with a relatively high nutrient content in the foliage.

#### 6.3.1e *Temporal variations in behaviour during nightly activities*

Each observation for any activity represents the first activity recorded during each 5 min period of each hour of the nightly period of emergence of *P. volans*. There can be 12 such observations per hour, but the number of hours may vary. For this reason, observations are expressed as a percentage of the maximum number of such observations possible in a night or over all the nights of a cited interval or period.

Seasonal variations in the activities of intensively-monitored *P. volans* were considered above (6.3.1d). The frequency of individual behavioural activities (e.g. feeding, moving, stationary) exhibited by male and female gliders at Wadbilliga and Morton also changed during the course of their respective nightly periods of emergence.

The mean cumulative percentage frequency of observations in each behavioural category (all seasons combined) for male and female *P. volans* (data for both Wadbilliga and Morton combined), in relation to hours after first emergence from their dens, is shown in Figure 6.2. There were no significant differences (one-way ANOVAS,  $P > 0.05$ , Table 6.3) in the percentage frequency of observations of each behavioural activity exhibited by animals during each hour of their period of emergence.

On a seasonal basis, the percentage frequency of observations on different behaviours exhibited by intensively-monitored male *P. volans*, in relation to hours since first emergence from their dens, was comparable. The same situation occurred for females, except for F1 at Wadbilliga and F2 at Morton forest type B which had similarly sized mean foraging areas (1.28 ha and 1.32 ha, respectively).

At 2 and 3 h after emergence, F1 showed significantly greater (Mann-Whitney test:  $P < 0.05$ , Table 6.4) mean cumulative per cent frequency of feeding than F2, during summer (Fig. 6.3). Otherwise there was no significant difference between them during this season (Table 6.4). Feeding by F1 decreased markedly during the last three hours of its nightly activity period (i.e. total mean cumulative % frequency of feeding observations: 44.3 at 2-4 h, 25.0 at 5-7 h, but this apparently large fall was not significant; Mann-Whitney test:  $n_1 = 18$ ,  $n_2 = 18$ ,  $U = 189$ ,  $P > 0.2$ ). The mean cumulative per cent frequency of feeding by F1 and F2 in winter was comparable. The mean cumulative per cent frequency of observations for movement by F1 and F2 during their nightly activities was comparable during summer and winter (Fig. 6.3).

The significantly higher frequency of observations for feeding by F1 (at 2 and 3 h) over those for F2 may be related to a greater abundance of food and/or the higher nutrient concentration in the

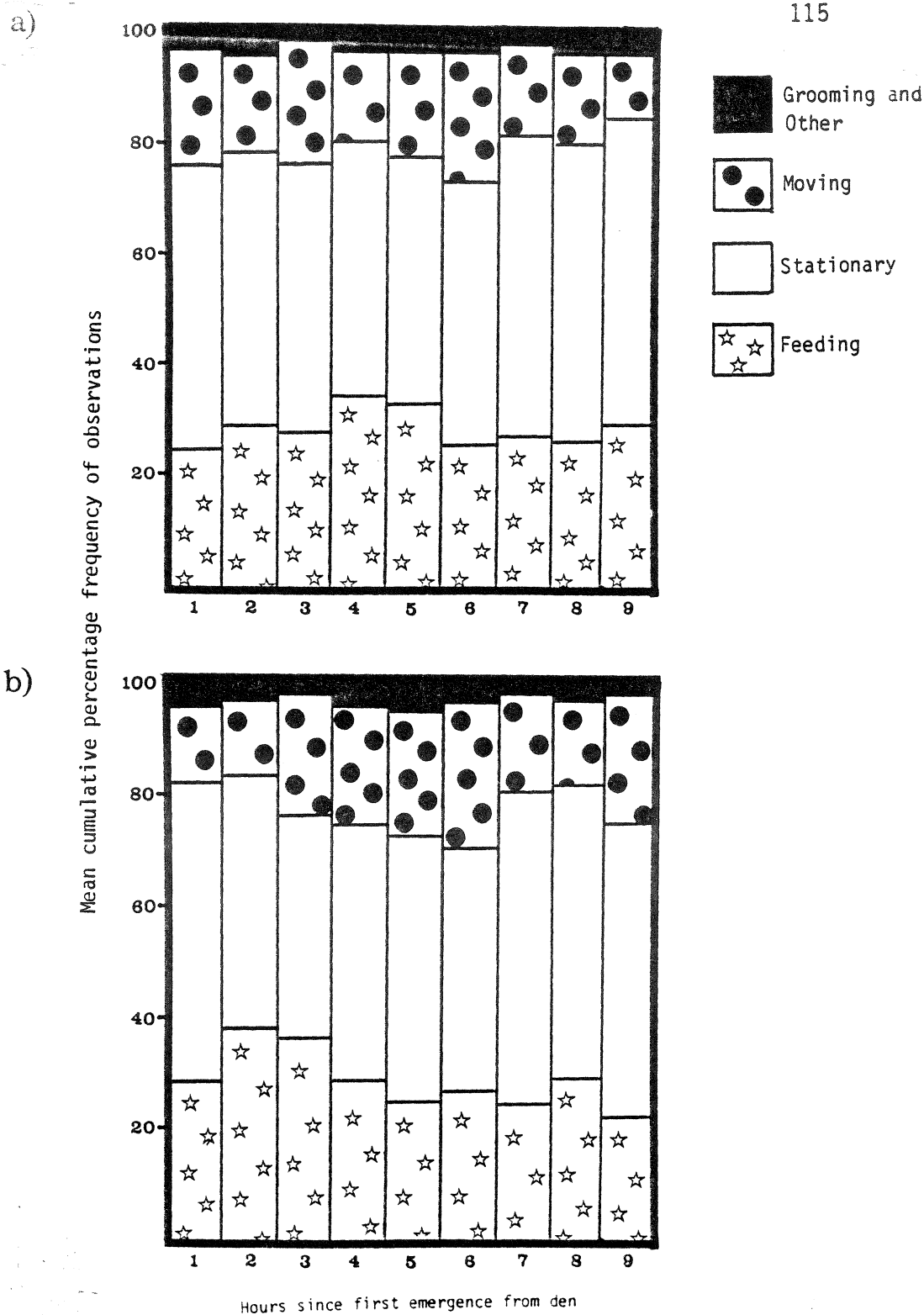


Figure 6.2 Mean cumulative percentage frequency of observations of behaviour (Grooming and Other, Moving, Stationary, Feeding) recorded for intensively-monitored male (a) and female (b) *P. volans*, data for both sites combined, in relation to the hours following first emergence from their dens.

Table 6.3 One-way ANOVAS (following Sokal and Rohlf 1969) comparing the cumulative percentage frequency of observations in each of four behavioural categories (Grooming and Other, Moving, Stationary, Feeding) exhibited by intensively-monitored male and female *P. volans* at Wadbilliga and Morton during each hour of their period of emergence from their dens. Note that for each analysis: all data were arcsine-transformed, data for all seasons were combined and data for both Wadbilliga and Morton were combined. Statistics shown are sample variance ratios ( $F_S$ ). For all analyses: df (among groups) = 8, (within groups) = 69; NS = not significant ( $P > 0.05$ ).

Activity	Males	Females	Significance level
Grooming and Other	0.83	0.69	NS
Moving	0.90	0.95	NS
Stationary	0.73	0.76	NS
Feeding	0.89	0.98	NS

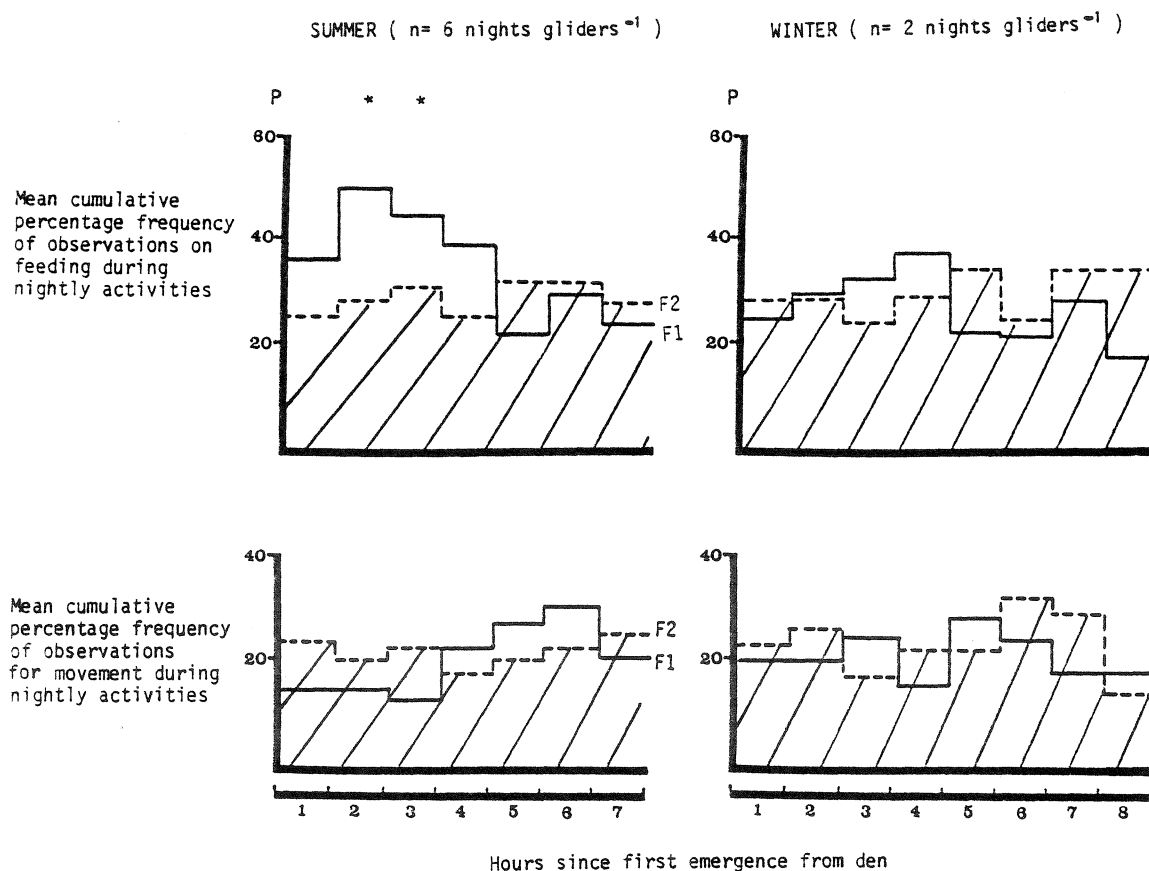


Figure 6.3 Comparison of the mean cumulative percentage frequency of Feeding and Moving behaviours during nightly activities, in relation to hours since first emergence from their dens, for intensively-monitored female *P. volans* F1 (Wadbilliga) and F2 (Morton forest type B; represented by shading) during summer and winter. Significance levels (\*) ( $P < 0.05$ ) between females at any given hour were determined by non-parametric Mann-Whitney tests (Sokal and Rohlf 1969) (Table 6.4).

Table 6.4 Comparison using Mann-Whitney tests (following Sokal and Rohlf 1969, p. 433) of the mean cumulative percentage frequency of observations on feeding during nightly activities, in relation to hours since first emergence from their dens, by intensively-monitored female *P. volans* F1 at Wadbilliga and F2 at Morton during summer. For all analyses  $n_1 = 6$ ,  $n_2 = 6$ ; \* =  $P < 0.05$ ; NS = non-significant.

	Hours since first emergence from den						
	1	2	3	4	5	6	7
U statistic	24	32	30.5	28	23.5	8.5	11
Significance level	NS	*	*	NS	NS	NS	NS

Probability levels:  $U_{0.1}[6,6] = 27$ ;  $U_{0.05}[6,6] = 29$ ;  $U_{0.01}[6,6] = 33$



foliage at Wadbilliga. F1 could stay and eat whereas F2 at Morton spent less time eating and more time foraging for food of suitable quality. These data were consistent with my field impressions that most intensively-monitored females in the relatively high productivity forest of Wadbilliga spent less time foraging for food than did female *P. volans* in the relatively low productivity forest of Morton forest type B (for full discussion see 6.3.3a).

#### 6.3.1f *Variations related to size of home range and foraging area*

Linear regression analyses indicated that the percentage frequency with which intensively-monitored female *P. volans* were observed moving each night was correlated strongly and positively with the size of their home range and foraging area (e.g. 'moving' versus size of foraging area: (correlation coefficient)  $r = 0.78$ ,  $P < 0.001$ ) (Table 6.5). Conversely, the amount of time spent stationary by females was negatively correlated with the size of their foraging area ( $r = -0.62$ ,  $0.001 < P < 0.01$ ; Table 6.5). In contrast to females, the percentage frequency with which male *P. volans* were observed moving or stationary was not correlated with the size of their home range or foraging area (Table 6.5).

#### 6.3.2 *Estimated nightly range of movement*

The estimated nightly range of movement (mean  $\pm$  S.D.) of intensively-monitored *P. volans*, based on the linear distance moved (metres) between successive trees (for definition see Sub-section 6.2.1e) was  $309.7 \pm 125.8$  for males and  $268 \pm 113.3$  for females. Linear regression analyses (Sokal and Rohlf 1969) demonstrated a positive correlation between the nightly range of movement by males and females and the size of their respective home ranges. Unlike males, the nightly range of movement of female *P. volans* was also positively correlated (correlation coefficient:  $r = 0.57$ ,  $P < 0.01$ ) with the size of their foraging area (Table 6.6).

Table 6.5 Equations of linear regression analyses\* (Sokal and Rohlf 1969) relating the percentage frequency of occurrence of observations of moving or stationary intensively-monitored male and female *Petauroides volans* at both Wadbilliga and Morton to the size (ha) of their home range or foraging area; r = correlation coefficient.

Linear regression:	'Moving' vs. home range size	'Stationary' vs. home range size	'Moving' vs. size of foraging area	'Stationary' vs. size of foraging area
Males	Y = -1.6 x + 21.4, r = -0.19, P>0.1	Y = -1 x + 50.5, r = -0.19, P>0.1	Y = -0.9 x + 20, r = -0.03, P>0.1	Y = 1.1 x + 47.5, r = 0.03, P>0.1
Females	Y = 7.1 x + 8.8, r = 0.65, 0.001< P<0.01	Y = -7.1 x + 8.8 r = -0.47, 0.01< P<0.02	Y = 11 x + 5.7, r = 0.78, P<0.001	Y = -12.1 x + 63.3, r = -0.62, 0.001< P<0.01

\*Data analysed represent seasonal means for each sex; number of observations was 24 per sex.

Table 6.6 Equations of linear regression analyses\* (Sokal and Rohlf 1969) comparing the estimated nightly range of movement (in metres) of intensively-monitored male and female *P. volans* at Wadbilliga and Morton to the size (hectares) of their home range or foraging area;  $r$  = correlation coefficient.

Linear regression:	Nightly ranging vs. home range size	Nightly ranging vs. size of foraging area
Males	$Y = 108.2 x + 141.9,$ $r = 0.49, P < 0.05$	$Y = -108 x + 443.4,$ $r = -0.27, P > 0.1$
Females	$Y = 104.7 x + 128.3,$ $r = 0.42, P < 0.05$	$Y = 141.7 x + 108.6,$ $r = 0.57, P < 0.01$

\*Data analysed represent seasonal means for each sex, number of observations was 24 per sex.

### 6.3.3 Feeding ecology

#### 6.3.3a Diet and availability of food

The diet of intensively-monitored *P. volans* at Wadbilliga and Morton was restricted to various *Eucalyptus* species. Gliders ate mature leaves and new leaf growth, buds, flowers and, at Wadbilliga, epicormic growth. Gliders at Wadbilliga occasionally were observed in Blackwood *Acacia melanoxylon* and at Morton frequently in Turpentine *Syncarpia glomulifera*, but they were never observed feeding on the foliage of these species.

The percentage frequency of seasonal observations of feeding on mature leaves, young leaves, and flowers and buds by *P. volans* at Wadbilliga and Morton was directly related to the abundance of new leaf growth on the eucalypt species at each site (Fig. 6.4). At both Wadbilliga and Morton the relative abundance of new leaf growth reached a maximum between about December and March of each year of the study. As a consequence, a large proportion (mean  $\pm$  S.D.),  $74.2 \pm 17.9$  per cent of the observations of feeding activity of gliders during this summer period were of harvesting of new leaves. Male and female *P. volans* at Wadbilliga were noted significantly more frequently (mean  $\pm$  S.D.) eating immature leaves during summer and autumn ( $81.5 \pm 8.3\%$ ) than in spring and winter ( $32.0 \pm 11.7\%$ ) (Mann-Whitney test: (summer vs. winter)  $n_1 = 36$ ,  $n_2 = 12$   $t = 2.41$ ,  $0.01 < P < 0.05$ ). Even so, all gliders consumed, some mature leaves during summer and early autumn despite the apparent super-abundance of new leaf growth, particularly at Wadbilliga.

All gliders spent similar (Mann-Whitney test:  $n_1 = 12$ ,  $n_2 = 12$ ,  $U = 76.5$ ,  $P > 0.05$ ) amounts of their feeding time (about 60% frequency of all observations of feeding) consuming mature eucalypt leaves during winter and spring when the relative abundance of new leaves was lowest (Fig. 6.4). Even during these seasons a minimum of about 30 per cent of

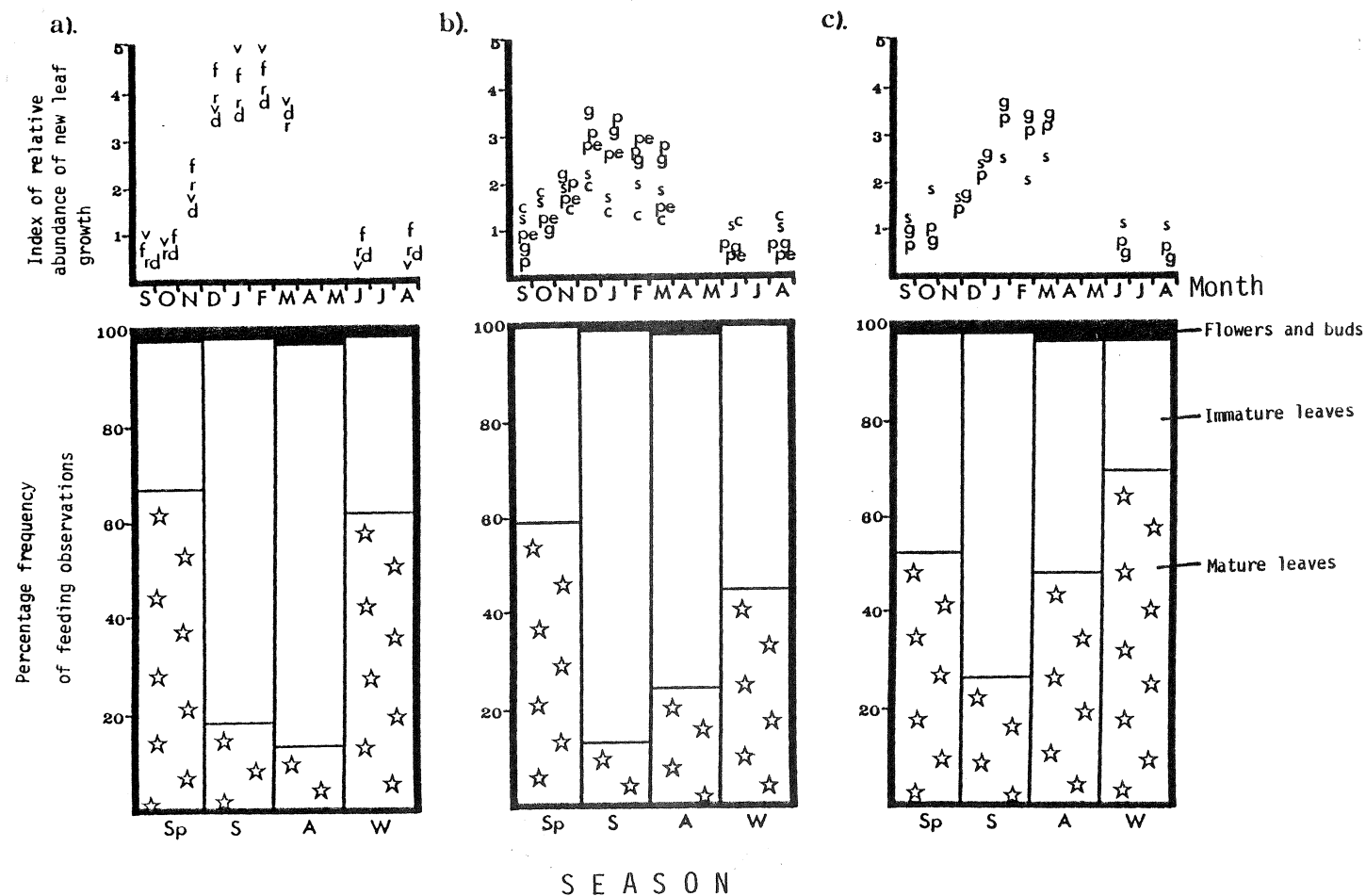


Figure 6.4 Comparative percentage frequency of seasonal observations of feeding on mature leaves (starred bars), young immature leaves (open), and flowers and buds (solid) by intensively-monitored *P. volans* at Wadbilliga (a) and Morton forest types C (b) and B (c) in relation to the relative abundance of new leaf growth of eucalypt species represented at each site (Wadbilliga: r - *E. radiata*, v - *E. viminalis*, d - *E. dalrympleana*, f - *E. fastigata*; Morton: p - *E. piperita*, g - *E. gummifera*, s - *E. sieberi*, pe - *E. pellita*, c - *E. consideniana*).

observations of feeding were for gliders eating new growth. The frequency of feeding on eucalypt flowers and buds during each season was minor (less than 3%; Fig. 6.4).

Not all of the four eucalypt species at Wadbilliga were encompassed by the foraging area or home range of every intensively-monitored Greater Glider. *Eucalyptus viminalis* was the main species, and represented at least 40 per cent of the basal area of trees in the home range of every glider. *E. radiata* occurred in the home range of five intensively-monitored *P. volans* while only three *P. volans* had home ranges encompassing all tree species.

The use of different eucalypt species as a food source ('food trees') by *P. volans* rarely differed from that expected from the relative availability indicated by the percentage contribution to total basal area of each eucalypt in the home range. *Eucalyptus viminalis* was the host tree for 52.6 per cent, and *E. radiata* the host tree for 40.4 per cent of the 2126 observations of feeding by gliders. These species accounted for 93 per cent of observations and were the most important source of food. When the home range of *P. volans* encompassed *E. fastigata*, as in the case of gliders M2, M3 and F3, they showed a strong preference for this species during winter and early spring (Chi-square test:  $df = 15, \chi^2 = 26.08, P < 0.02$ ), apparently because it had more new growth of leaves than the neighbouring tree species.

In contrast to Wadbilliga, the foraging areas and home ranges of all intensively-monitored *P. volans* at Morton encompassed all of the eucalypt tree species occurring in the two sites, three in forest type B and five in forest type C.

Differential use of food tree species by *P. volans* in forest type B appeared related to other factors in addition to the relative abundance of new leaf growth. During summer and autumn, for example, when the relative abundance of new growth on each eucalypt species peaked, gliders fed far more than expected on the young leaves of *E. sieberi* (observed vs. expected frequency of food tree use: Chi-square test:  $df = 271, \chi^2 = 417.31, P < 0.001$ ). Young leaves of *E. piperita* were taken at the expected frequency (Chi-square test:  $df = 271, \chi^2 = 263.85, P > 0.2$ ), but new leaf growth of *E. gummifera* which was readily available was not taken as frequently as expected from its abundance (Chi-square test:  $df = 271, \chi^2 = 359.14, P < 0.05$ ). This preference also occurred in other seasons when young leaves were consumed.

In contrast to the preference for young leaves, whenever *P. volans* consumed mature eucalypt leaves, particularly in winter and spring, they rarely took those of *E. sieberi*. Of the 569 observations of *P. volans* consuming mature leaves, less than 2 per cent of these occurred in *E. sieberi*. Gliders spent similar amounts of time consuming mature leaves of *E. gummifera* and *E. piperita*.

Of the 532 observations of feeding (young and old leaves) recorded for M4 and F6 in forest type C at Morton, 35 per cent were in *E. piperita*, 22 per cent in *E. sieberi*, 19 per cent in *E. gummifera*, 16 per cent in *E. pellita*, and 8 per cent in *E. consideniana*. The number of observations of feeding by gliders recorded in *E. sieberi*, *E. gummifera* and *E. piperita* was comparable to that expected, based on their relative contributions to total basal area (see Table 4.2). On the other hand, both gliders showed a strong preference for *E. pellita* (Chi-square test:  $df = 84, \chi^2 = 119.42, P < 0.01$ ) and *E. consideniana* (Chi-square test:  $df = 42, \chi^2 = 89.07, P < 0.001$ ). Both the immature and mature foliage of these two species were eaten regularly. As observed in Morton forest type B, *P. volans* rarely consumed the mature leaves of *E. sieberi*.

### 6.3.3b *Feeding heights and sites*

The location of intensively-monitored male and female *P. volans* when observed feeding was remarkably consistent, irrespective of the season of monitoring or the location of the forest site. All gliders had at least 75 per cent of their feeding observations (total  $n = 4072$ ) recorded while located in the mid-outer branches of the upper canopy of food trees. The actual height above ground of these feeding sites varied with the height of the food tree in question. For example, gliders at Wadbilliga and Morton forest type C were occasionally observed feeding in the tops of small eucalypt saplings which were only 2.5-4 m in height. These observations were consistent with the hypothesis that the foraging behaviour of *P. volans* was primarily directed towards maximising the amount of new leaf growth in its diet.

### 6.3.3c *Food selection*

*P. volans* appeared highly selective in the food items they consumed. Animals fed by grasping foliage branchlets or the foliage with the manus of one foreleg and drew the food to their mouth. Either foreleg was used for food manipulation, while the other foreleg provided support for the animal. Food items were sniffed before eating commenced. Food items were most frequently rejected after sniffing, but sometimes immature and mature leaves were rejected only after gliders had bitten them.

Measurement of the number and type of food items gliders consumed during timed bouts of feeding proved unsuccessful. *P. volans* were rarely in suitable positions for accurate longer-term monitoring and, when they were, animals frequently placed several food items into their mouth at the same time. Also, animals sometimes consumed only a portion of the food item they had selected. Feeding bouts were interspersed with periods of resting, moving or sometimes scratching and grooming.



During each nightly monitoring period, *P. volans* generally browsed on all of the eucalypt species that occurred within their home range. F6 and M4 in forest type C at Morton often consumed food items from the five different eucalypt species present, and F2 at Wadbilliga consumed both *E. viminalis* and *E. dalrympleana*, the only two species within its home range. Of the 13 nights that F2 was monitored, both food tree species were browsed on 11 nights. The only two occasions that F2 did not browse both food tree species were during spring when she had a large dependent sibling which appeared to restrict her movements.

The observed frequency of use of food trees as a source of new leaf growth by *P. volans* during summer and autumn, and winter and spring is shown in Figure 6.5. Although the foraging behaviour of gliders was primarily aimed at maximising the amount of new leaf growth in their diet during each season, *P. volans* appeared to exert minimal or relatively low browsing pressure on most of the food trees.

During summer and early autumn when the relative abundance of new leaf growth reached a maximum at all forest sites, a grazing frequency of 1-5 occasions was recorded for 49 per cent of food trees at Wadbilliga, 45 per cent at Morton forest type C, and 66 per cent at Morton forest type B. The percentage of food trees used more than 10 times was 35 per cent at Wadbilliga, 12 per cent at Morton forest type C and 15 per cent at Morton forest type B (Fig. 6.5). Of those trees relatively more heavily browsed by *P. volans* (e.g. some individuals of *E. pellita* and *E. consideriana* in Morton forest type C) none showed any external signs of ill-health such as die-back. Similarly, browsing on mature leaves, buds and flowers by *P. volans* appeared to have a minimal impact on the health or productivity of food trees.

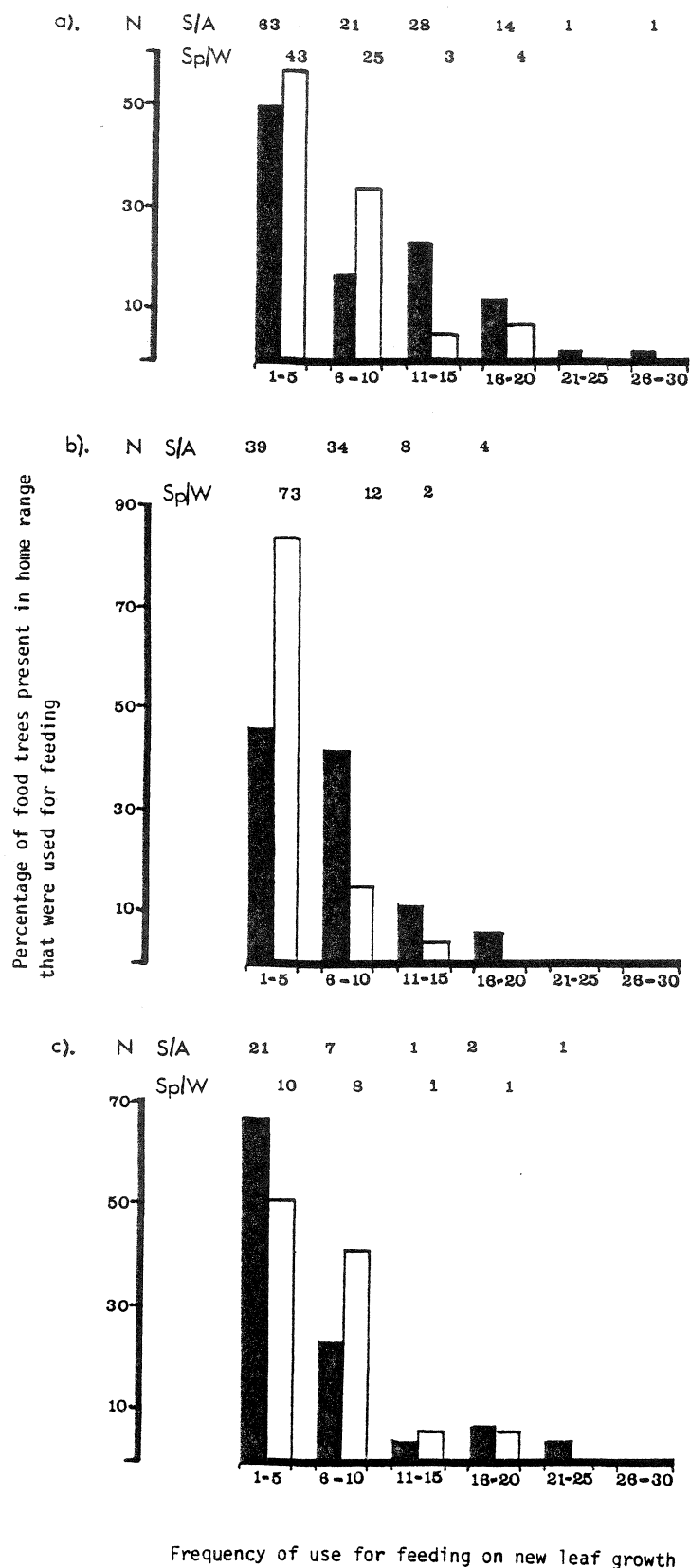


Figure 6.5 Observed frequency of use of food trees as a source of new leaf growth by intensively-monitored male and female *P. volans* at Wadbilliga (a), and Morton forest types B (b) and C (c) (N represents the number of food trees in each frequency-of-use category; summer and autumn: solid histogram, winter and spring: open histogram).

In spring/winter, about 90 per cent of trees at all sites were used 10 times or less. This occurred because, in contrast to summer and early autumn, the availability of new growth on individual food trees was relatively low and *P. volans* had to visit more food trees to exploit this resource.

#### 6.3.3d *Social interactions*

Social interactions between *P. volans* while feeding were generally restricted to paired adults, and to mothers and their dependent young. When closely associated (see Fig. 5.5), paired adults routinely fed in the same tree crown but rarely in the same sub-canopy region. The time when dependent young first commenced eating eucalypt foliage could not be determined. However, during the first few weeks of feeding on foliage (during spring), young animals were generally accompanied by their mothers and typically selected and ate juvenile leaves that had been first sampled by their mothers.

The only agonistic behaviours observed between gliders occurred at Morton forest type B and were between resident females F1 and F3 (Fig. 5.7) in the region where their home ranges and foraging areas overlapped. These agonistic behaviours occurred in winter or early spring when females were apparently exploiting and defending trees with relatively abundant new leaf growth when compared to their neighbouring trees. There was no apparent pattern of dominance by female antagonists. Generally, the resident female first to enter and exploit an area of forest which was overlapped by two adjacent home ranges or foraging areas, was able to assume dominance and force the 'intruding' female to retreat to another part of her home range.

#### 6.3.4 Comparative phenology of eucalypts in Morton forest types A, B and C

*Eucalyptus gummifera* and *E. piperita* were the only two eucalypt species common to forest types A, B and C at Morton. The

timing of new leaf growth, production of buds and flowering of trees of each of these species across the site was generally in synchrony. However, production of new leaves and buds, and the extent of flowering in forest type A at Morton was lower than for trees in the forest types occupied by gliders.

Flushes of new leaf growth occurred on several individuals of both *E. piperita* and *E. gummifera* in forest type B and, to a lesser extent, forest type C during both winters of the study, but were rarely observed on trees in forest type A. The index of relative abundance (mean  $\pm$  S.D.) used to assess new leaf growth for each species during summer and early autumn (both periods sampled for each of 3 years) was consistently lower for *E. gummifera* ( $2.4 \pm 0.5$ ) and *E. piperita* ( $2.2 \pm 0.4$ ) in forest type A than for trees of the same species in forest type B and C during the study. Mean values  $\pm$  S.D. were  $3.4 \pm 0.6$  for *E. gummifera* and  $3.0 \pm 0.6$  for *E. piperita* in forest types B and C, but the sampling and Index method were inadequate to demonstrate that the differences between these forests and forest type A were significant.

The relative differences in the phenology of *E. gummifera* and *E. piperita* across forest types was consistent with the hypothesis that the site productivity of forest types B and C (particularly the latter) was relatively higher than that of forest type A (see Chapter 4, Section 4.4).

## 6.4 DISCUSSION

### 6.4.1 Behaviour

The most notable aspects of the behaviour of *P. volans* in this study were the similarities across sites and seasons. Irrespective of their sex, location of site or season of monitoring, gliders spent

about 8 hours active each night. During these periods, about one-third of the time was spent in feeding (about 29%) and grooming and 'other' behaviours (about 4%). About two-thirds of their time was taken in moving around or remaining stationary. The amount of time spent moving or stationary was one variable that did vary between sites and was related to forest site productivity (see Sub-section 6.4.2). In general, data for all variables were consistent with the less intensive observations of Kehl and Borsboom (1984) and Robinson (1984) (but particularly the former) which were the only two studies comparable to this research.

Feeding time consumed approximately one quarter of the waking time of *P. volans* (♂: n = 3, ♀ : n = 5) at Wongi S.F., south-east Queensland (Kehl and Borsboom 1984). The most significant difference between male and female gliders was in movement; males spent double (22%) the time moving in their home ranges compared to females, despite the home ranges of both sexes being comparable in size. As a consequence, males spent less time (36 per cent) stationary compared to females (47 per cent). Kehl and Borsboom (1984) suggested that greater activity by male gliders would allow them to establish a 'stronger presence' in their home range.

Most *P. volans* emerged from their dens within about one and a half hours of sunset. Since their activity periods were similar, irrespective of night-length, animals returned to their dens 'earlier' in the night during winter when night-length was longest. This pattern of behaviour was similar to that reported for *P. volans* at Glengarry North by Henry (1985) and may be related to energy conservation and predator avoidance.

Male and female *P. volans* monitored in this study spent similar amounts of time (about 2.5 h) feeding, irrespective of night-length. As no significant sexual dimorphism occurs in *P. volans* and all intensively-monitored adult gliders had comparable body weights their food harvesting efficiency and stomach capacity should also be comparable. Observations on captive *P. volans* and related marsupial browsing herbivores such as *Phascogalea cinerea* and *Pseudocheirus peregrinus* (Cork and Warner 1983; Hume *et al.* 1984) indicate that the consistent amounts of time spent feeding by *P. volans* in my study might best be explained if their daily food intake was limited by their stomach capacity and the rate of food passage through the gut.

During most nights male *P. volans* at both sites were more active in terms of time spent moving and linear distance moved than their female counterparts. These observations were consistent with the behaviour of *P. volans* noted at Wongi State Forest by Kehl and Borsboom (1984) and follow behaviour predicted by theory (Wittenberger 1980; Smith and Lee 1984). In contrast, Robinson (1984) found that, of the two *P. volans* that she monitored in Kioloa S.F., the female generally spent more time moving and ranged further than the male.

*P. volans* at Wadbilliga and at Morton avoided unnecessary volplaning and would walk or jump between tree crowns whenever possible. This behaviour was also reported by Robinson (1984) and I have observed the same behaviour by *P. volans* at Kioloa State Forest and Coolangubra State Forest, N.S.W. and at Cambarville, Victoria. Avoidance of volplaning may be related to conservation of energy and/or avoidance of predators. At first sight, volplaning may appear to be an efficient way to save energy or avoid predators. However, unless approached by a predator, this may not be true for gliders which inhabit forests with a closed canopy. *P. volans* lose considerable height when volplaning

and usually land low on the bole of the target tree. As a result they have to expend a substantial amount of energy to climb the target tree, and during the climb are more exposed to predators. The impact noise made when landing after volplaning often betrayed the location of animals. In contrast, the noise created by *P. volans* walking or jumping between tree crowns was relatively minor and often was undetectable on windy nights.

#### 6.4.2 Feeding ecology

*P. volans* is reported to feed almost exclusively on the mature and immature leaves of *Eucalyptus* spp. (How 1978; McKay 1983), although buds, flowers, bark, and the foliage of several non-eucalypt species including *Acacia* spp. (Marples 1973; Kavanagh 1984; Robinson 1984; S.M. Davey pers. comm.) and *Casuarina* spp. (Troughton 1965) may occasionally be taken. Russell (1980) recorded them licking nectar from eucalypt blossoms and Veron (1966) observed them eating new, green bark. Henry (1985) observed *P. volans* feeding on *Muellerina eucalyptoides* and *Pomaderris aspera* although neither appeared to be major components of the diet. Fleay (1947) found that the main diet of gliders in Victoria was the foliage of *Eucalyptus australiana* (now *E. radiata*) and *E. eleophora* (now *E. goniocalyx*) while Smith (1965) reports *P. volans* feeding on *E. robertsoni*, *E. viminalis*, *E. pauciflora* and *E. dalrympleana*. These four eucalypt species were the dominants in the Tumut study region of Smith (1965) (for site descriptions see Tyndale-Biscoe and Smith 1969a). The research of Tyndale-Biscoe and Smith (1969a), Griffith (1973) and Marples (1973) led How (1978) to suggest that the preferred food species of *P. volans*, although varying geographically, are principally the dominant eucalypts of the glider's habitat.

The diet of *P. volans* in my study was restricted to *Eucalyptus* species. Most *P. volans* favoured some eucalypt species that were growing within their foraging range, and preferred new leaf growth. At Wadbilliga, all four of the eucalypt species in the home ranges of *P. volans* were regularly browsed, but the new leaf growth of *E. viminalis* was most often selected during summer and early autumn when this food was very abundant. New leaf growth declined during winter but gliders continued to maintain a relatively high intake of new leaf growth by feeding more on species such as *E. fastigata*. This species maintained more new growth than the other tree species that were used for food. These changes in preferences were seasonal and fairly consistent within sites and were related mainly to changes in the availability of new leaf growth on food trees. Although Smith (1965) did not note any temporal variations in the diet of *P. volans*, both Kavanagh (1984) and Henry (1985) indicated marked seasonal changes in preferences for food tree species. The observations of Kavanagh (1984), in particular, were very similar to those for the patterns of food selection by gliders at Wadbilliga. This could be expected as the floristics at Kavanagh's site at Coolangubra State Forest were like those at Wadbilliga. The studies of Kavanagh (1984) and Henry (1985), however, should be treated with some caution since neither researcher had specific information on the frequency of occurrence of tree species in the home ranges of individual *P. volans* and hence the food selection options available to them.

All gliders consumed at least a few mature eucalypt leaves during each night of the year, but selection of these leaves was not random between the available tree species. *P. volans* at Morton nearly always avoided eating the mature leaves of *E. sieberi* although they regularly consumed the new leaves of this species. *P. volans* in Kioloa State Forest, N.S.W. also exhibit similar behaviour (S.M. Davey



pers. comm.). Kavanagh (1984) reported that *P. volans* preferred the mature foliage of *E. radiata* and *E. ovata* over that of *E. viminalis* during winter and early spring when the availability of new growth was low and animals spent much of their feeding time consuming mature foliage. Similar preferences were not shown by *P. volans* at Wadbilliga in my study. Although *P. volans* fed slightly more frequently during winter and spring on the mature leaves of *E. radiata* than on those of *E. viminalis*, when both species were available, the difference was not significant.

During this study the foraging behaviour of *P. volans* at both sites differed little. All gliders maintained a high intake of new leaf growth in their diet, so foraging was closely related to the spatial and temporal availability of this food. It remains unclear why all intensively-monitored *P. volans* also regularly ate at least some mature leaves, although it is possible they may have been seeking additional dietary fibre. This aspect warrants further study (see also Chapter 7).

All gliders regularly patrolled and scent-marked most of their home range. Most female *P. volans* occupied a forest area, their home range, not much larger than the foraging area required to meet the majority of their annual food requirements. The frequency of observations of stationary female *P. volans* was inversely correlated with the size of their home range and foraging area. As a consequence, females foraging in a small forest area (F6 at Morton forest type C and all females at Wadbilliga) would expend less energy foraging than female gliders in Morton forest type B which had to travel further for food. These data were also consistent with the observations that the forest site quality (Chapter 4) and, probably as a consequence, the amount and/or quality of potential food such as new leaf growth was higher at Wadbilliga and Morton forest type C compared to Morton forest type B and A (Sub-

sections 6.3.1, 6.3.4). However, the estimate of the size of the foraging area of each glider did not take into account the amount of overlap in foraging areas between breeding partners or, very occasionally adjacent resident females. Such overlap could lead to competition for the available resources (see below and Chapter 7).

With the exception of M4 and F6 at Morton forest type C, the amount of overlap of foraging areas was similar and always less than 15 per cent. The foraging area of M4 nearly always completely overlapped that of F6. It is doubtful that these two animals competed for mature foliage, but some competition may have occurred for new leaf growth, particularly in winter and early spring. Hence the amount and/or dietary quality of new leaf growth food in Morton forest type C may have been higher than that indicated by the size of the foraging areas of M4 and F6.

Unlike the situation at Wadbilliga where the home range of resident female *P. volans* was exclusive, the home range (and foraging area) of females at Morton forest type B overlapped. Altmann and Altmann (1970) have proposed two hypotheses to account for the overlap of home ranges of animals and these apply as well for foraging areas:

1. The amount of overlap of home ranges between animals will depend primarily upon those essential resources that have the most restricted spatial distribution.
2. The amount of time that animals will spend simultaneously in the area of overlap will depend primarily on the temporal availability and rate of utilisation of those essential resources.

For females in Morton forest type B, both hypotheses were applicable. New leaf growth was an essential resource. In summer, it was relatively abundant and as a result females did not exploit all of their foraging area. During winter, however, this resource appeared to be particularly scarce and females utilised most of their respective foraging areas. Females frequently made use of new growth on trees near or at the edge of their foraging area and home range. As the harvesting and consumption of this resource was relatively slow, females with adjacent or abutting home ranges often encountered each other and sometimes engaged in agonistic behaviours.

The basis of food selection by arboreal marsupial herbivores has received considerable attention, particularly for *Phascogalea cinereus* (Cork 1984; Hindell *et al.* 1985; Chapter 2), but remains problematic. Several authors have suggested that specific foliar constituents act as limiting factors (for a further discussion see Chapter 7). Degabriele (1981, 1983), for example, considered that nitrogen is a limiting factor in the life of *P. cinereus*. However, while high nitrogen level may be the *ultimate* factor, he postulated that the *proximate* factor determining the choice of browse by *P. cinereus* is the fibre content of the leaf. This hypothesis was based on the assumption that *P. cinereus* is unlikely to have the ability to determine the nitrogen level of a leaf. Recently, Landsberg (1986) found that *Trichosurus vulpecula* selectively browsed *E. blakelyi* seedlings which had relatively sweeter and less astringent foliage. These seedlings had been positioned on platforms in the crowns of fully grown *E. blakelyi* for a quite unrelated experiment. Although no data were available as to the number of animals browsing her seedlings, Landsberg's observations were consistent with the hypothesis of Bates-Smith (1972) that sweetness may be a universal attractant in determining the food preferences of higher animals, and that astringency may be a powerful repellent.

*P. volans* in my study selected food items first by sight, then by touch, smell and taste, a sequence also recorded by Henry (1985). The majority of food was rejected after it was touched and smelt. If food passed this selection process it was nearly always consumed. However, since the *P. volans* that were regularly monitored were adults and had probably been residents of each site for a number of years, it is possible that they had 'fine-tuned' their food selection and did not need to taste food as frequently as they may have done in the past. Young gliders may acquire their initial food preferences from their mothers (see Sub-section 6.3.3), as is observed in sloths (Montgomery and Sunquist 1978). In the short-term (until independence) this would be advantageous to juveniles because they also probably acquire their mother's gut flora such as cellulose-digesting bacteria (Bauchop 1978; Cork 1981). In the long-term the acquisition of food preferences from the mother would only be advantageous to juveniles that were recruited into the resident population or dispersed to forests with comparable floristics. However, even the latter option may not be viable since the foliar composition (and possibly food quality) of eucalypts may vary geographically and with site quality (Mak 1982; S.M. Davey pers. comm.). As a consequence, many *P. volans* may be forced to acquire their food preferences by trial and error. Similarly, if proximate cues are used to discern food quality, it is possible that these cues may vary spatially and/or temporally. The use of touch and smell by *P. volans* to select food clearly warrants further investigation.

At both Wadbilliga and Morton during this study, intensively-monitored *P. volans* consistently foraged for and browsed eucalypt foliage that was high in nitrogen concentration (see Table 4.3 for mean concentrations of foliar nutrients). The only exception to this pattern was the mature foliage of *E. sieberi* at Morton. However, the

relationship between foliar nitrogen concentration and food quality is unknown and may be spurious. In eucalypt foliage where there are large and variable proportions of free amino acids (Journet and Cochrane 1978; Cork 1984; Landsberg 1986), an estimate of the concentration of total foliar nitrogen or of the concentration of ammonium nitrogen (as measured in my study) may not reflect reliably the concentration of foliar protein-nitrogen which is more important for folivores (Cork 1984; Cork and Pahl 1984; Cork 1986; S.J. Cork unpubl. data). Hence the above data are insufficient to implicate foliar nitrogen as the ultimate factor determining browse selection by *P. volans*.

## CHAPTER 7

## GENERAL DISCUSSION

7.1 COMPARATIVE ECOLOGY OF *P. VOLANS* AT WADBILLIGA AND MORTON IN  
RELATION TO THE FIRST RESEARCH OBJECTIVE

The first main objective of my study was to investigate why population densities of *P. volans* are low in eucalypt forests with relatively low concentrations of nutrients (N,P,K) in mature foliage of the eucalypts and high in eucalypt forests with relatively high concentrations of nutrients in their mature foliage. Forest sites at Morton ('low nutrient') and Wadbilliga ('high nutrient') were chosen for a comparative study and their respective relative nutrient status was confirmed (Chapter 4). Data presented in Chapter 4 also demonstrated that the forest site at Morton was actually comprised of three distinct forest types (A,B,C) which varied in productivity.

An apparent gradient in forest productivity was noted which decreased from Wadbilliga through Morton forest types C, B and A. Many aspects of the social organisation of *P. volans* were related to this gradient (Chapter 5). For example, there was a marked contrast in the distribution of resident adult *P. volans* at the two sites. *P. volans* at Wadbilliga had a relatively even distribution across the site and most of the site was permanently occupied. In contrast, *P. volans* at Morton had an extremely clumped distribution. The majority of the site was unoccupied (forest type A) and resident animals were restricted to two relatively small areas of more favourable habitat (forest types B and C) within the site. The annual population fecundity of *P. volans* was also related to forest productivity. Resident animals at Wadbilliga and Morton forest type C successfully raised young during each year of the study while those in Morton forest type B did not, although their

social cycle was comparable to gliders elsewhere. Neither Wadbilliga or Morton appeared to have experienced major disturbances such as wildfire in recent years (Chapter 3), and predation or the availability of den sites did not appear to influence the distribution of resident *P. volans*. Therefore, the hypothesis generated (Chapter 5) to explain the observed distribution and social organisation of *P. volans* in each forest was that the availability of high-quality food was limiting and that this factor was an important determinant of habitat quality. At Morton, for example, the amount of such foods in forest type A was postulated to be insufficient to support resident *P. volans* while in forest type B the availability of high-quality food, at least during the study, was postulated to be insufficient for the successful production of offspring by resident *P. volans*.

The majority of data on the behaviour and feeding ecology of *P. volans* presented in Chapter 6 were consistent with this hypothesis. Since all *P. volans* probably had comparable rates of food intake (Chapter 6) and food digestion and assimilation (Hume *et al.* 1984), the amount of 'excess energy' (i.e. above that required for their own body maintenance) available to males and females for reproduction and other activities would depend primarily on the quality of their diet and the energy expended in obtaining that diet. However, as neither of the latter parameters were quantified, the quality of the habitat of *P. volans* in each forest can only be inferred from circumstantial evidence.

All *P. volans* preferred new leaf growth to other foods and attempted to maintain a high intake of this food in their diet throughout the year. During summer and early autumn new leaf growth was very abundant at both Wadbilliga and Morton and feeding on this food by *P. volans* represented about 75 per cent of their total feeding time (Chapter 6, Fig. 6.4). During winter and spring, however, the availability

of new growth at both sites was considerably reduced. *P. volans* in Morton forest type B consumed slightly less new growth compared to animals in forest type C and at Wadbilliga, most probably because of the slightly reduced availability of new leaf growth in forest type B. Unfortunately the sampling intensity used was not adequate to statistically validate these differences and more work is required. The differences in the amount and availability of new leaf growth were related to the differences in forest productivity between sites, particularly in relation to the diversity of eucalypt species (Chapter 4) and their phenologies (Chapter 6). The concentration of nitrogen in the juvenile foliage consumed at Wadbilliga and Morton forest type C was typically higher than that of the new growth consumed by *P. volans* in Morton forest type B. During winter and early spring all *P. volans* relied predominantly on mature eucalypt foliage for sustenance. The concentration of nitrogen in the mature foliage of food trees at Wadbilliga and Morton forest type C was also considerably higher than that of food trees in Morton forest type B. These data suggest that the amount and quality of potential food at Wadbilliga and Morton forest type C may have been considerably greater than that in Morton forest type B. The reduced diversity of species of eucalypts in forest type A, compared to other forest types at Morton, and their very low production of new growth during winter was also consistent with the hypothesis that the food resources of this forest type were insufficient to support resident *P. volans*.

A qualitative comparison of aspects of the behaviour, feeding ecology and social organisation of resident adult female *P. volans* at Morton and Wadbilliga in relation to the spatial and temporal availability of food is shown in Table 7.1. Resident female *P. volans* at Wadbilliga and Morton forest type C were able to obtain the majority of their annual food requirements from a forest area considerably smaller than



Table 7.1 Qualitative comparison of aspects of the behaviour, feeding ecology and social organisation of resident adult female *P. volans* at Morton and Wadbilliga in relation to the spatial and temporal availability of food. Note that forest site productivity appeared to increase from Morton forest type A (relatively lowest productivity) through forest types B and C to Wadbilliga (relatively highest productivity) (Chapter 4). Data presented summarise that given in Chapters 5 and 6.

	Morton			Wadbilliga
	FT/A	FT/B	FT/C	
Site occupied	no	yes	yes	yes
Apparent preferred food	-	new leaf growth (NLG)	NLG	NLG
Relative availability of preferred food:				
Summer & early autumn	abundant	abundant	abundant	abundant
Rest of year	minimal	low	low	low
Relative size of foraging area	-	large	small	intermediate
Distance covered during nightly activities which appeared directed primarily at foraging	-	large	small	intermediate
Relative amount of overlap in home ranges which appeared related to foraging	-	high	none	very low
Presence of female <i>P. volans</i> with young	-	no	yes	yes
Sample size <sup>+</sup>	-	4	1	8

<sup>+</sup>based on mean data for females as given in Chapter 5, Table 5.9

that required by females in Morton forest type B (e.g. the mean foraging area of female *P. volans* in Morton forest type C was 0.76 ha compared to 1.33 ha in forest type B. It appeared that the amount and/or quality of food resources was higher in the former two forests. Female *P. volans* at Wadbilliga and Morton forest type C also almost certainly expended less energy foraging, compared to females in Morton forest type B, since they spent less time moving around in search of food (Table 7.1). The situation for resident male *P. volans* at each site was less clear than for females but appeared to be consistent with the hypothesis. Males in all forests had similar sized foraging areas (i.e. about 1.15 ha) but male *P. volans* at Wadbilliga and in Morton forest type C, on the basis of their activity, apparently derived more 'excess energy' from these foods than the males in Morton forest type B. This enabled male gliders at Wadbilliga and Morton forest type C to retain larger areas of relatively infrequently-used food ('spare' food, for a full discussion see Section 7.2) than males in Morton forest type B as well as successfully pairing, and siring young. For example, the mean size of the home range of male *P. volans* which contained less than 5 per cent of their annual observations of feeding was 0.33 ha in Morton forest type C compared to 0.13 ha in forest type B.

The Wadbilliga site was typically considerably colder than the Morton site, particularly during winter (Chapter 4), and would probably require more expenditure of energy by resident gliders for thermoregulation than animals at Morton. Despite this, female *P. volans* at Wadbilliga still regularly raised young, probably because of the 'excess energy' available from the greater amounts and/or higher-quality of food at this site.

In general, the data were consistent with the hypothesis that the availability of high-quality food limited the distribution, and

fecundity of *P. volans* at Morton. That is, the spatial and temporal availability of high-quality food was an important determinant of habitat quality for this species.

Although concentrations of N, P and K in the mature foliage of eucalypts were demonstrated to be positively correlated with the population density of *P. volans* by Braithwaite *et al.* (1983), the exact form of this correlation remains to be demonstrated. Clearly, from my study, the spatial and temporal availability of high-quality food (i.e. new leaf growth) is important for *P. volans* although the dietary quality of the available mature foliage of eucalypts may be of some importance when new leaf growth is least abundant (see 7.3.2a). Particularly, for example, during the late stages of lactation in female *P. volans* which often occurs before the commencement of new leaf flushes. While *P. volans* consistently foraged for and browsed eucalypt foliage that was high in nitrogen concentration, it should be noted that my data are insufficient to implicate foliar nitrogen as the ultimate factor determining browse selection by this species. Clearly, many other foliar constituents, either independent of or in association with nitrogen, may be implicated in browse selection and influence the dietary quality of foliage for *P. volans*. As notable differences appeared to occur in the amount of energy that animals, particularly females, expended in searching for food at Wadbilliga and Morton forest type C compared to Morton forest type B, the availability of readily digestible carbohydrates may have been a limiting factor in the latter forest type. This aspect warrants investigation.

Figure 7.1 shows the possible manner in which the availability of high-quality food and the distribution of *P. volans* may interact and, in turn, influence the mating association, and population fecundity, adopted by *P. volans*. From the outset, however, it should be

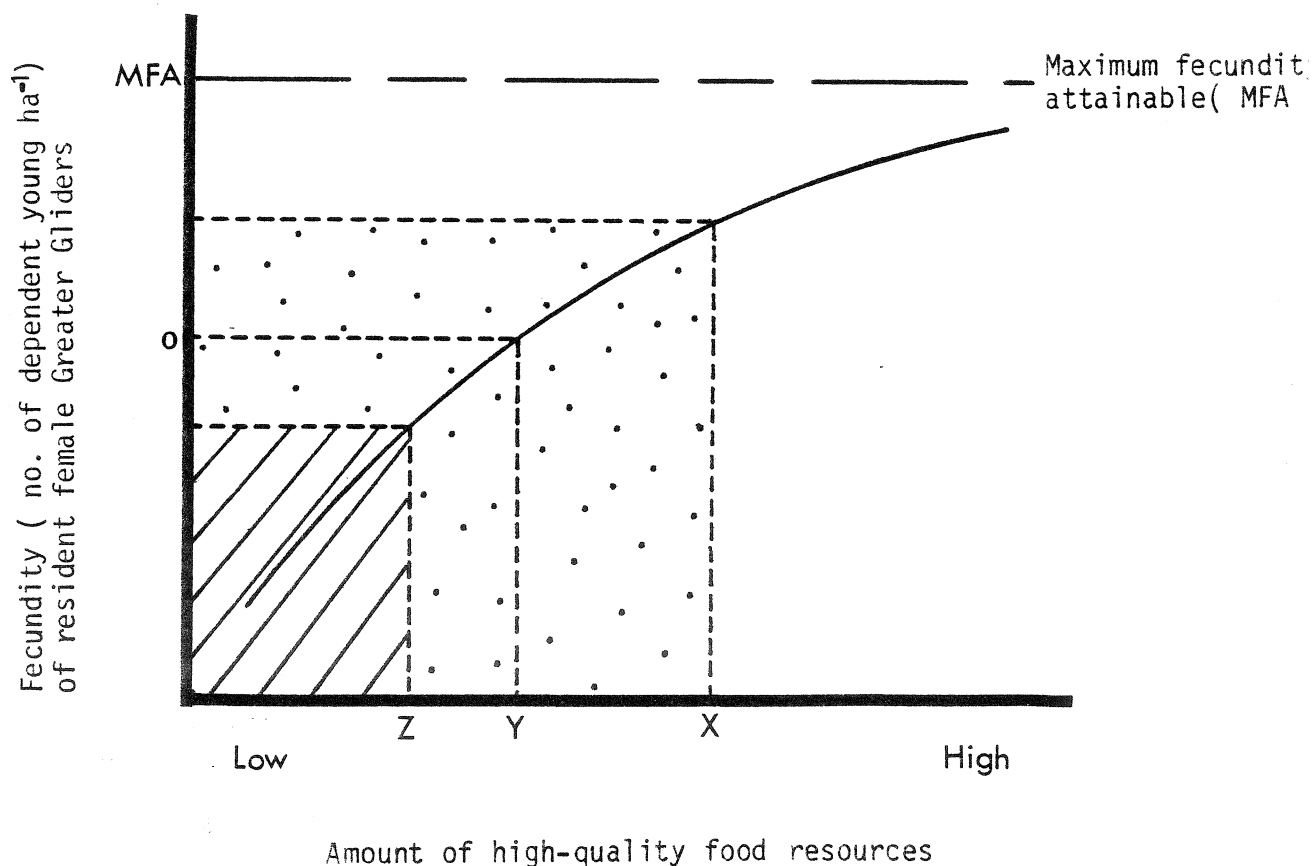


Figure 7.1 A hypothetical relationship between the distribution, mating association and fecundity of resident populations of *Petauroides volans* and their habitat quality, as measured by the annual availability (e.g. amount) of high-quality food. Cross-hatching indicates that gliders are absent from forests with high-quality food resources below Z. Resident gliders in forests with an amount of high-quality food between X and Z are monogamous (as shown by dots). In forests with an amount of high-quality food above X, gliders are frequently bigamous. See text for full explanation.

emphasised that given the low sample size and the lack of replication of study sites in my study, the following model is clearly speculative. The model is proposed primarily to facilitate the generation of new hypotheses, the testing of which may shed light on the adaptive character of the facultative mating association exhibited by *P. volans*. Note that the number of young per hectare raised annually by resident females is used in the model as a measure of population fecundity, rather than annual population fecundity which does not accurately reflect the population density of females in an area. The availability of high-quality food is based on the amount that is available to gliders on an annual basis. Also it is assumed that (i) all populations of *P. volans* live under similar constraints of behaviour and feeding, (ii) abiotic or other biotic factors such as population density and predation do not influence significantly the distribution and fecundity of resident *P. volans* and (iii) the dietary quality of the food remains constant.

In forests where the density of high-quality food falls below Z, gliders cannot harvest enough food to meet their daily basal metabolic requirements (Fig. 7.1). For example, the energetic 'cost' of ranging widely to forage in forest with a poor supply of high-quality food outweighs the nutritional gains from the high-quality food finally located and consumed. Hence these forests cannot support animals in the medium to long-term (cross-hatching in Fig. 7.1). In forests with an amount of high-quality food between Y and Z, gliders can harvest enough of this food to meet most of their energetic requirements. However, little or no 'excess' energy is available for reproduction. The fecundity of resident populations of *P. volans* in these forests is zero and the population is not viable in the long-term without immigration of young animals. Forests which have amounts of high-quality food above Y (Fig. 7.1) fall into two categories: X denotes the threshold above which

bigamy and polygyny are possible (cf. Verner and Willson 1966). When the amount of high-quality food is between Y and X gliders can harvest efficiently enough of this food to sustain reproduction. However, the amount of food is insufficient to support more than one adult female in an area small enough to be monopolised by a resident male glider: monogamy is the norm. Resident populations of gliders in forests with amounts of high-quality food above the level of the threshold (X) for bigamy and polygyny should attain the highest fecundity since males can monopolise two or more females and, as a consequence, the population is highly female-biased. Above this threshold the fecundity of the resident population approaches a maximum (MFA) which is set by the minimum space requirements of each resident female rather than by the amount of high-quality food.

Within this model, however, the area of habitat available to gliders may also influence their observed distribution and mating association. For example, some relatively small forest areas may support a quantity of high-quality food above the level represented by Z (as defined on a  $ha^{-1}$  basis) but the absolute quantity of the food in the small area may be insufficient to support gliders. Similarly, some forest areas may have an amount of high-quality food which is above the threshold for bigamy or polygyny but their area may be insufficient to support more than one female (and her partner), hence monogamy will be the observed mating association.

In nature, however, numerous deterministic and stochastic processes may influence the amount and quality of food available to gliders and it would be extremely rare to encounter relatively large forest areas that supported a spatially contiguous large amount (i.e. above X in Fig. 7.1) of high-quality food (cf. Wootton *et al.* 1986). Where these areas did occur they have largely been cleared for agriculture. Further, gliders occurring in these areas could be subject

to predation by owls (see Section 7.3) which would reduce the population density below that which the area theoretically was capable of supporting. Studies which monitor large forest areas would almost certainly encounter considerable spatial variability in the population density of resident *P. volans*, and a combination of monogamy and bigamy. This situation occurred at Wadbilliga where both bigamy and monogamy were observed. Henry (1984, 1985) observed both of these mating associations in a population of *P. volans* at Glengarry North. He found that bigamous males and their partners tended to occupy moist, relatively higher quality forest on east- and south-facing slopes while monogamous males and their partners occurred in forest where favourable habitat was restricted. Three monogamous males occupied dry forest on west-facing slopes while one resided in a relatively small, isolated pocket of moist forest at the head of a gully (Henry 1985, p. 198).

The amount of high-quality food available to *P. volans* resident in a forest area may also vary annually. For example, female gliders living in areas with high-quality food, on average, just above the level represented by Y in Figure 7.1, might not be able to support reproduction in poor years (e.g. drought) when the production of new leaf growth was minimal. Females occupying forest areas with, on average, an amount of high-quality food that was just below the level represented by Y would probably only successfully raise young in good years. During this study, female gliders in Morton forest type B failed to raise young (i.e. the amount of high-quality food available to them was, theoretically, between Y and Z, Fig. 7.1). The climate at Morton during the study was similar to the average conditions recorded for the general region although the general region was recovering from an extended severe drought (Chapters 3 and 5). Good years certainly occur in which it might be possible for females in Morton forest type B to raise young. Whether the frequency of offspring production (assuming it occurs) by

resident female *P. volans* is sufficient to maintain the existing population without immigration is not known. The quantity of high-quality food in Morton forest type A appeared to be below the theoretical level Z in Figure 7.1 and could not support resident animals in the short- or long-term.

## 7.2 LIFE HISTORY OF *P. VOLANS*

In this study, *P. volans* showed some variation in certain parameters of its life history (e.g. social organisation) which appeared related to habitat quality. Within a forest type, populations were stable with low rates of loss and recruitment of adults. However, population density varied markedly between different sites, as did annual fecundity. In large part, these differences could be attributed to variation between forests in the availability of high-quality food eaten by *P. volans*. *P. volans* tended to be monogamous in poorer quality sites and bigamous in better quality sites. Although the mating system changed with habitat quality, males probably attempted to monopolise and mate with as many females as possible in any habitat. Kleiman (1977, 1981) has termed this mating association facultative monogamy. She distinguishes it from obligate monogamy where the assistance of both parents is required to successfully raise progeny.

The general behaviour exhibited by *P. volans* was conservative. That is, it was comparable to most other species of specialised arboreal browsing herbivore, particularly animals like *Pseudocheirus peregrinus* which have a similar adult body weight. For example, *P. volans* apparently attempted to minimise energy expenditure during all of its behaviour. Gliders spent long periods (ca. 40-60%) of their nightly emergence period stationary. Further, when they were active, movements were typically relatively slow which is similar to other arboreal marsupial herbivores. Agonistic encounters and volplaning were avoided if possible; other strategies that appeared related to conserving energy.



*P. volans* apparently attempted to minimise their energy expenditure when foraging. Foods postulated to be of high-quality (new leaves), when available, formed the major proportion of their diet although dietetic diversity and, as a consequence, nutrient balance was probably maximised whenever possible.

Several reviews of the social organisation exhibited by birds and mammals conclude that intrasexual competition for primary resources (i.e. food, mates, breeding sites) plays an important part in the evolution of mating systems (Emlen and Oring 1977; Wittenberger 1979, 1980; Mace *et al.* 1983; Lee and Cockburn 1985). Intrasexual competition for resources appears to be a consequence of the greater investment by females, compared to males, in the production of offspring (Trivers 1972). Such was the case in *P. volans*. With the exception of male gliders in Morton forest type B, resident male *P. volans* maintained forest areas considerably larger than those required to meet the majority of their annual food requirements. Even allowing for an expansion of their foraging areas during periods of relatively limited food availability (e.g. drought), these observations suggested that male *P. volans* may employ resource defence (see Smith and Lee 1984) as the primary means of maximising their reproductive success (but see also Ostfeld 1987). Habitat quality may influence this behaviour in two ways. First, a relatively high-quality habitat could potentially support several females in a relatively small area thus facilitating bigamy or polygyny if a resident male could monopolise these females. Second, a relatively high-quality habitat would, theoretically, enable males to meet the energetic requirements of a more active life style such that bigamy or polygyny might be possible. As a consequence, male gliders could maximise their resource defence and hence their reproductive potential.

Comparative studies of the mating associations of several different species have shown a similar pattern to that observed in *P. volans*. In primates (Clutton-Brock and Harvey 1977), ungulates (Jarman 1974) and birds (Verner and Willson 1966), for example, the mating association is linked to resource dispersion and the temporal availability of mates. Davies and Lundberg (1984) have demonstrated this in a population of hedge sparrows, *Prunella modularis*. This species is of some interest as it may exhibit monogamy, polygyny, polygynandry and polyandry within the same population. When Davies and Lundberg (1984) provided extra food on the territories of some females their ranging was reduced and the mating success of males increased (e.g. from monogamy to polygyny or polygynandry). In contrast, where food patches were scarce, ranging by females was larger and they were difficult for one male to monopolise. Thus a reduced male mating success was observed (polyandry). Clearly, food supplement experiments in *P. volans* warrants investigation (see Section 7.4).

Polygyny in *P. volans* may not be possible because sufficient 'excess energy', to permit a male to overlap 3 or more home ranges of females, may not be available because of the size of the animal, the relatively poor nutritional quality of eucalypt foliage and the slow rate of passage of food through the animal's gut (see Chapter 2). Polygyny has never been observed in this species. Henry (1984) observed that the home range of one resident male at Glengarry North partially overlapped the home range of three female gliders. However, the association between one of the females and the male appeared incidental. They were never observed in proximity and the female was regularly associated with another resident male, particularly during the mating season (S.R. Henry pers. comm.). Hence it appears more likely that this situation represented the partial overlap of the home ranges of a bigamous male and a female in a monogamous association with another male.

The similarities of the size of home ranges and foraging areas of most female gliders at each study site fits the hypothesis (Trivers 1972; Wilson 1975; Wittenberger 1979) that range size of females is set by the minimum area necessary to supply critical resources (e.g. food, shelter) and to raise young.

Two interesting observations noted during my study were that some resident female *P. volans* apparently remained unmated (i.e. at Morton forest type B), yet males appeared to suffer costs in long-distance dispersal (e.g. predation). A similar situation was observed at Glengarry North by Henry (1984). The occurrence of resident but unmated females of a species appears to be rare in, at least, marsupials (A. Cockburn\* pers. comm.) but may also be due to the dearth of detailed studies in this area. The reason for this apparent contradiction is unknown and warrants investigation. It is possible that both female *P. volans* at Morton forest type B were unacceptable as partners to males. On the other hand, neither female may have encountered males that were considered to be acceptable partners. Alternatively, the forest occupied by these females may not have been of suitable quality to sustain additional animals (i.e. male *P. volans* acceptable as partners).

Despite the specialised adaptations exhibited by *P. volans* in its relatively nutrient-poor feeding niche, this niche still appears to impose severe restrictions on any great change in its life history, particularly its fecundity and hence ultimately its distribution. *P. volans* may not have the luxury of increasing its food intake and reducing its energy expenditure in relatively low-quality habitats. Rather, food intake is probably maximised and energy expenditure minimised in all habitats in an attempt to meet field metabolic

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requirements (FMR). This behaviour may be due to the body weight of *P. volans* which appears close to the minimum for a marsupial that is capable of sustaining FMR requirements in this niche, particularly since it appears to lack the option of caecotrophy (Hume *et al.* 1984). Consequently, relatively small changes in the spatial and temporal availability of high-quality food may significantly influence the nutritional state and ultimately the reproductive performance of individuals.

The importance of the availability of high-quality food for reproduction has been demonstrated or inferred for many animal species, both vertebrate and invertebrate (White 1978; Gaughwin 1981; Ohmart *et al.* 1985; White 1985; Sedinger and Raveling 1986; Tyndale-Biscoe and Renfree 1987). Freeland and Winter (1975) studied *Trichosurus vulpecula* in a sclerophyll forest with an open, grassy understorey. They found that this species spent about two thirds of its feeding period consuming eucalypt foliage with the remainder devoted to feeding on non-eucalypt foods. Freeland and Winter (1975) suggested that although *T. vulpecula* derived the majority of its energy requirements from eucalypt foliage, it relied on other sources of food to subsist. Thus the availability of other suitable foods, rather than that of eucalypt foliage, was postulated to limit the population density of this species. Freeland and Winter (1975) also hypothesised that the occurrence of toxic secondary compounds in the mature eucalypt foliage available to *T. vulpecula* indirectly limited its population density. More recent data, however, do not entirely support this hypothesis (Kerle 1984).

Bell (1981) monitored the reproductive performance of female *Trichosurus vulpecula* in New Zealand over a five year period. Oestrus in this species occurs in autumn and Bell (1981) found that

female *T. vulpecula* weighing more than 2.4 kg in this season were able to maintain adequate body weight in the subsequent winter to successfully rear young. In contrast, females weighing less than 2.4 kg in autumn continued to lose weight in winter and either lost their young or failed to breed altogether. Bell (1981) considered that female *T. vulpecula* attempted to accumulate fat reserves in autumn and early winter and utilised them in late lactation when the demands of lactation were highest and food was generally scarce.

Strong evidence of a direct relationship between the availability of suitable food (in this case fruit, arthropods and nectar) and reproduction has been shown for *Caluromys philander* and *Philander opossum* in French Guyana (Charles-Dominique *et al.* 1981; Atramentowicz 1982). Atramentowicz (1982), for example, studied *Caluromys philander*. This species breeds twice during the year. Litters born in October-December survived to independence while litters born in April-June, after the first litters had been weaned, did not. Atramentowicz (1982) suggested that females were unable to raise a second litter because the main fruiting season of the forest ceased in June and there was insufficient food resources for them to sustain lactation.

The life history of *P. volans* in this study appeared comparable to that known from all other studies on this species (e.g. How 1978; Henry 1984). Since the life history of *P. volans* exhibits many characters which tend towards the *K*-selected end of the *r-K* continuum (e.g. stable population density, relatively small litter size, relatively low fertility, relatively prolonged period of lactation, increased longevity; for a review see Horn and Rubenstein 1984; Lee and Cockburn 1985), several authors (e.g. How 1978; Henry 1985) have

suggested that *P. volans* is a *K*-selected species. The adaptive significance of this life history might be to enable *P. volans* to maximise the range of eucalypt forest habitats it can successfully exploit; a feature which could be particularly important on continental Australia which, by world standards, is an excessively dry and nutrient-deficient environment. Due to its longevity and population stability, *P. volans* could exploit environments (for definition see Coulombe 1978a,b) which only permit successful reproduction during infrequent and unpredictable episodic events (i.e. when the availability of critical food resources was maximised). These environments provide a relatively stable resource base compared to the life span of *P. volans*, and may be marginal or unexploitable to shorter-lived species. Southwood *et al.* (1974) have postulated that species exhibiting life histories dominated by *K*-selected characteristics should be subject to low predation and parasite pressure. Of the populations of *P. volans* adequately studied, most of these conditions appear to hold.

In terms of the evolutionary success of this species, marginal or relatively low-quality habitats may act as important refugia for gliders since foraging theory (Schoener 1971; Krebs 1978; Pyke 1984) would predict that these areas would be considerably less subject to predation (particularly by owls) compared to high-quality habitats which supported a relatively high population density of resident gliders. Further, the capacity to utilise marginal habitats may also enable *P. volans* to cross extensive barriers, such as unfavourable environments, between biogeographic zones of high-quality habitat. However, marginal habitats often occur in relatively dry climatic regions and, combined with their relatively high flammability (Mak 1982), may be more susceptible to major wildfires than high-quality habitats.

### 7.3 IMPLICATIONS OF CURRENT RESEARCH

#### 7.3.1 Observation of *P. volans*

Robinson (1984) appraised the techniques available for observing *P. volans*. Unlike her study, however, the behaviour of intensively-monitored animals in my study was not significantly influenced by the presence of an observer.

A less intrusive means of observing gliders was the method employed during this study for the monitoring of tagged animals. To minimise noise and disturbance I always arrived in the forest area encompassed by the home range of the glider to be monitored before sunset. A red filter was used on spot- and back-up lights for observations. If it could be avoided, light was never shone directly at the animal. Instead the periphery of the light beam was shone on the animal. During twilight or full moon it was often not necessary to use light for recording behaviour. If possible, gliders with distantly-separated home ranges were monitored on consecutive nights of the sample period to minimise disturbance. These procedures are recommended for future studies of *P. volans*.

#### 7.3.2 *P. volans* and forest management

The theoretical model illustrated in Figure 7.1 could integrate and explain the distribution, fecundity and mating associations exhibited by resident populations of *P. volans* monitored in this study. This model can also explain the distribution, population fecundity and mating association adopted by *P. volans* throughout its entire range, and is consistent with all of the current observations on this animal. However, the predictive value of the model needs to be tested widely. To do this, a rigorous definition of 'amount of high-quality food' is required. Deriving a function to calculate reliably this variable,

however, is extremely difficult since numerous factors which contribute to it are hard to quantify and may vary temporally. Such a function would need to calculate the biomass and dietary quality of mature and juvenile eucalypt foliage available to *P. volans* on at least an annual basis. To further complicate matters, little is known of the time scale that is important to the ecophysiology of *P. volans*. In terms of reproduction, for example, the availability of high-quality food resources may only be critical for resident adult females in marginal habitats during a short phase of their annual reproductive cycle (see also Sub-section 7.4).

In terms of the delineation of forests which are potentially capable of supporting high-quality habitat for gliders it may be possible to circumvent the above problem. Eucalypt forests in the general <sup>study</sup> region appear able to provide an amount of high-quality food which is above the threshold  $Y$  in Figure 7.1 (i.e. enough to sustain annual reproduction in resident populations of *P. volans*) in two general ways. First, forests may provide high-quality habitat for gliders if the eucalypt species forming them have mature foliage of high dietary quality. Hence any marked seasonal or annual fluctuations in the availability of new leaf growth would not detract significantly from the reproductive potential of resident female gliders. In these forests, the diversity of eucalypt species present would not be of importance unless the dietary quality of the mature foliage of some species (e.g. possibly *E. sieberi*) varied considerably between seasons. Even so, forests with a high diversity of eucalypt species with mature foliage of high dietary quality, including species that produced new growth in winter, would be expected to approach the optimum habitat for gliders. On the other hand, forests represented by eucalypt species with mature foliage of relatively low dietary quality may provide high-quality habitat if these species can supply an adequate amount of new leaf growth over all



seasons. Since the phenology of individual trees within a species is fairly well synchronised (Kavanagh 1984), these forests would almost certainly consist of a relatively high diversity of eucalypt species that provided predictable flushes of new leaf growth in all seasons, particularly winter and early spring. However, as shown in this study, eucalypt species that appear to have the potential to provide new growth need not necessarily do so since new growth production may vary according to factors such as tree age, soil moisture, solar radiation and precipitation (Jacobs 1955; Pook 1984; Norton and Davey 1986). As a consequence, the identification of forests which support eucalypt species with mature foliage of high dietary quality should provide the best means of predicting where high-quality sites suitable for *P. volans* will occur.

Currently, there is no unequivocal method of determining the dietary quality of mature eucalypt foliage or, in fact, the dietary quality of any foliage eaten or avoided by *P. volans* or any other arboreal marsupial (Chapter 2; Cork and Pahl 1984; S.J. Cork pers. comm.). Nor does a reliable technique to determine the dietary quality of food items eaten by these animals appear likely to become available for some time. Despite this, the concentration of N, P and K in mature eucalypt foliage provides a **coarse correlate** of its quality for food. Forests supporting potential high-quality habitat for *P. volans* could be identified provisionally by mapping forests containing eucalypt species with a relatively high concentration of N, P and K in their adult foliage (Kavanagh 1984; Norton 1985, 1986). This is consistent with field observations (Section 1.1; L.W. Braithwaite pers. comm.; S.M. Davey pers. comm.; S.R. Henry pers. comm.).

Initial identification of potential high-quality habitat for *P. volans* would have to be verified from the ground as forests may not realise the potential indicated by their composition of eucalypt species. This might occur because of factors such as an unfavourable age class distribution of trees which resulted in a lack of mature trees containing den sites; unfavourable topography (Braithwaite *et al.* 1983); or the temporal unpalatability of the mature foliage of dominant tree species. Forests confirmed to support *P. volans* could be assessed quickly for relative quality by determining the population density of resident adults. Note, however, that the population density of *P. volans*, if considered alone, may not be a reliable correlate of habitat quality (cf. Van Horne 1983). This problem arises since the size of the home range used by gliders, but particularly males, may not be directly related to their own requirements for food. For example, if resident male *P. volans* regularly employ resource defence as a means of maximising access to partners and the quality of the occupied habitat is insufficient to support many bigamous mating associations, then the realised population density of resident *P. volans* may be more comparable to that observed in less favourable habitat (e.g. Wadbilliga versus Morton forest type B). Hence my use of the concept of foraging area in this study. A far more accurate measure of habitat quality, but more time-consuming to obtain, would be to assess population density and annual fecundity or the density of breeding females in the resident population.

There is now considerable debate as to the best strategy or strategies to adopt for conserving wildlife in commercially productive eucalypt forests (Shaw 1983; Loyn 1985; S.M. Davey pers. comm.). In formulating policies for management of habitat for *P. volans* or a suite of species which includes *P. volans*, two points generated from my study are important. Firstly, the highest population density of resident gliders monitored in this study was slightly below 2 animals

per hectare and was within the range reported, for the maximum population densities attained by *P. volans*,<sup>from</sup> all other studies for which data are available (Chapter 5, Table 5.10). Gliders used between 2 and 3 den trees per hectare, so a resident population would require at least 5-6 den trees per hectare in relatively high-quality forests, otherwise the lack of shelter sites becomes limiting. As relative habitat quality decreases, the minimum number of den trees ( $\text{ha}^{-1}$ ) required by gliders would also decrease but would rarely fall below 1 den tree per hectare. However, a forest area which supports a range of species that are dependent on hollows in trees as well as *P. volans* will require the presence (and long-term maintenance) of a lot more hollow trees in an area than based on the requirements of *P. volans* alone (cf. Mackowski 1984; Inions 1985). Secondly, the presence of a resident population of *P. volans* in a forest may not be indicative of its ability to support such in the longer-term. This will depend primarily on the quality of the habitat (i.e. its ability to support successful reproduction within the lifetime of resident animals) and its proximity to other viable populations (i.e. probability of recruitment of dispersing young).

### 7.3.3 The problems of sampling scale and spatial heterogeneity in ecological field studies

An important but often neglected axiom in ecology is that the choice of a sampling strategy depends on the objectives of the study (Johnson 1981). Recently, researchers examining the ecology of selected species of arboreal marsupial, or a suite of species (e.g. Davey 1984; Kavanagh 1984) have attempted to interpret their data in relation to the nutrient hypothesis of Braithwaite *et al.* (1983). The interpretation of these data has given equivocal results. In some cases the hypothesis put forward by Braithwaite *et al.* (1983) is supported, in others it is refuted or can be neither supported or rejected. The lack of strong support for the nutrient hypothesis may in most, if not all, cases be

explained by the inadequacy of the sampling strategy employed rather than the inadequacy of the hypothesis itself. This is not to suggest that the various studies were poorly conducted; rather, the objectives they were designed for and the data that were collected to meet the various objectives were either insufficient, inappropriate, or difficult to interpret, to also adequately test the nutrient hypothesis.

The main problem of sampling is the spatial heterogeneity of resources within an environment, and the design of sampling methods to minimise, or allow for, the effect of this heterogeneity so that the data collected will have valid ecological value when interpreted (Weins 1974, 1976; Johnson 1981; Connell and Sousa 1983; Kaiser 1983; Hodda, Williams and Norton, in prep.). Some of the problems relate to data collection and logistics. Ideally, each forest type requires several sampling 'replicates' (for statistical rigour), with no spatial heterogeneity of resources important to *P. volans* within each 'replicate'. Further, each 'replicate' requires a peripheral area sufficient to counteract potential interference such as emigration or immigration of resident gliders from adjacent forest types. Finally, each of the forest types studied would, ideally, have occurred within the same climatic region, have similar topography and be large enough to contain a large population of gliders from the same genetic 'pool'. No study so far has met these requirements, mainly because the heterogeneity of the forests makes it virtually impossible to meet the ideal requirements. My study met several important criteria that, if neglected (see below), could have markedly influenced the interpretation of the data collected. Both study sites, for example, were located in forest areas that were sufficiently buffered to prevent significant interference from populations of *P. volans* in adjacent forest types.

One of the problems associated with interpreting data collected from areas with considerable spatial heterogeneity of resources is that a mosaic of communities is present over relatively small distances and considerable inter-change or movement of animals may occur between or through them. Spot-lighting along a transect crossing such a mosaic of forest types can pick up high populations of *P. volans* in both low- and high-quality food areas. A large number of *P. volans* may exist in areas of low-quality food because there is ample opportunity for them to move easily to adjacent small areas of the mosaic to supplement their diet with high-quality food. I experienced this situation in a pilot survey in 1984-85 at Kioloa State Forest, N.S.W (T.W. Norton unpubl. data). Hence studies attempting to identify the habitat requirements of this species in a forest region can produce misleading results if they are based solely on estimates of population density; a detailed knowledge of the ecology of local populations of *P. volans* is also required.

#### 7.4 FURTHER RESEARCH

Desirable research projects, which could lead to a significant improvement in our knowledge of the dynamics of arboreal marsupial communities in the eucalypt forests of south-east Australia are outlined below:

1. A mathematical function could be derived to quantify the amount and distribution of high-quality food in a given forest area. These data could then be compared: i) to the occurrence of regularly breeding female *P. volans* with bigamous partners and those with monogamous partners; ii) to the occurrence of regularly breeding females with monogamous partners and non-breeding (as observed) females with monogamous partners, and iii) for forests that are regularly occupied by gliders and those that are not.

With sufficient data, an idea of the absolute values for X, Y and Z in Figure 7.1 could be gained. Methods are available to quantify the biomass of potential food resources in a given forest area (Young 1971; Whittaker *et al.* 1974; Stewart *et al.* 1979; Davey 1984) but there are major problems in quantifying the nutritional value of food items to consumers. Until these problems are resolved the mathematical model cannot achieve its potential.

Measurement of the energy turnover of free-living *P. volans* in forest types of different (relative) food quality provides a second way of assessing the 'quality food' model. This would enable comparison of energy requirements of different mating associations or of regularly breeding and 'non-breeding' animals. A quantitative measure of the time budget and energy expenditure of *P. volans* such as this would provide a means of assessing the validity of the conclusions drawn from the time budget data of *P. volans* collected in my study. However, the problem remains of quantifying the quality of the habitat in which the monitored gliders were living. This technique has already been tested on several marsupial species in Australia (Nagy *et al.* 1978; Smith *et al.* 1982).

A third way of assessing the 'quality food' model would be by manipulating the habitat of resident populations of *P. volans*. If the availability of high-quality food is limiting the distribution, density or fecundity of *P. volans* this can be tested by:

- i) reducing the availability of high-quality food by removal of trees or erection of barriers to exclude gliders from their foraging areas in high-quality forests. The response of the population would then be monitored.

- ii) supplementing the food resources of gliders resident in relatively poor-quality habitat by providing selected foods (e.g. eucalypt foliage from nearby 'high-quality' habitat) *ad libitum* and observing the response of the population.

The effect on breeding success might be tested by providing food supplements to certain 'non-breeding' females while using other females as controls in the manner used by Grant (1978) and Krebs *et al.* (1986).

2. Studies on the basis of food selection by arboreal folivorous mammals have typically produced equivocal results. In terms of food selection by *P. volans*, it may prove more reliable to sample directly the eucalypt foliage accepted or rejected by this animal during its nocturnal feeding. If gliders select food primarily on the basis of its sweetness this may be more evident in foliage collected at night since there are data which show that sugar levels in eucalypt foliage fluctuate diurnally and reach a maximum overnight (Landsberg 1986; Jill Landsberg\* pers. comm.).

It may also be possible to examine food selection in *P. volans* by removing known preferred food trees and/or applying selected fertiliser to non-preferred food trees (see Dick and Longman 1985) and observing the effects on the feeding behaviour of resident gliders. In the latter situation, temporal changes in the composition of the foliage of the fertilised trees would also have to be monitored.

3. The availability of high-quality food appeared to increase the success of resident adult females in raising young each year. Provision

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of food supplements to male and female gliders resident in Morton forest type B would provide the opportunity to test this hypothesis, particularly if it could be arranged to provide food supplements to: i) some male gliders but not their partner; ii) some female gliders but not their partner, and iii) both partners. This should establish if the reproductive status of both sexes was diminished by the availability of high-quality food or whether one sex was more influenced than the other.

During this study I developed the idea that most forest environs provide female *P. volans* with relatively little 'excess energy' for reproduction. Even in relatively high quality forests only females which exploit the best habitat and expend little energy foraging (i.e. usually those in bigamous mating associations) appear able to retain enough 'excess energy' to sustain reproduction each year. In contrast, most resident females probably only retain enough 'excess energy' between breeding cycles to successfully raise young every other year. This would explain the observed (50-60%) moderate annual fecundity of most resident populations (e.g. Henry 1984). Currently, however, there exist no data to support this idea. The body weights of females occurring at Wadbilliga and Morton were similar, as were the body weights of females at Wadbilliga associated with bigamous and monogamous partners. However, since females known to have mated at Morton did not have small pouch young (in contrast to those at Wadbilliga) the critical period, if any, for determining annual breeding success may have already passed when these animals were assessed (cf. Bell 1981). It was assumed that body weight is a reliable measure of general body and reproductive condition (see Humphreys *et al.* 1984). These observations raise the questions whether or not body weight is a reliable indicator of reproductive condition in *P. volans*, and what is the most critical period of the reproductive cycle of female gliders. Also, is the body weight of females at the commencement of breeding critical in determining



the success of reproduction? Do females actively cease or limit development of the blastocyst as is observed in other marsupials (Tyndale-Biscoe 1973, 1979); if so are dietary (foliar) compounds implicated in this process? Food supplement experiments which manipulated the timing and duration of food availability and the types of food available to resident female *P. volans* in Morton forest type B may help resolve some of the above questions.

4. A study of the mechanisms involved in the dispersal of young *P. volans* from the paternal/maternal group would provide useful data for testing evolutionary theories (e.g. evolution of mating associations; see Lee and Cockburn 1985) and has several applied uses. Such a study would markedly improve our understanding of the population dynamics of this species, particularly the mortality rates of young. By following selected individuals (both sexes) it may be possible to assess parameters which can influence the probability of uninhabited forest areas becoming permanently occupied. Combined, the above data may provide insights into the potential of this species to colonise regenerating or disturbed forests. Similarly, such data may also elucidate ways of making regenerating or disturbed forests more readily colonisable by *P. volans*. To obtain a suitable sample size, this project would almost certainly involve monitoring individuals by radio-tracking (see Robinson 1984).

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