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Foraging Ecology, Behaviour and Management of the Mahogany Glider *Petaurus gracilis*

Thesis Submitted by
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In partial fulfilment of the requirements for the degree of Doctor of Philosophy in the Department of Zoology and Tropical Ecology of James Cook University of North Queensland.

The Gliding Ability of Petaurids.

"On board a vessel sailing off the coast of New Holland was a Squirrel *Petaurus*, which was permitted to roam about the ship. On one occasion it reached the mast-head, and as the sailor who was despatched to bring it down approached, it made a spring from aloft to avoid him. At this moment the ship gave a heavy lurch, which, if the original direction of the little creatures course had been continued, must have plunged it into the sea. All who witnessed the scene were in pain for its safety; but it suddenly appeared to check itself, and so to modify its career that it alighted safely on the deck".

From: Penny Cyclopedia (1839) Marsupialia, Charles Knight & Co. Vol xiv p. 460-461.

A Mahogany Glider Launching Into a Glide.

Photo by John Young

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Abstract

The mahogany glider *Petaurus gracilis* is a large species of gliding possum that was rediscovered in 1989, after not having been formally seen since 1886, and has a naturally very limited distribution, between the Hull River near Tully and approximately 30km south of Ingham in North Queensland. As a result of habitat loss, its naturally limited distribution, the potential for further habitat loss and the small amount of habitat protected within national parks it is considered endangered. The objective of this study was to examine the ecology and habitat requirements of the mahogany glider so that this information can be used in its long term management. To achieve this, the aims were to:

1) Examine the demography, reproductive biology, population density and longevity of the mahogany glider and sugar glider *Petaurus breviceps* in sympatry in both continuous and fragmented habitat.
2) Identify the habitat characteristics that determine the local distribution of both the mahogany glider and sugar glider, as the use of the different habitat types has important implications in managing the habitat of the mahogany glider. Compare the preferred habitat used by the mahogany glider to that used by the sugar glider when both species occur in sympatry.
3) Determine the diet of the mahogany glider and how it changes seasonally. Examine the timing and success of flowering for species of trees which are utilised by the mahogany glider and the potential availability of insects.
4) Determine the area of habitat required to supply adequate food and shelter. Determine the distance individuals move each night in maintaining their home range and finding food. Determine the number of dens required and interpret the social system.
5) Determine the gliding efficiency of the genus *Petaurus* using the mahogany glider and the sugar glider, and compare this genus of gliding mammals with other gliding mammals.
6) Examine the distribution of the mahogany glider with respect to its close relative the squirrel glider and examine their evolutionary history.
7) Examine the probability of extinction of different sized populations of the mahogany glider and the impact of a one in a one hundred year catastrophe.

The ecology and social behaviour of the mahogany glider was studied in an area of continuous forest and an adjacent area of fragmented forest between Cardwell and Ingham in North Queensland, between December 1994 and December 1996. A mark recapture study was undertaken to examine the life history of the mahogany glider and sugar glider *Petaurus breviceps*. A radiotracking study was also completed to examine the home-range, social behaviour and foraging strategies of the mahogany glider. Food availability was also determined to allow a comparison with the observed diet.

The mahogany glider has a distinct breeding season, with births occurring between April and August/September each year. This appears to synchronise the weaning period with a peak in the availability of insects and acacia arils, which are presumably needed to supply nitrogen and lipids to subadult animals during this growth phase.

The mean litter size for the mahogany glider was 1.55, and females appear to be able to raise only one litter per year, although they can re-mate and replace a litter if it is lost early in the breeding season. The sugar glider had an average litter size of 1.83, and was able to produce more than one litter per year. Both male and female mahogany gliders and sugar gliders appear to be able to live until at least 5 years of age. Female mahogany gliders appear to mature between 12-18 months of age.

Trapping information revealed the density of mahogany gliders was on average 0.24ha^{-1}, with the density of sugar gliders being 0.26ha^{-1} in the continuous forest. However in the discontinuous fragmented forest, the density of the mahogany glider was greatly less than the continuous habitat (0.16ha^{-1}), while the density of sugar gliders was greatly more than found in the continuous habitat (0.46ha^{-1}). An examination of the habitat utilised by the mahogany glider and sugar glider in the continuous and fragmented areas, revealed the mahogany glider to prefer open habitat dominated by eucalypts and *Albizia procera*, while the sugar glider favoured closed habitat, with an understorey of acacias. As corridors are typically comprised of a greater understorey of acacias this helps to explain the significant decrease in

mahogany glider density within riparian strips in fragmented forest (although the results do show that corridors may be used by mahogany gliders).

The mahogany glider fed on a diverse variety of food items, including nectar and pollen from Myrtaceae species such as eucalypts, bloodwoods and melaleucas. Sap, from *Acacia mangium* and especially *Albizia procera* were important. Lerps and honeydew, insects, acacia arils and fruit from mistletoes were also consumed. In obtaining this variety of food the mahogany glider depended on complex seasonal cycles of food availability, requiring a high species diversity of plants with distinct periods of availability.

The annual home-range averaged 19-20ha for both males and females in continuous forest and 10 hectares for females and 16 for males in the riparian fragmented linear habitat. Individual males and females formed pairs with home-ranges overlapping by approximately 86%, whereas they overlapped only 8-10% on average with other animals of either sex, suggesting that they are socially monogamous. Both males and females have 6-13 dens within their combined home-range, which they either share with their mate (and offspring) or often den apart. The use of a number of dens, and denning apart, appears to be a cost effective means of jointly defending a territory.

In traversing their home-range, the mahogany glider has a glide angle of 28.26° (or 1.91m distance per 1m loss in elevation), which was not significant to the sugar glider that had a glide angle of 29.69° (or 1.82m distance per 1m loss in elevation). Significant differences were found between them for height of launch (19.75 and 11.96m respectively), height of landing (4.48 and 1.95m respectively), diameter at breast height of landing tree (44.12 and 23.22cm respectively), and glide distance (29.71 and 20.42m respectively). Although both gliders do make short glides, direct observations, and the significantly greater height of launch and landing points, show the much larger mahogany glider preferred more open habitat and to glide from the top of tall trees, where longer glides could be made. In contrast the sugar glider clearly preferred the mid storey with a higher density of trees, where shorter glides would be preferred.

Bioclimatic prediction of the potential distribution of the mahogany glider using the BIOCLIM program, suggested their distribution was unlikely to extend much beyond their presently known range or much greater than 500m elevation. The predicted distribution of the closely related squirrel glider overlapped almost entirely with that of the mahogany glider, although there is no known overlap of these two species as the closest records are 25km apart. It is proposed that an isolation event resulted in the separation of a population of squirrel gliders (or a common ancestor) and consequently allowed the evolution of the mahogany glider in the highly productive area where they occur.

The population viability analysis program VORTEX showed that populations up to 300 individuals (1500ha) have a negative population growth rate, high losses of genetic diversity and a greater than 5% chance of extinction within 100 years. A population of 800 individuals (4000ha) was needed for the population size to stabilize. Sensitivity analysis showed adult mortality of greater than 25% to be important in decreasing the viability of populations. Populations of 400 were resistant to a one in 100 year catastrophe which had a 20% mortality and 20% decrease in reproduction. As only approximately 50% of the available habitat appears to be occupied, an area approximately 8000ha (800 individuals) is suggested to be required to maintain viable populations of mahogany gliders.

In order to manage this species over the long term a number of management issues need to be addressed. These include: (1) the establishment of reserves of adequate size to maintain viable populations; (2) establishment and maintenance of corridors between key areas of habitat to allow individuals to move between populations; (3) monitoring and controlling rainforest expansion within corridors and in key habitat; (4) use plain wire instead of barbed wire where possible; (5) minimise the distance of gaps in habitat for tracks and roads so that these can be crossed easily, reducing the opportunity for predation on the ground or being run over; and (6) conduct research to determine the most appropriate fire regime to control rainforest expansion.

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Chapter 1

Introduction.

1.1 History and Taxonomy of the Mahogany Glider

The mahogany glider *Petaurus gracilis* was described in 1883 by Charles De Vis as *Belideus gracilis* from a specimen obtained from "north of Cardwell" by Kendall Broadbent. The generic name *Petaurus* means ‘tightrope walker’ or ‘rope-dancer’ (Strahan 1981) and the specific name *gracilis* means thin, slender or lean.

In his description, De Vis (1883) described the mahogany glider as intermediate in size between the squirrel glider *Petaurus norfolcensis* and the yellow-bellied glider *Petaurus australis* although differing from both of these "in its markings and in having shorter ears, and a rather slender and less hairy tail". In 1886 three further specimens were collected by Broadbent (Van Dyck 1993). Of the specimens collected as *P. gracilis*, a holotype was apparently not chosen and no specimen of the mahogany glider was officially catalogued at the Queensland Museum. Therefore further references to this species were ambiguous and it was generally thought that *Petaurus gracilis* was a synonym of the closely related squirrel glider. After 1886 no further specimens were collected and because of the lack of a holotype in the collection the species appeared to be lost, or at least forgotten! In 1888, Thomas synonymised *P. gracilis* with *P. norfolcensis* and one hundred years later McKay (1988) and Van Dyck (1990) did the same. A number of authors have placed *P. gracilis* as a northern subspecies of the squirrel glider, ie. as *P. norfolcensis gracilis* (Iredale & Troughton 1934; Troughton 1941; Tate 1945; Fleay 1954; Colgan & Flannery 1992).

In 1986, during the movement of the Queensland Museum to a new location, three large glider skins and their skulls were found, from Mt Echo in north-east Queensland, which appear to be specimens of *P. gracilis* (Van Dyck 1990). Several surveys of the mountains around Ingham, Tully and Cardwell failed to find the mahogany glider. It was not until October 1989 when a further specimen (collected in February 1974 at Barrett's Lagoon) was found in the Queensland Museum that the gliders true locality was identified. Finally, in the early hours of December 6 1989 living specimens of *P. gracilis* were located on freehold land at Barrett's Lagoon (18°02'S, 145°58'E), 14km southeast of Tully (Van Dyck 1990).

Colgan and Flannery (1992) used biochemical techniques to assess the relationship of the genus *Petaurus* and although they suggested that *P. gracilis* and *P. norfolcensis* were genetically distinct, they elevated the mahogany glider only to sub-species status. However as suggested by Van Dyck (1993), it appears that none of these authors had examined the few *P. gracilis* specimens, relying instead on interpreting the rather vague description of De Vis in 1883. The mahogany glider was formally reassigned as a full species by Van Dyck (1993), 110 years after it was first described. It is distinguished from *P. norfolcensis* by its significantly larger body size, weight and skull measurements, and from *P. australis* by its smaller size and grey to buff-brown colour (Van Dyck 1993). The mahogany glider has a head-body length of 250 ± 12cm and the vent-tail length is generally one and a half times longer than the head body length with an average of 370 ± 15cm (Chapter 3). There is significant variation in the depth of toning in both the dorsal and ventral fur (Van Dyck 1993), however most specimens appear to have a grey dorsal surface, with a black dorsal stripe extending from between the eyes to the base of the tail, and typically a creamy/yellow ventral surface (similar to that in sugar and squirrel gliders). It appears that within the limited distribution of the mahogany glider, two colour morphs occur (grey and "mahogany") with each being dominant in different sub-populations.

The mahogany glider is a member of the family Petauridae. This family contains eleven species, six from Australia and eight from New Guinea and surrounding islands (the sugar glider *Petaurus breviceps* and the striped possum *Dactylopsila trivirgata* are found in both Australia and New Guinea) (Flannery 1994). The Petauridae is divided into two subfamilies, the Dactylopsilinae that contains four species of striped possums and the Petaurinae that contains seven species including the gliders (*Petaurus* spp.) and Leadbeater's possum *Gymnobelideus leadbeateri* (Table 1.1).

Table 1.1. Species within the family Petauridae and their distribution.

Species	Distribution
Dactylopsilinae	
Dactylopsila megalura	New Guinea; Central Cordillera, from the Weyland range in the west to the Telefomin area in the east.
Dactylopsila palpator	New Guinea; Central Cordillera, from the Arfak Mountains in the west to the mountains in the extreme south-east in Milne Bay Province.
Dactylopsila tatei	Fergusson Island in the D'Entrecasteaux Group, SE of New Guinea.
Dactylopsila trivirgata	Australia; North-east. South to Townsville, Qld. New Guinea; Aru, Japen and Waigeo Islands.
Petaurinae	
Gymnobelideus leadbeateri	Australia; 1000km^2 area in the central highlands of Victoria.
Petaurus abidi	New Guinea; North coast ranges - Mt. Somoro-Mt Sapau.
Petaurus australis	Australia; East. from Portland Victoria to Sarina near Mackay, Qld. A second population exists on the western slopes of the Atherton Tablelands.
Petaurus biacensis	Irian Jaya; Biak-Supiori and Owi Islands.
Petaurus breviceps	Australia; East and north coast including Tasmania. New Guinea; widespread; and Adi, Bagabag, Bam, Batjan, Blup Blup, Duke of York, Fergusson, Gebe, Goodenough, Halmahera, Japen, Kadovar, Kai Besar, Karkar, Koil, Misima, Misool, New Britain, Normandy, Numfoor, Salawati, Sudest, Ternate, Vokeo, Wei and Woodlark Islands.
Petaurus gracilis	Australia; Between Tully and the Bambaroo Foothills, 30km south of Ingham. A distance of approximately 108km north to south.
Petaurus norfolcensis	Australia; East coast. from south-western South Australia to northern Queensland.

(derived from Flannery 1994, 1995a, 1995b and Strahan 1995).

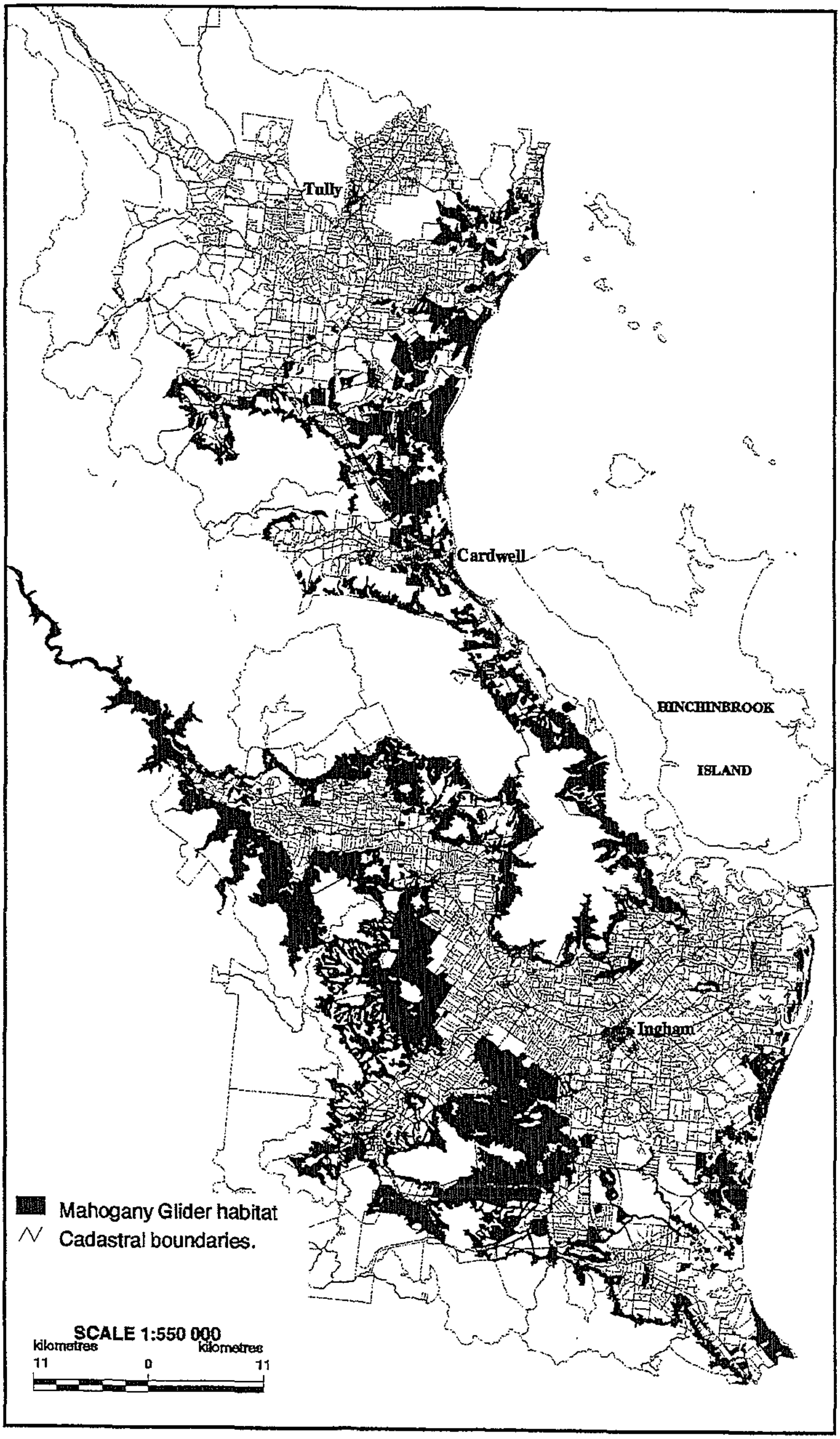
1.2 Distribution

The known distribution of the mahogany glider is very restricted despite numerous surveys (Eyre 1993; Lyon 1993; Van Dyck 1993; Goldingay & Carthew 1996; Smith 1996; McKay 1997; per. obs.). The species has been recorded only in a narrow and highly fragmented band of medium to low woodland on coastal lowlands between the Hull River near Tully and Crystal Creek some 30km south of Ingham, a north-south distance of approximately 108km and enclosing a total area of only 720km^2 (Fig. 1.1; Blackman *et al.* 1994; Chapter 8). Within this band the mahogany glider has been found (with several exceptions) only at altitudes below 120m elevation, so the maximum remaining habitat is approximately 87.2km^2. However, as most records are between 0-80m elevation, the area could be as small as 68.9km^2.

Blackman *et al.* (1994) suggested that within the known range of the mahogany glider, populations utilise at least two distinct woodland and forest environments, one associated with coastal forest complexes occurring on floodplain alluvials and on siliceous sands of beach dunes, the other associated with woodlands and forests of foothills and colluvial fans.

1.3 Land Use Within the Distribution of the Mahogany Glider

Approximately 80% of the species' potential habitat has been cleared for agriculture or forestry purposes on the coastal floodplain (Van Dyck 1993; Blackman *et al.* 1994). Primary production of the area includes pine plantations (*Pinus carribea*), bananas, fruit trees, pineapples, cattle and, most importantly sugar cane. The remaining habitat is very fragmented and vulnerable to wildfires and continued clearing (Blackman *et al.* 1994). The composition of land tenure (below the 120m elevation) can be seen in Fig. 1.2. Only 16% of the remaining mahogany glider habitat is protected within National parks, while 34% is leasehold land and 22% is freehold land, which requires no permit to be cleared.


Tully
Cardwell
HINCHINBROOK
ISLAND
Ingham
Mahogany Glider habitat
Cadastral boundaries.
SCALE 1:550 000
kilometres
kilometres
11
0
11

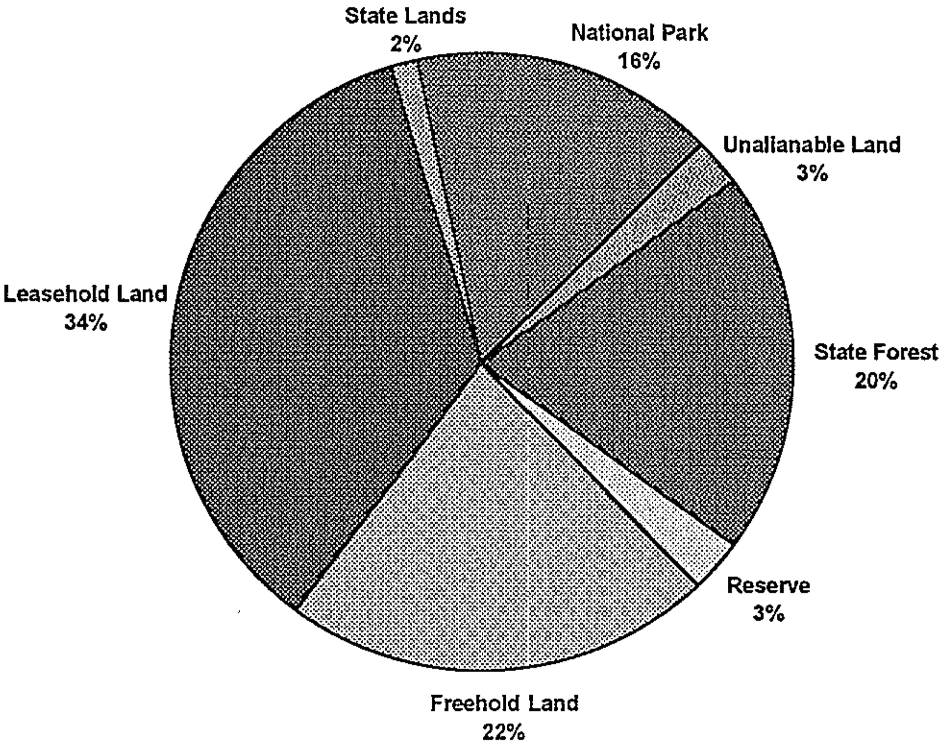


Figure 1.2. Land tenure of remaining mahogany glider habitat. Based on the 120m elevation area of 87, 200ha. Values from the Queensland Dept. of Environment.

As a result of the limited natural distribution, large scale loss of habitat, continuing clearing of land and the very small amount of available habitat in protected areas, the mahogany glider is considered one of Australia's most endangered species (Van Dyck 1993; Blackman *et. al.* 1994). It is scheduled as an endangered species in Queensland under the Nature Conservation (Wildlife) Regulation 1994, by the Federal Endangered Species Protection Act 1992, and the ANZECC (Australian and New Zealand Environment and Conservation Council) list of endangered vertebrate fauna.

1.4 Objective of this Study

The mahogany glider has recently been rediscovered, re-elevated to full species status, and found to occur in an extremely restricted distribution in coastal lowland eucalypt woodland in north Queensland, which has been mostly cleared for agriculture. The aim of this study was to examine the ecology and habitat requirements of the mahogany glider so that this information can be used in its long term management. To achieve this, the specific objectives were to:

1) Examine the demography, reproductive biology, population density and longevity of the mahogany glider and sugar glider in sympatry in both continuous and fragmented habitat (Chapter 3).
2) Identify the habitat characteristics that determine the local distribution of both the mahogany glider and sugar glider, as the use of the different habitat types has important implications in managing the habitat of the mahogany glider. Compare the preferred habitat used by the mahogany glider to that used by the sugar glider when both species occur in sympatry (Chapter 4).
3) Determine the diet of the mahogany glider and how it changes seasonally. Examine the timing and success of flowering for species of trees which are utilised by the mahogany glider and the potential availability of insects (Chapter 5).
4) Determine the area of habitat required to supply adequate food and shelter. Determine the distance individuals move each night in maintaining their home range and finding food. Determine the number of dens required and interpret the social system (Chapter 6).
5) Determine the gliding efficiency of the genus *Petaurus* using the mahogany glider and the sugar glider, and compare this genus of gliding mammals with other gliding mammals (Chapter 7).
6) Examine the distribution of the mahogany glider with respect to its close relative the squirrel glider and examine their evolutionary history (Chapter 8).
7) Examine the probability of extinction of different sized populations of the mahogany glider and the impact of a one in a one hundred year catastrophe (Chapter 9).

1.5 Ecological and Energetic Constraints on the Exudivore/ Insectivore Marsupials

1.5.1 Introduction

There are a number of ecological and energetic constraints that act on exudivore/ insectivore marsupials such as the mahogany glider. These factors in turn determine the life history and habitat use of a species, including the diet, area requirements, optimal body size and ultimately the distribution of species. The aim of this review is to examine the constraints that influence exudivore/insectivore marsupials and compare them with folivorous marsupials.

1.5.2 Body Size

A species typical body size is an important biological parameter as it influences or correlates with the required rates of energy acquisition, metabolism, and surface area to volume ratios (McNab 1971). Body size also has important effects on reproduction through its influence on rates of growth, metabolism, litter size and duration of lactation (Tuomi 1980; Smith & Lee 1984). There are a number of factors that can influence body size; however, it is generally considered that energetics (metabolic rate) is the major factor influencing the evolution of body size particularly as it relates to other factors such as climate, food quality and fasting endurance (Speakman 1992, 1993). The mass specific metabolic rate (KJ/Kg/d) has been found to be proportional to $(\text{body mass})^{-0.25}$ (Poczopko 1979). This relationship shows that small mammals have higher energy requirements on a mass-specific basis than larger mammals. Amongst the Australian members of the Phalangeroidea, body mass ranges from 6g to 4900g, with the koala *Phascolarctos cinereus* (not in the Phalangeroidea) weighing up to nearly 15,000g (Strahan 1995). The variation in body mass is reflected in large differences in metabolism, diet and habitat requirements between the different species of possums. It is unknown, however, why the mahogany glider has a very large body size compared to its close relative the squirrel glider (Colgan & Flannery 1992; Van Dyck 1993), or what evolutionary events may have led to this large size.

1.5.3 Food Quality

Within Australia there are 18 genera and 27 species of Phalangeroidea and Phascolarctidae, each occupying their own dietary niche (Table 1.2). The dietary niche of a species has been suggested to limit body size amongst mammals with larger species being folivorous and small species being limited to energy rich food items such as nectar, sap and arthropods (Table 1.2; Smith & Lee 1984; Lee & Cockburn 1985; Goldingay 1989). There are a number of ecological and energetic constraints on exudate- and insect-eating marsupials, with interactions between food quality and food availability placing limitations on their body size and distribution.

Of the different food types, plant material such as leaves and stems are high in structural carbohydrates and low in material that is easily metabolised (Eisenberg 1981). Utilisation of plant fibre is more efficient for larger mammals because of their lower energy requirements relative to gut capacity (Van Soest 1982; Justice & Smith 1992; Freudenberger *et al.* 1989). Although plant material is generally a more ubiquitous food resource than other food types (such as exudates or flesh) for arboreal folivores, the consumption of eucalypt and other foliage as the major component of the diet of Australian mammals has several problems. These include the presence of toxic secondary compounds (xenobiotics) such as essential oils and tannins, and the generally low digestible energy and crude protein content of the leaves (Hume 1982; Hume *et al.* 1984). Among the arboreal marsupials, the greater glider *Petauroides volans* and the koala *P. cinereus* appear to be the only strict folivores. Arboreal folivores such as these have low field metabolic rates (FMR) and therefore low energy requirements and food intake (Hume *et al.* 1984). Hume *et al.* (1984) showed that arboreal folivores such as the koala and the greater glider have a FMR half that of exudivore omnivores such as the sugar glider *Petaurus breviceps* and Leadbeater's possum *Gymnobelideus leadbeateri*.

Table 1.2. Weights, diet and torpor of members of the Phascolarctidae and Australian members of the Phalangeroidea. * Uses hibernation.

Species	Weight (g)	Diet	Torpor	Ref.
Phascolarctos cinereus	4100-14900	Almost exclusively leaves.	N	1
Spilocuscus maculatus	1500-4900	Leaves, fruits, flowers, some meat.	N	1
Trichosurus caninus	2500-4500	Eucalypt leaves, fruits, buds, flowers, fungi, occasionally meat and bark.	N	1
Trichosurus vulpecula	1200-4500	Eucalypt leaves, fruits, buds, bark, pasture, occasionally meat	N	1
Phalanger intercastellanus	1500-2200	Leaves, fruits, flowers, little meat.	N	1
Wyulda squamicaudata	1350-2000	Leaves, flowers, fruit, insects.	N	1
Petropseudes dahli	1280-2000	Flowers, fruits, leaves.	N	1
Petauroides volans	900-1700	Almost exclusively leaves. Some buds and flowers.	N	1,2,
Pseudochirulus herbertensis	800-1530	Leaves, fruits, flowers.	N	1
Pseudochirulus cinereus	700-1450	Leaves, fruits.	N	1
Pseudochirops archeri	670-1350	Almost exclusively leaves.	N	1
Hemibelideus lemuroides	750-1140	Almost exclusively leaves.	N	1
Pseudocheirus occidentalis	900-1100	Eucalypt leaves, flowers, fruit.	N	1
Pseudocheirus peregrinus	700-1100	Eucalypt leaves, flowers and fruit.	N	1
Petaurus australis	450-700	Exudates, invertebrates, nectar	N	1,3,4
Dactylopsila trivirgata	246-528	Exudates? fruit, invertebrates, honey	N	1,7,8,9,10
Petaurus gracilis	320-460	Exudates, invertebrates, nectar	N	5, 6.
Petaurus norfolcensis	190-300	Exudates, invertebrates, nectar	N	1,11
Gymnobelideus leadbeateri	100-166	Exudates, invertebrates, nectar	Y	1,12
Petaurus breviceps	95-160	Exudates, invertebrates, nectar	Y	1,13,14, 15
Burramys parvus	30-82	Seeds, fruits, invertebrates.	Y*	1,16,17, 18, 19,20.
Cercartetus caudatus	25-40	Nectar, pollen, invertebrates?	Y*?	1,21.
Cercartetus nanus	15-43	Nectar, pollen, invertebrates.	Y*	1,22,23, 24,25.
Acrobates pygmaeus	10-14	Nectar, manna, sap, blossoms, insects.	Y*	1,26,27, 28,29
Cercartetus concinnus	8-20	Nectar, pollen, invertebrates?	Y*	1,30
Tarsipes rostratus	7-12	Nectar, pollen only.	Y	1,31,32, 33, 34.
Cercartetus lepidus	6-9	Nectar, pollen, invertebrates?	Y*	1,24,35.

References : 1 Strahan 1995; 2 Marples 1973; 3 Henry & Craig 1984; 4 Smith & Russell 1982; 5 Chapter 5; 6 Van Dyck 1993; 7 Rand 1937; 8 Fleay 1942; 9 Smith 1982a; 10 Handasyde & Martin 1996; 11 Menkhorst & Collier 1987; 12 Smith 1984a; 13 Fleming 1980; 14 Howard 1989; 15 Smith 1982b; 16 Geiser 1994; 17 Fleming 1985a; 18 Mansergh 1984; 19 Mansergh & Broome 1994; 20 Mansergh *et al.* 1990; 21 Atherton & Haffenden 1982; 22 Hickman & Hickman 1960; 23 Bartholomew & Hudson 1962; 24 Turner 1984a; 25 Arnould 1986; 26 Frey & Fleming 1984; 27 Fleming 1985b; 28 Turner 1984b; 29 Huang *et al.* 1987; 30 Geiser 1987; 31 Vose 1973; 32 Wooller *et al.* 1981; 33 Renfree *et al.* 1984; 34 Richardson *et al.* 1986; 35 Ward 1988.

Several authors have predicted that mammals below the mass range of 15 to 20kg should have severe problems meeting energy requirements from fibrous diets (Parra 1978; Demment & Van Soest 1985). The greater glider (0.9-1.7kg) appears to be on the lowest mass margin a species can be and be strictly folivorous. This diet doesn't appear to provide much energy as Foley *et al.* (1990) found that male greater gliders spent only 22% of their time outside the den moving, while females spent only 11% of their time outside the den active. In both cases, the majority of these movements were within, rather than between trees. Even the much larger koala does not gain much energy from eucalyptus leaves and spends some 20 hours per day inactive (Lee & Martin 1988).

Apart from the greater glider, all other members of the Pseudocheiridae and the Phalangeridae appear to supplement their diet with other vegetation more easily digested such as blossoms, flowers, fruit and even meat (Table 1.2). The common ringtail possum *Pseudocheirus peregrinus* and the green ringtail possum *Pseudochirops archeri* are the smallest arboreal marsupials (700-1100 and 670-1350g respectively) with a predominantly folivorous diet and appear to be at the limit in size to be folivorous. To maximise food digestion the common ringtail possum is caecotrophic (reingesting soft faeces of high nutritive value derived from caecal contents) in order to obtain access to protein, energy, and vitamins that would otherwise be lost because of poor absorption in the caecum and proximal colon (Hume *et al.* 1984; Chilcott 1984; Chilcott & Hume 1985). Cork and Foley (1991) noted that virtually no utilisation of tree foliage is seen in primate, marsupial or rodent species smaller than approximately 700g. Cork and Foley (1991) proposed this as the absolute evolutionary limit for foliage to be a major part of the diet, without supplementation of the diet with other more easily digestible matter such as flowers and fruit. Indeed the smallest pseudocheirid possum, the pygmy ringtail *Pseudochirulus mayeri*, which has a body weight of only 105-206g, appears to eat more digestible food types such as epiphytic lichens and mosses, and to eat only very small portions of leaves (Flannery 1995b). Similar observations have been made of the slightly larger (335-380g) lowland ringtail possum *Pseudochirulus canescens* (Flannery 1995b).

All members of the Petauridae, Burramyidae, Acrobatidae and Tarsipedidae (Table 1.2) weigh less than the common ringtail possum and all have a diet that is more easily digested. Their diet consists of insect and plant exudates such as nectar (and pollen), fruit, tree sap, manna and insect honeydew in order to obtain their energy requirements (Table 1.2). However as these substances are very low in protein, the dietary requirements of protein are supplied through the consumption of arthropods, pollen and occasionally small vertebrates.

Within the Petauridae, Burramyidae, Acrobatidae and Tarsipedidae protein is obtained from a variety of sources (Table 1.2). The striped possum *Dactylopsila trivirgata* eats large numbers of ants, small stingless bees *Trigona* spp., termites, wood boring larvae and the larvae of several other insects (Troughton 1941; Smith 1982a; Handasyde & Martin 1996), and Fleay (1942) found captive striped possums to catch and eat house mice *Mus musculus.* Mahogany gliders consume green ants and various other insects, spiders, pollen and acacia arils (Van Dyck 1993; Chapter 5); Leadbeater's possum consumes tree crickets, beetles, moths and spiders (Smith 1984a); the yellow-bellied glider *Petaurus australis* eats a variety of arboreal arthropods, primarily tree crickets, adult and larval beetles, caterpillars, spiders and moths (Henry & Craig 1984; Smith & Russell 1982); squirrel gliders *Petaurus norfolcensis* consume pollen and various insects such as caterpillars and beetles (Menkhorst & Collier 1987). Squirrel gliders have also been known to kill mice in captivity (Troughton 1941), and there is a record of one killing a magpie-lark *Grallina cyanoleuca* in the wild and eating its eggs (Winter 1966). Sugar gliders consume moths, scarabaeid beetles and pollen (Smith 1982b; Howard 1989); pygmy possums *Cercartetus* spp. eat insects and pollen (Hickman & Hickman 1960); feathertail gliders *Acrobates pygmaeus* eat pollen, while the honey possum *Tarsipes rostratus* consumes pollen and has been observed eating mealworms and small moths in captivity (Richardson *et al.* 1986; Turner 1984a and b; Vose 1973).

Although pollen is high in protein, this may be inaccessible because pollen grains are protected by a tough exine coat (Stanley & Linskins 1974). Despite apparent difficulties in the digestion of the nitrogenous cell contents, pollen is a large component of the diet of several marsupials including the honey possum, eastern pygmy possum, and feathertail glider (Richardson *et al.* 1986; Wooller *et al.* 1983; Turner 1984a; Turner 1984b). The use of pollen as a significant protein source also occurs in larger possums including sugar gliders (Goldingay et al. 1987; Howard 1989), squirrel gliders (Menkhorst & Collier 1987), mahogany gliders (Chapter 5) and yellow-bellied gliders (Goldingay 1990; Quin *et al.* 1996a).

Exudivorous marsupials are able to survive on a plant exudate (carbohydrate) and low protein diet, as Smith and Green (1987) found that the dietary requirement of nitrogen in the sugar glider was 87mg N $kg^{-0.75}$ per day^{-1}, the lowest yet recorded for a marsupial. Smith and Green (1987) also proposed that their results provided evidence for efficient recycling of amino acids by marsupials and suggested that free-living adult male sugar gliders may be able to satisfy their nitrogen requirements on a diet of plant exudates (saps, gums, nectar) alone. However they proposed that growing juveniles and reproducing females may need to consume invertebrates and pollen to meet the additional nitrogen demands of tissue production and lactation. This appears to be the case, as Smith (1982b) found sugar gliders to eat more insects during spring and summer, coinciding with late lactation, even though exudates were most abundant during these seasons.

1.5.4 Food Availability

Omnivores and particularly carnivores do not have uniformly distributed and abundant food resources (which folivores generally have) and find food to be patchily distributed throughout their habitat. Therefore insectivore/omnivores such as the Petauridae must spend more time travelling between patches in order to obtain food than herbivores. McNab (1963) demonstrated that herbivores have smaller home ranges than similar sized carnivores and that home range increases in proportion to body size. Home-range size increases with the mean body mass and metabolic rate of species, and decreases with an increase in the abundance of food supplies (McNab 1983). Likewise Harestad and Bunnell (1979) found significant relationships between home range and body size for herbivores, omnivores and carnivores. In light of Harestad and Bunnell's (1979) conclusions, Goldingay and Kavanagh (1993) compared a regression of mammals that feed predominantly on exudates with the Harestad and Bunnell (1979) exudivore mammal regression, but found no significant difference. The use of gliding was suggested by Goldingay and Kavanagh (1993) to facilitate the efficient movement between patches to find food. It has generally been considered that gliding evolved as an adaptation to the opening up of Australia's forests as the climate dried in the late Miocene and Pliocene (Archer & Clayton 1984; Flannery 1994). However, the use of gliding as a mechanism for obtaining adequate food, and the effect that gliding may have an optimal body size has not been examined.

Charles-Dominique (1974) proposed that the small size of insectivorous species is caused by the low biomass of their food and the difficulty of harvesting it rapidly enough to satisfy energy requirements from only this source. Smith (1982a) and Kay and Hylander (1978) noted that most arboreal insectivores weigh less than 220g, suggesting that this reflects the size and dispersion of arthropod prey. Smith and Russell (1982) suggested the larger size of petaurids such as the yellow-bellied glider means that they must rely more heavily on exudates than the smaller sugar glider, as their larger size does not increase their insect harvesting potential as they don't move much faster, and indeed probably move slower than smaller species such as sugar gliders. Therefore, as body size increases in insectivorous/exudivorous species, the proportion of arthropod biomass in the diet decreases, with exudates becoming more important (Smith & Russell 1982; Goldingay 1989). Kay and Hylander (1978) pointed out that the only truly insectivorous mammals that attain large size are those that feed upon social insects such as ants, bees and termites, because of the high feeding efficiency allowed by this resource. Mammals that feed on social insects include pangolins (Manidae), the aardvark *Orycteropus afer*, giant anteaters (Mymecophagidae), aardwolf *Proteles cristatus*, short-beaked echidna *Tachyglossus aculeatus*, and the numbat *Myrmecobius fasciatus*.

When food is always readily available there it has been suggested that there is no selection on body size, however when food has unpredictable availability, large sizes is selected for (Millar & Hickling 1990; Lindstedt & Boyce 1985). Speakman (1993) proposed that in any environment, even the most harsh and unpredictable, there will be times when food is readily available. Although larger animals have greater total food requirements, they will be favoured in unpredictable environments because of a greater ability to store fat (Millar & Hickling 1990). Therefore larger animals appear have a greater 'fasting endurance' which will make them better able to survive periods of food shortage. Alternatively, if food is always available, but in limited amounts, the smaller individuals could be advantaged because of the lower maintenance costs per animal and higher fecundity.

Hickling and Millar (1993) suggested that fasting endurance is not necessarily the most important component of an argument based on energetics. They proposed that small size could be advantageous for a species where periods of fasting are rarely life threatening, by allowing for rapid recouping of maintenance requirements when the fast ends. For some species fasting endurance could be relatively unimportant in determining body size. For example, differences in body size could reflect character displacement among sympatric species or predator-prey interactions (Hickling & Millar 1993).

1.5.5 Climate

Clinal variation in the body masses of animals with temperature, altitude and/or latitude is apparent in many species (Mayr 1956). Bergmann's rule states that populations from cooler climates tend to be larger than populations of the same species living in warmer climates (Mayr 1963). Large animals expend less energy for thermoregulation because of their smaller surface-to volume ratios, therefore it is more economical for large animals to live in colder climates (McNab 1971). An analysis of geographical variations in body size by Quin *et al.* (1996b) found a clinal change in body size for both the sugar glider and squirrel glider consistent with Bergmann's rule.

The high metabolic rate and high surface area to volume ratios (as a result of small body size) impose a constraint on small mammals, particularly those in cold climates (Lyman 1982). This can be compensated for in part by insulation. However, smaller animals cannot fully compensate heat loss through their proportionally large body surface by increasing their surface insulation (Lyman 1982). Lyman (1982) suggested that there is a critical point when insulation becomes so bulky that its survival value as a protection against the cold is outweighed by an inevitable increase in clumsiness.

The thermoregulatory disadvantages of small size have been significantly reduced in the smaller members of the Petauridae and in all the Burramyidae, Acrobatidae and Tarsipedidae by the use of group huddling, nest construction (in tree hollows) and daily or seasonal torpor (Smith & Lee 1984). Torpor and hibernation have been suggested by a number of authors to be mechanisms to conserve energy and increase fasting endurance during poor weather, lower temperatures and during periods of food shortage (Fleming 1980; Wooller *et al.* 1981; Renfree *et al.* 1984; Jones & Geiser 1992).

Wang (1989) described two types of torpor, one involving daily torpor with minimum body temperatures that are metabolically defended during torpor (11-28°C), and a second type of torpor involves deep and prolonged torpor (hibernation) with minimum body temperatures (1-6°C) and torpor bouts lasting between one and three weeks. Larger species that undergo torpor do so for only short periods while those of lower weights, except the honey possum, undergo periods of hibernation (Table 1.2). The honey possum may require torpor rather than hibernation because of the milder temperatures experienced in the areas where they are found in the south-west of Western Australia.

1.5.6 Limits on Distribution

Quin (1993) proposed four hypotheses to explain the regional distribution of large petaurids: (1) larger species are restricted to more productive environments because of their greater overall dietary needs; (2) larger species are restricted to aseasonal environments because of their greater fasting endurance; (3) contrary to hypothesis 2, that larger species are restricted to seasonal environments with reliable, heavy winter flowering of eucalypts and banksias; and (4) increased body size allows the use of resources potentially unavailable to smaller species.

When comparing squirrel gliders with sugar gliders Quin *et al.* (1996b) found the larger squirrel gliders were better able to live in aseasonal environments where food was less predictable than the smaller sugar glider. However Quin (1993) suggested that where the squirrel glider and sugar glider co-exist, the smaller sugar glider is favoured during periods of low food abundance because of its lower absolute energy needs. Quin (1993) also suggested that the higher absolute energy needs associated with larger size of the squirrel glider restricts the range of habitats it can occupy.

1.5.7 Conclusion

Exudivore / insectivore marsupials such as the mahogany glider are restricted to a readily digestible diet as a result of their small body size. Yet due to the intermediate body size of the mahogany glider means that may be more severely constrained ie. they are too small to use foliage (and have high nitrogen requirements), but are unable to harvest insects on a proportionally larger scale than small petaurids so they must rely more on exudates such as nectar and pollen. Their diet consists primarily of exudates such as nectar, sap, lerps and honeydew which are high in sugar and low in protein, so pollen and invertebrates are consumed to supply nitrogen. Little is known of the patchy distribution of the different dietary items of the mahogany glider (Chapter 5) and the movement patterns required to find adequate food and shelter (Chapter 6). The combination of diet, the availability of food, climate (which affects food availability and thermoregulation) ultimately influences the distribution of species such as the mahogany glider (Chapter 8). There is also little information available on the population ecology, density, reproduction (Chapter 3) or habitat requirements of the mahogany glider (Chapter 4) which will in turn assist in the management of this threatened species.

Chapter 2

Description of Study Site.

2.1 Location of the Study Site

The site chosen to study the mahogany glider contained a number of different habitat types and was located approximately 25km south of Cardwell in north Queensland on the eastern side of the Cardwell Range, at an elevation of approximately 10m (Fig. 2.1). It had no previous research conducted on it apart from spotlight surveying to determine the mahogany gliders presence. This area is approximately midway between the northern and southern known distribution limits. This area contained two strata or zones that were immediately adjacent to each other. The first was a 100ha area of continuous habitat located at Mullers Creek (18°26'13''S, 146°07'15''E). The second zone was located immediately south at Porters Creek (18°26'57''S, 146°07'35''E). This was an area of discontinuous or fragmented habitat that was composed of the buffer strips corridors along Porters Creek and its tributaries, an area of approximately 45ha, and was surrounded by a plantation of the introduced caribbean pine *Pinus caribaea*.

Selection of the study site was based on the presence of the mahogany glider (Van Dyck 1993) and its possession of the general attributes of high quality habitat (pers. obs.; Van Dyck pers. comm.). Access, particularly during the wet season, was very important as in many potential sites access was impossible for up to six months of the year. Because of the severe pressure from clearing, the site needed to be secure from further clearing. The presence of the fragmented habitat allowed a comparison with the continuous zone.

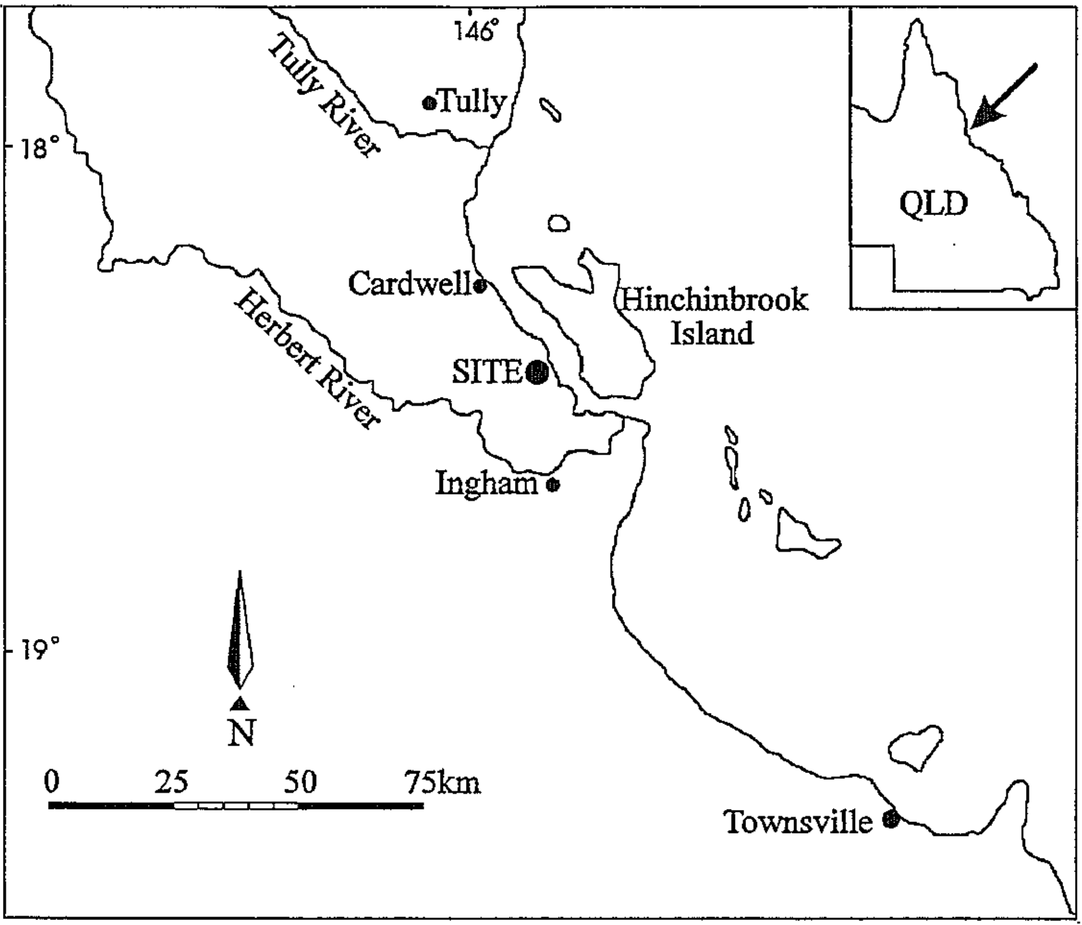


Figure 2.1. The location of the Mullers Creek and Porters Creek study areas.

2.2 Land Use

The study area was part of the Conn logging area which was managed by the Department of Primary Industry (DPI), Forestry Division. The area contained a large section of habitat that was uncleared, with a plantation of the introduced pine *Pinus caribaea* adjacent to it. There was also a grazing lease over the pine plantation and surrounding area.

2.3 Climate

The climate in the region has two distinct seasons. The wet season commences in November/December and ends in March/April, with the highest average monthly temperatures occurring in December (32.4° C) prior to the highest rainfall in January (462 mm). The dry season commences in April and continues until November during which time the lowest average monthly rainfall and lowest average maximum temperatures occur in July (29 mm and 24.8° C respectively) (Fig. 2.2). The mean yearly rainfall is 2166 mm. The average monthly temperatures and total monthly rainfall experienced during the present study period from November 1994 to December 1996 are given in Fig. 2.3.

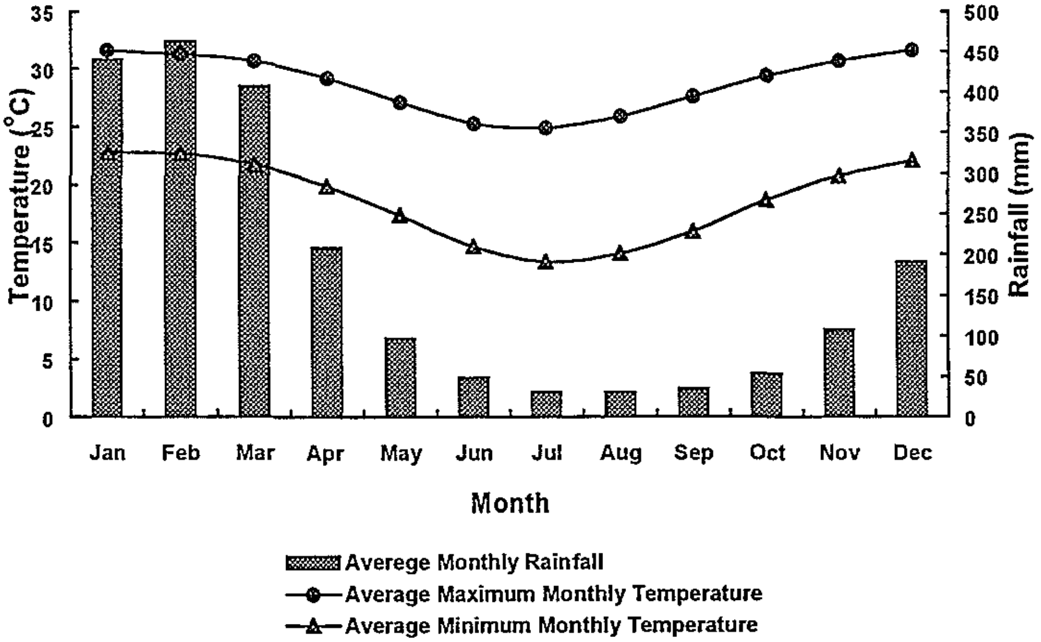


Figure 2.2. Mean monthly maximum and minimum temperatures and average monthly rainfall for Cardwell. Data from the Townsville Bureau of Meteorology.

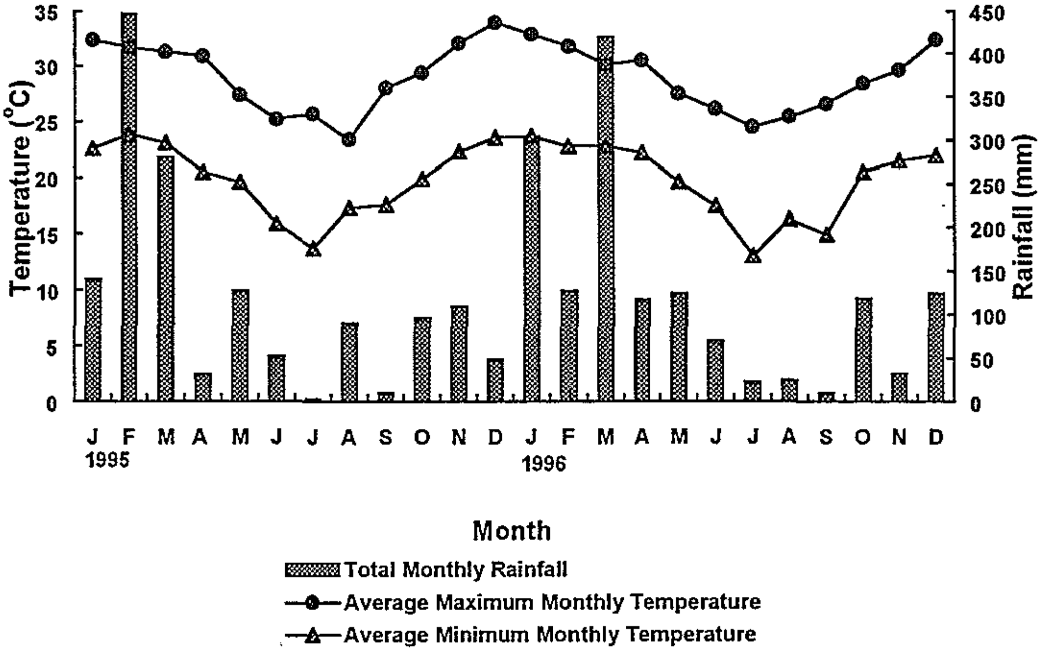


Figure 2.3. Mean monthly maximum and minimum temperatures and total monthly rainfall recorded in Cardwell throughout the present field study. Data from the Brisbane Bureau of Meteorology.

2.4 Fauna of the Area

Other mammals found in the area that could compete with the mahogany glider for food include the sugar glider *Petaurus breviceps*, feathertail glider *Acrobates pygmaeus*, spectacled flying-fox *Pteropus conspiculatus*, black flying-fox *Pteropus alecto* and the little red flying fox *Pteropus scapulatus*, all of which were commonly seen. A brushtail possum *Trichosurus vulpecula* was observed once during spotlighting but none were trapped. A list of mammals that were found in the Mullers Creek and Porters Creek areas during this study is given in Table 2.1.

Table 2.1 List of mammals observed at Mullers creek and Porters creek during nightly observations and caught during trapping sessions between 1994 and 1996.

Common Name	Genus and Species	Family
Peramelomorphia		
Northern brown bandicoot	*Isoodon macrourus*	Peramelidae
Diprotodontia		
Feathertail glider	*Acrobates pygmaeus*	Acrobatidae
Sugar glider	*Petaurus breviceps*	Petauridae
Mahogany glider	*Petaurus gracilis*	Petauridae
Agile wallaby	*Macropus agilis*	Macropodidae
Rodentia		
Grassland melomys	*Melomys burtoni*	Muridae
Fawn-footed melomys	*Melomys cervinipes*	Muridae
White-tailed rat	*Uromys caudimaculatus*	Muridae
Carnivora		
Dingo	*Canis lupus dingo*	Canidae
Chiroptera		
Black flying-fox	*Pteropus alecto*	Pteropodidae
Little red flying-fox	*Pteropus scapulatus*	Pteropodidae
Spectacled flying-fox	*Pteropus conspiculatus*	Pteropodidae
Artiodactyla		
Feral pig	*Sus scrofa*	Suidae
Domestic cattle	*Bos taurus & B. indicus*	Bovidae

2.5 Establishment of the Trapping Grid

A grid was marked out in the continuous forest at Mullers Creek site before the study began to trap mahogany gliders and sugar gliders to record weights and measurements, examine reproduction, density, ages, collect various samples, mark individuals, put radio collars on for home range and dietary observations. The grid also provided reference points for plant phenology examination, which had not been conducted previously in this region on the species examined during this study. The grid measured 1km by 1km, enclosing an area of 100ha. The grid was marked with twenty-two 1km long transect lines (11 running N/S and 11 running E/W), each separated by 100m (Fig. 2.4). The intersecting lines produced a total of 121 grid points. At each of the grid points reflectors were nailed to the nearest tree on all four sides, and a grid position was written on the reflectors according to the column and row. From the 22 grid lines, every second transect line was chosen for measurement of plant phenology, giving a total of ten transect lines (5 orientated N/S and 5 orientated E/W). At the 25 intersecting points created from these ten lines the phenology of 10 trees was assessed making up a total of 250 trees. A detailed description of plant phenology can be found in Chapter 5.

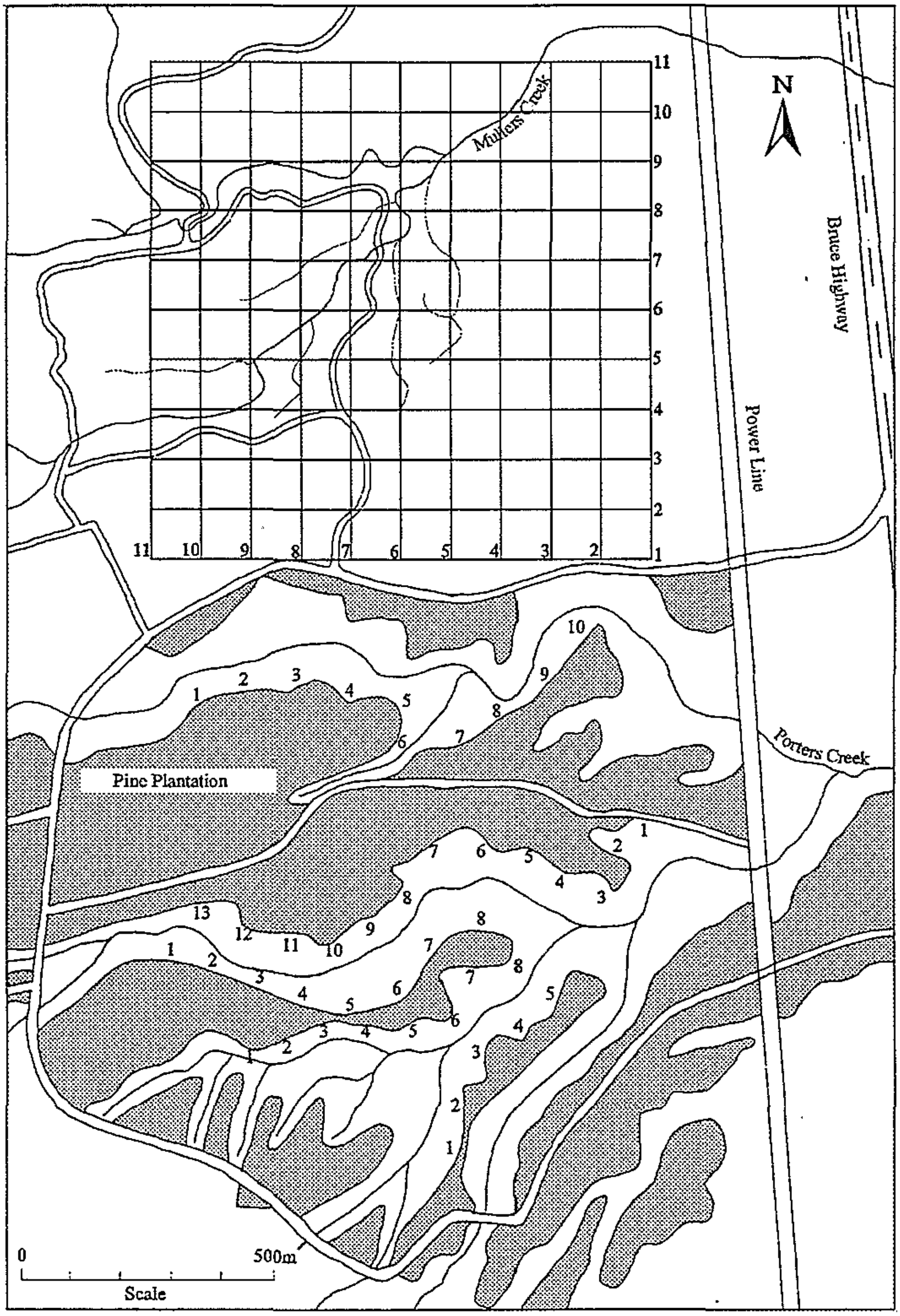


Figure 2.4. The study grid of continuous habitat at Mullers Creek and the trapping transects in fragmented habitat at Porters Creek. The numbers in the fragmented area represent trap locations.

In the area of fragmented habitat at the Porters Creek study area, establishing a grid was not feasible because of the linear nature of the buffer strips. This area was set up with trapping transects along the edges of the buffer strips with traps 100m apart, as shown in Fig. 2.4. No trees were marked or recorded for phenology within the Porters Creek study area.

2.6 Vegetation and Soil Types at the Site

The vegetation in the area of continuous forest at Mullers Creek comprised primarily open woodland and was dominated by the bloodwood *Corymbia clarksoniana*, poplar gums *Eucalyptus platyphylla*, swamp mahoganys *Lophostemon suaveolens* and several species of acacia (*Acacia mangium, Acacia crassicarpa, Acacia flavescens* and *Acacia leptocarpa*) with an understorey of spear grass *Heteropogon triticeus* (Cumming & Thomas (1992) vegetation type 14). In several areas there were poorly drained swamps that were dominated by the broad-leafed tea-tree *Melaleuca viridiflora* (with the occasional *Eucalyptus tereticornis*) with grass trees *Xanthorrhoea johnsonii* dominant in the understorey (Cumming & Thomas (1992) vegetation type 18). At the extreme north west side of the grid rainforest occurs (Cumming & Thomas (1992) vegetation type 4), with riparian rainforest being present along most of Mullers Creek (Cumming & Thomas (1992) vegetation type 5). This was dominated by numerous rainforest species as well as *E. tereticornis* and *Eucalyptus pellita*, with the occasional *Corymbia intermedia, Corymbia tessellaris* and *Melaleuca leucadendra*.

The vegetation within the fragmented site at Porters Creek consisted of riparian rainforest (Cumming & Thomas (1992) vegetation type 5) close to the creek with woodland species (Cumming & Thomas (1992) vegetation type 14) further away. There were also several areas of *M. viridiflora* with an understorey of *Xanthorrhoea johnsonii* (Cumming & Thomas (1992) vegetation type 18). Some species such as *Allocasuarina torulosa* were more common in some areas along the buffer strip than in the continuous area at Mullers Creek.

The major plant species found within Mullers Creek and Porters Creek are listed in Table 2.2 and are allocated to one or more of four vegetation types with the abundance of each species in each vegetation type also shown. The vegetation types used here are mapped on a finer scale (1: 10 000) than those used by authors such as Cumming and Thomas (1992) who used a scale of 1: 50 000 and Tracey (1982) who used a scale of 1: 100 000. Primarily because of the scale used the vegetation types described within the study area do not closely match the broad categories used by either Cumming and Thomas (1992) or Tracey (1982). However, the nearest vegetation types of these authors have been added after the definitions of each vegetation type (Fig. 2.5 & Table 2.2). Photographs representing the three most dominant vegetation types can be seen in Plates 2.1-2.3.

The soil was generally a grey-brown sandy loam soil (Van Dyck 1993). There were two distinct soil types in the area. On the eastern part of the Mullers Creek and Porters Creek sites towards the coast, the soils were quaternary alluvium lagoonal deposits. Further inland the soils are carboniferous to permian and are derived from hornblende-biotite adamellite, biotite granite, riebeckite granite, microgranite and alaskite (de Keyser *et al.* 1972).

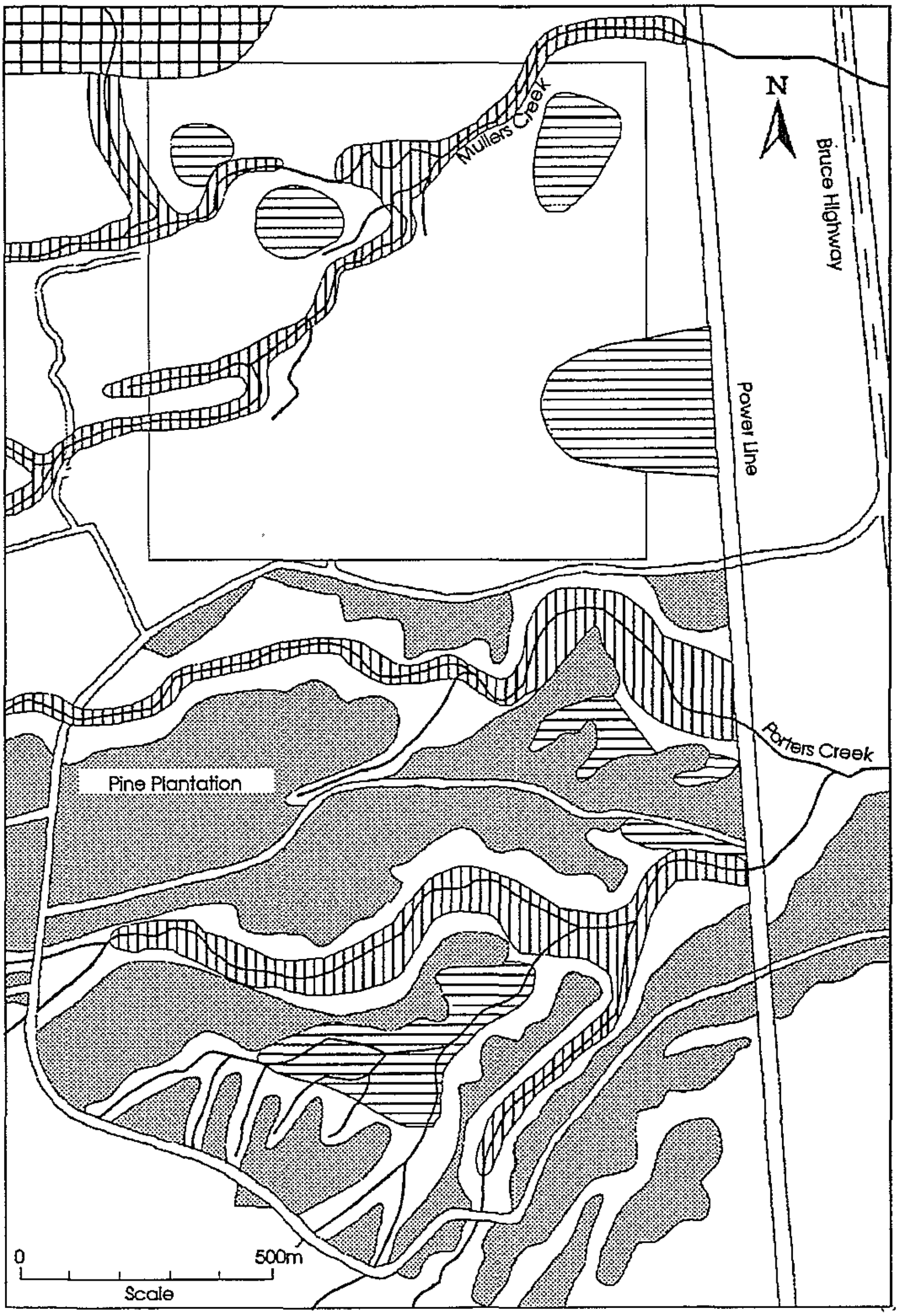


Figure 2.5. Map of vegetation types in the continuous forest at Mullers Creek and the fragmented at Porters Creek, based on observations at each grid point. Rainforest = cross hatching, Riparian Forest = vertical lines, Eucalypt forest = white, *Melaleuca* woodland = horizontal lines.

Table 2.2 List of plant taxa found at the study site.

Species Name	Common Name	Vegetation Type (abundance)
Upper Storey		
Acacia crassicarpa	Brown salwood	3 (C)
Acacia flavescens	Wattle	3 (C)
Aleurites moluccana	Candlenut	1 (O), 2 (O)
Allocasurina torulosa	Casurina	3 (O)
Alstonia scholaris	Milky pine	1 (O), 2 (R)
Archontophoenix alexandrae	Alexander palm	2 (R)
Carallia brachiata	Carallia	2 (O)
Castanospermum australe	Blackbean	1 (C)
Cryptocarya sp.	Laurel	1 (O), 2 (C)
Corymbia clarksoniana	Clarkson's bloodwood	2 (O), 3 (A)
Corymbia intermedia	Pink bloodwood	2 (O)
Corymbia tessellaris	Moreton bay ash	3 (R)
Corymbia torelliana	Cadargi	2 (O)
Deplanchea tetraphylla	Golden bouquet Tree	2 (R)
Eucalyptus pellita	Red mahogany	2 (C)
Eucalyptus platyphylla	Poplar gum	3 (A)
Eucalyptus tereticornis	Forest red gum / Blue gum	2 (C), 3 (O), 4 (O)
Ficus opposita	Sandpaper fig	2 (O), 3 (R)
Ficus racemosa	Cluster fig	2 (O)
Ficus variegata	Variegated fig	1 (O)
Livistona drudei	Palm Tree	2 (R)
Melaleuca dealbata	Cloudy tea-tree	3 (R)
Melaleuca leucadendra	Long-leafed paperbark	2 (O)
Melaleuca viridiflora	Broad-leafed tea-tree	3 (O), 4 (A)
Melicope elleryana	Euodia/Ulysses butterfly tree	2 (O)
Nauclea orientalis	Leichhardt tree	2 (C)
Neolitsea dealbata	Red kamala	1 (O), 2 (R)
Pongamia pinnata	Pongam	2 (C)
Schefflera actinophylla	Umbrella tree	2 (O)
Syzygium tierneyanum	River cherry	2 (C)
Terminalia sericocarpa	Damson tree	1 (O), 2 (O)
Xanthostemon chrysanthus	Golden Penda	2 (O)
Mid Storey		
Acacia leptocarpa	Wattle	3 (O)
Acacia mangium	Brown wattle	1 (O), 2 (C), 3(O)
Albizia procera	Forest siris / albizia	3 (O)
Canarium australianum	Mango bark / cudgerie	1 (R), 2 (O), 3 (O)
Casuarina littoralis	Coastal she oak	3 (O)
Chionanthus ramiflora	Native olive	1 (O), 2 (C)
Dillenia alata	Red beech	2 (C)
Diploglottis diphyllostegia	Northern Tamarind	2 (O)
Ficus opposita	Sandpaper fig	3 (O)
Ficus hispida	Hairy fig	2 (O)
Glochidion lobocarpum	Cheese tree	3 (C)
Glochidion ? sumatranum	Cheese tree	2 (C)
Grevillea parallela	Silky oak grevillea	3 (R)
Grevillea pteridifolia	Golden parrot grevillea	3 (R)
Guioa acutifolia	Guioa	1 (O), 2 (C)
Jagera pseudorhus	Foambark	1 (O), 2 (O)
Lantana camara	Lantana	2 (C), 3 (C)
Lophostemon suaveolens	Swamp mahogany	3 (C)
Macaranga involucrata	Macaranga	2 (O)

Table 2.2 - continued.

Species Name	Common Name	Vegetation Type (abundance)
Mid Storey (continued)		
Macaranga tanarius	Macaranga	2 (O)
Mallotus philippensis	Red kamala	2 (O)
Pandanus whitei	Pandanus / screw pine	2 (O), 3 (O), 4 (R)
Pittosporum ferrugineum	Pittosporum	2 (O)
Planchonia careya	Cocky apple	3 (C)
Polyscias australiana	Ivory Basswood	1 (O), 2 (O)
Polyscias elegans	Celerywood	2 (O)
Randia fitzalanii	Yellow mangosteen	1 (O), 2 (O)
Timonius timon	Tim tim tree	2 (O), 3 (C)
Tristaniopsis exiliflora	Water Gum	2 (O)
Lower Storey		
Acacia simsii	Wattle	3 (R)
Abelmoschus moschatus		3 (O)
Adiantium hispidulum		2 (O)
Allopteropsis cimicina	Cockatoo grass	3 (C)
Breynia cernua	Breynia	2 (O)
Breynia oblongifolia	Breynia	3 (O)
Brunoniella acaulis	Brunoniella	3 (C), 4 (O)
Calytocarpus vialis		3 (O)
Ceratanthus longicornis		3 (O)
Chamaecrista mimosoides		3 (O)
Cheilanthus tenuifolia		3 (C)
Chrysopogon acicularis		3 (C)
Commelina cyanea		3 (O)
Cycas media	Cycad	3 (O)
Dianella caerulea	Blue flax lilly	3 (R)
Flemingia parviflora		3 (C)
Flemingia lineata		3 (O)
Galactia tenuiflora		3 (O)
Geodorum neocaledonicum		3 (R)
Grewia retusifolia	Dogs balls	3 (O)
Heteropogon triticeus	Giant spear grass	3 (O)
Hybanthus stellarioides		3 (C)
Imperata cylindrica	Blady grass	3 (A), 4 (O)
Lindsaea media		2 (O)
Lomandria longifolia	Mat rush	3 (O), 4 (O)
Melastoma affine	Native lasiandra	4 (C)
Mimosa pudica	Sensitive weed	3 (O)
Mnesithea rottboellioides		3 (C)
Murdannia graminea	Pink swamp lily	3 (O)
Oplismenus aemulus		2 (O)
Phyllanthus virgatus	Phyllanthus	3 (O)
Psychotria loniceroides		2 (R)
Pteridium esculentum	Bracken fern	2 (O), 3 (C)
Pycnospora lutescens		3 (C)
Rostellularia adscendens	Rostellularia	3 (O)
Tacca leontopetaloides	Native arrowroot	3 (O)
Themeda triandra	Kangaroo grass	3 (A)
Thysanotus banksii		4 (O)
Tricoryne anceps		3 (C)
Uraria cylindracea		3 (C)
Xanthorrhoea johnsonii	Grass tree	3 (O), 4 (C)

Table 2.2 - continued.

Species Name	Common Name	Vegetation Type (abundance)
Parasites / Epiphytes/Vines		
Amyema sanguineum	Mistletoe	3 (O)
Cymbidium madidum	Cymbidium orchid	1 (O), 2 (O)
Drynaria rigidula	Basket fern	1 (C), 2 (C)
Dendrobium canaliculatum	Tea-tree orchid	4 (R)
Dendropthoe sp.	Mistletoe	3 (O)
Myrmecodia beccarii	Ant plant	4 (R)
Platycerium bifurcatum	Staghorn fern	1 (O), 2 (O)
Smilax australis	Barbed wire vine	1 (O), 2 (O)

Note: A = abundant, C = common, O = occasional, R = rare.

Note: The bloodwoods which were previously within the Genus *Eucalyptus* are now within the Genus *Corymbia* (Hill & Johnson, 1995).

Description of Vegetation Types.

1 = Rainforest, dominated by *Aleurites moluccana*, *Alstonia scholaris*, *Castanospermum australe*, *Neolitsea dealbata* and *Terminata sericocarpa*, with *Drynaria rigidula*, *Cymbidium madidum* and *Platycerium bifurcatum* being epiphytes. Found at the extreme back, left corner of study area. Cumming & Thomas (1992) vegetation type = 4. Tracey (1982) vegetation type = 1c.

2 = Riparian rainforest or gallery rainforest, dominated by *Eucalyptus pellita*, *Eucalyptus tereticornis*, *Pongamia pinnata*, *Syzygium tierneyanum*, *Chionanthus ramiflora*, *Dillenia alata* and *Guioa acutifolia*, with the occasional *Corymbia intermedia*, *Corymbia tessellaris* and *Melaleuca leucadendra*. Found along creeks. Cumming & Thomas (1992) vegetation type = 5. Tracey (1982) vegetation type = no equivalent vegetation type.

3 = Eucalypt forest, dominated by *Corymbia clarksoniana*, *Eucalyptus platyphylla*, *Acacia crassicarpa*, *Acacia flavescens* and *Lophostemon suaveolens*, with *Albizia procera* being found occasionally to common. *Imperata cylindrica* and *Themeda triandra* are the dominant grasses. Widepread, the most dominant vegetation type. Cumming & Thomas (1992) vegetation type = 14. Tracey (1982) vegetation type = 19.

4 = *Melaleuca* woodland, dominated almost exclusively by *Melaleuca viridiflora* (with the occasional *E. tereticornis*) with *Xanthorrhoea johnsonii* being very common underneath. Very limited patches of habitat. Cumming & Thomas (1992) vegetation type = 18. Tracey (1982) vegetation type = 20.

Plate 2.1. Riparian or gallery rainforest (vegetation type 2) along the margins of Muller Creek.

Plate 2.2. Open eucalypt forest (vegetation type 3) at the Mullers Creek study area.

Plate 2.3. *Melaleuca* woodland dominated by *Melaleuca viridiflora* and *Xanthorrhoea johnsonii* (vegetation type 4).

Chapter 3

Population Dynamics and Life History of the Mahogany Glider and Sugar Glider.

3.1 Introduction

Since its rediscovery in 1989, very little information has been collected on the life history of the mahogany glider *Petaurus gracilis*, with the available information being limited largely to a study by Van Dyck (1993). Throughout its limited distribution, the mahogany glider lives sympatrically with the sugar glider *Petaurus breviceps*, which in contrast to the mahogany glider, has a very wide distribution, occurring along the east coast of Australia from Tasmania to north Queensland and across northern Australia. The sugar glider is also found outside Australia, occurring in New Guinea and numerous surrounding islands (Flannery 1995a & Flannery 1995b). The ecology of the sugar glider has been studied extensively in southern Australia (Smith 1980; Goldingay 1984; Henry & Suckling 1984; Suckling 1984; Henry 1985; Quin 1995), while in northern Australia it has been studied little or not at all.

The aim of this chapter is to compare the demography, reproductive biology and longevity of the mahogany glider and the sugar glider in sympatry. Differences in the population densities of the mahogany glider and the sugar glider in both the continuous habitat at Mullers Creek and the fragmented habitat containing linear vegetation at Porters Creek are also examined.

3.2 Methods

3.2.1 Trapping Censuses

Demographic and life history information was obtained from live-trapping (capture-mark-recapture) in both the continuous habitat at Mullers Creek and the adjacent fragmented habitat at Porters Creek. Wire cage traps, 20 x 20 x 56 cm in size (Mascot Wire Works, Enfield, NSW) were used to catch gliders. These traps were attached to wooden brackets which were approximately 4m above the ground (on trees with a diameter at breast height greater than 20cm) using elastic straps and with the entrance facing the trunk of the tree. Brackets for the traps were made using two pieces of timber 920mm long and 75 or 100mm wide, and screwed together in a 'T" shape. These were supported with a cross bracket of hardwood that was set at 45° to the other two pieces. These brackets were placed 100m apart in the grid established in the continuous habitat at Mullers Creek, or as transects in the fragmented habitat at

Porters Creek. In the fragmented habitat at Porters Creek trap points began 200-300m into each end of the corridors to target animals that were resident in the corridors and not 'visitors'. The area sampled by the traps in the buffer strips was approximately 45 hectares.

A trial trapping session was conducted in the continuous habitat at Mullers Creek from December 1994 to February 1995, during which the entire grid was trapped. Because of the limited number of traps available (80), and the time required to move and service traps, only the central area at Mullers Creek was trapped after this initial trapping period (an area enclosing 63ha). Therefore the front row, transect 11 and the back two rows (10 and 11) were not retrapped (See Fig. 2.4). The remaining trapping area was broken into two during each trapping session, with transects 1-5 (40 traps) then 6 to 10 (40 traps) being trapped. These grids were trapped every eight weeks from February 1995 until December 1996. The fragmented habitat at Porters Creek was trapped from December 1995, every eight weeks until December 1996.

During each trapping session, traps were set over 3-4 nights (except for October 1996 when only two nights of trapping were undertaken in transects 1-5 because of torrential rain) and baited with a mixture of creamed honey and rolled oats, wrapped in grease proof paper. A honey/water solution (approximately 1:8) was sprayed as far as possible up the tree above the trap bracket, on the bracket and bait to attract gliders to the tree and the trap. The honey/water solution was resprayed each day to keep the bait and trail fresh.

3.2.2 Handling, Marking and Measurements

Traps were inspected from dawn until all traps were cleared, which was generally by mid-day. Captured animals were restrained in cloth bags, sexed, measured, and weighed (± 1g) with Salter scales. Females with pouch young had their weight taken by subtracting the estimated weight of pouch young from the recorded weights of females with pouch young. Pouch young weights were estimated using head measurements and modified regression estimates of Smith (1979) to determine their weight. The following measurements were taken with Vernier callipers for all new animals caught: (1) snout to vent length; (2) vent to tail tip length (from the cloaca to the last vertebra of the tail tip); (3) snout to tail tip length; (4) head length (from occiput to snout tip); (5) head width (maximum width across the zygomatic arches); (6) length of right tibia; (7) length of right pes not including the claw; (8) length of testis; (9) width of scrotum; and (10) length of lower incisors. All three body-length measurements (snout-vent, vent-tailtip and total length) were taken to allow a more accurate measurement of total body length. Individuals that were recaptured during subsequent trapping sessions were weighed and the head length, head width and tibia length recorded only.

A condition index was determined for both the mahogany glider and sugar glider following that derived by Krebs and Singleton (1993). The estimation of a condition index involved three steps: (1) estimating the regression between skeletal size (tibia length, head length, head width and total body length were used) and body weight; (2) using the most significant regression to predict body weight from the appropriate measure of skeletal size for each individual; and (3) estimating the condition of each individual by taking the ratio of the observed to the predicted body weight.

Faecal samples were collected whenever possible and stored in 70% alcohol for later dietary analysis. Gliders were tagged in each ear with a hamster eartag (Sieper & Co., NSW) to which Scotchlite reflective tape (3M Australia Pty Ltd, Victoria) was attached. Reflective tape of various colour combinations was used so that individuals could be identified at night in a spotlight beam. Although ear tags generally enabled identification of each individual, occasionally both ear tags were lost so implanted identification chips were used to verify individuals. A passive integrated transponder (PIT tag) (Life chip, Animal Electronics ID Systems) was placed under the skin between the scapulars using a single use syringe. The implant chips were read with a Pocket Reader (Destron - Fearing, Spain).

When required, a radio transmitter was placed around the neck of individuals. Two types of collars were used, including single stage transmitters (Sirtrack, New Zealand) and 2-stage transmitters (Holohil, Canada and Sirtrack, New Zealand). Both types of transmitters weighed approximately 10-12g, had whip antennas approximately 15cm long, and had a PVC or leather collar. Because of problems with gliders chewing the aerials, cayenne pepper was applied to discourage chewing.

3.2.3 Age Estimation

Age of individual gliders was established using a combination of parameters modified from Alexander (1981), Suckling (1984) and Quin (1995) (Table 3.1). Parameters included a combination of tooth wear, patagium colour, weight and reproductive condition. Three methods were used to determine tooth wear: (1) the categories of tooth wear of Alexander (1981), based on the degree of flattening of the upper incisors when viewed from the anterior; (2) based on those used by Suckling (1984) which use the degree of wear and proportion of dentine exposed on the upper incisors when viewing the ventral surface; and (3) the colour and wear of the lower incisors and the presence of lateral cracks. Young animals have white lower incisors with no lateral cracks, whereas older animals have teeth that are more discoloured and develop increasing number of lateral cracks with age. In old animals part of the lower incisors can be completely chipped off. The patagium colour was used following Quin (1995), Suckling (1984) and personal observations of captive squirrel gliders *Petaurus norfolcensis*. As in other studies (eg. Quin 1995; Suckling 1984) body weight was a useful indicator of age until approximately 18 months for both species. The weights used to determine age (Table 3.1) for the mahogany glider were derived by multiplying the weights used by Quin (1995) for squirrel gliders by the ratio difference of adult squirrel and mahogany glider weights. Sugar glider weights to determine age were calculated by multiplying the weights used by Suckling (1984) for sugar gliders in southern Australia by the ratio difference of adult southern sugar gliders and sugar gliders in the present study to determine approximate weights.

If pouch young of either the mahogany glider or sugar glider were present, the head length of each pouch young was recorded and an approximate month of birth was estimated using regression estimates from Smith (1979). This was done by finding the ratio difference of head length between the adult mahogany glider in this study and adult squirrel gliders, and between the adult sugar gliders in the present study and the sugar glider in Smith (1979). This was done because sugar gliders in this area are smaller than those studied by Smith (1979) in southern Australia. The head lengths of mahogany gliders and sugar gliders in the present study were then adjusted by this ratio and an approximate age (and month of birth) was determined from the squirrel glider or sugar glider regressions respectively.

The reproductive status of male and female animals could also be used to gain an indication of age. Females less than one year of age usually had not previously bred and had very small teats (<1mm) and a shallow clean white pouch. Females greater than one year of age had teats greater than 1mm long (indicating previous breeding) or had pouch young or were lactating, and pouches which were larger and generally discoloured (Quin 1995). The frontal gland of males was generally classed as either: (1) not developed (indicating a juvenile); (2) partially developed; or (3) well developed (adult animal normally 2-3 years of age). Using a combination of these parameters each individual was assigned to one of four age-classes: <1 year or juveniles (not including pouch young); 1-2 years; 2-3 years; and >3 years.

Table 3.1. Age-estimation parameters of mahogany gliders and sugar gliders at Mullers Creek and Porters Creek (modified from Suckling 1984 and Quin, 1995).

Parameter	**Estimated age (years)**			
	<1	**1-2**	**2-3**	**>3**
Weight of mahogany gliders (g)				
Males	< 300	> 300	> 370	> 370
Females	< 280	> 280	> 330	> 330
Weight of sugar gliders (g)				
Males	< 60	> 60	> 80	> 80
Females	< 50	> 50	> 70	> 70
Mahogany Gliders and Sugar Gliders				
Wear of upper incisors	None to slight	None to slight	Slight to moderately heavy	Moderately heavy to very heavy
Wear of lower incisors	White, no cracks	Slight discolouration, lateral cracks slight	orange discolouration, lateral cracks obvious. Occasionally chipped teeth in old animals.	
Patagium colour	White	Cream-yellow	Yellow	Yellow-orange
Frontal gland (males)	Not developed	Partially to well developed.		
Pouch	Small and shallow with fine white hairs; teats 1mm long	Larger and deeper than in females that had not bred. Yellow/orange hairs with black scale. Teats >1mm.		

3.2.4 Reproductive Condition

Female gliders were classed into one of 6 reproductive categories following Quin (1995): (1) juvenile nulliparous females (small tight pouch, white hairs and teats < 1mm); (2) adult female non-breeding (pouch larger and deeper than nulliparous females, but reproductive activity not apparent, hairs yellow/brown, often with black scale; teats >1mm); (3) pregnant females (pouch lining thickening; pouch wall glandular; muscular and richly vascularised; may or may not have bred previously); (4) females with pouch young; (5) lactating females (females with loose pouch and one or two large lactating teats; or (6) females recently bred (pouch large with elongated teats but non-lactating, or expressing only a clear fluid).

3.2.5 Estimates of Population Size and Density

Two methods were used to determine the population size of mahogany gliders and sugar gliders at both the continuous habitat at Mullers Creek and the fragmented habitat at Porters Creek. In the first method Petersen estimates were used, in which the number of animals present is determined by multiplying the number of animals marked and released in the first sample, by the total caught in the second sample, and dividing this by the number of animals that were marked when caught in the second sample. This method assumes the population is closed, with no recruitment of new animals or loss of animals through dispersal (Krebs 1994). As ratios can lead to an overestimation, the bias can be corrected (Baily 1951, 1952) by:

$$Y = (M(n+1))/(m+1)$$

where "M" is the number of animals marked and released in the first sample, "n" is the number of animals captured in the second sample of which "m" have previously been marked, and "Y" is the unknown size of the population.

The second method used the minimum number of individuals known to be alive (MNKTBA). An individual was determined to be alive during each trap session if it had been caught before and after that trap session. Although this method can lead to an underestimate of the true population size, it has the advantage of using numbers of individuals physically observed rather than being a calculated estimation, and it includes trap-shy animals which are captured only occasionally but more than once.

Density estimates were derived by dividing the modified Petersen estimates of population size and the MNKTBA by the area of the trapping grid, plus a boundary strip equal to half the width of the mean home-range area assuming the home-ranges are roughly circular (Chapter 6). The boundary strip was estimated to be 200m for the mahogany glider and 100m for the sugar glider (Chapter 6; Quin 1992). Transients (individuals caught only once) were included in density estimates. In the fragmented habitat, the entire width of the riparian habitat was included in the density estimate with a 200m addition at each end in the area to determine glider density. The pine plantation area was not included in the area as the gliders were never observed to utilise the pine trees during the study.

Quin (1995) suggested two problems in assuming that individuals captured only once were transients. First, many gliders caught only once are likely to be on the edge of the trapping grid. This is because animals living on the edge of the grid have a low number of traps within their home-ranges and are therefore less likely to be caught. Second, individuals that are in the <1 year and 1-2 year age classes may well have been born on the grid and then trapped during dispersal. Dispersing individuals can also be caught on the edge of the trapping grid.

3.3 Results

3.3.1 Glider Trap Success and Capture Type

Between February 1995 and December 1996, 69 mahogany gliders (42 males, 27 females) and 63 sugar gliders (38 males, 25 females) were captured and marked in the continuous area of habitat at Mullers Creek. These accounted for a total of 412 and 313 captures, respectively. The mahogany glider proved to be readily caught in the continuous area of habitat with an average capture success of 11.93% (range 7.50 - 15.00%) over 3400 trap nights (Table 3.2). Trap success was low in August and October in 1996 because of poor weather. The trap success for the sugar glider over the same number of trap nights averaged 9.65% (range 0.88-16.24%; Table 3.2).

Sugar gliders were rarely caught in the initial trapping sessions in the continuous forest at Mullers Creek and then built up in number over subsequent trapping trips. There was no significant difference in trap success between the mahogany glider and the sugar glider in the continuous area at Mullers Creek when treating individual trap sites as sample units ($t_{22} = 1.33$; $P > 0.2$).

Table 3.2. Trap success for the mahogany glider and sugar glider in the continuous habitat at Mullers Creek.

Year and Month	No. of trap nights	No. of mahogany glider captures	Trap success (%)	No. of sugar glider captures	Trap success (%)
1995					
February	340	48	14.12	3	0.88
April	320	35	10.94	8	2.50
June	320	42	13.13	17	5.31
August	320	36	11.25	21	6.56
October	280	39	13.93	18	6.43
December	300	33	11.00	25	8.33
Total	1880	233	12.39	92	4.89
1996					
February	240	31	12.92	34	14.17
April	240	26	10.83	38	15.83
June	280	42	15.00	39	13.93
August	240	21	8.75	33	13.75
October	200	15	7.50	25	12.50
December	320	44	13.75	52	16.25
Total	1520	179	11.46	221	14.41
Overall total	3400	412	11.93	313	9.65

Note the February 1995 figure includes the single transect trapped in December 1994.

In the fragmented area at Porters Creek, 23 mahogany gliders (13 males, 10 females) and 51 sugar gliders (29 males, 22 females) were trapped between December 1995 and December 1996. The trap success for the mahogany glider in the fragmented area was significantly less than in the continuous area ($t_{17} = 6.2$; $P < 0.01$; Table 3.3). In contrast, the trap success for the sugar glider in fragmented habitat was significantly greater than in the continuous area ($t_{16} = 2.59$; $P < 0.05$). The trap success of the mahogany glider in the fragmented area was significantly less than the sugar glider in the fragmented area ($t_{11} = 4.65$; $P < 0.01$).

Table 3.3. Trap success for the mahogany glider and sugar glider in the fragmented habitat at Porters Creek.

Year and Month	No. of trap nights	No. of mahogany glider captures	Trap success (%)	No. of sugar glider captures	Trap success (%)
1995					
December	120	4	3.33	4	3.33
1996					
February	173	17	9.83	17	10.18
April	132	6	4.55	21	15.91
June	176	10	5.68	16	9.09
August	176	10	5.68	41	23.30
October	176	7	4.00	39	22.16
December	176	7	4.00	38	21.59
Total	1009	57	5.65	172	17.05
Overall total	1129	61	5.40	176	15.59

Although sugar gliders and mahogany gliders were the most common species trapped, fawn-footed melomys *Melomys cervinipes* were often caught along or near the creek lines, with white-tailed rats *Uromys caudimaculatus* also caught several times along the creeks. Several juvenile lace monitors *Varanus varius* were caught throughout the trapping area.

All gliders caught were placed into one of three categories to provide an indication of recruitment, transients and edge animals: "new" (never caught before), "last" (caught during the last trap session), and "previous" (not caught in the last trap session but had been caught previously; Figs. 3.1-3.2). "New" animals include juveniles and adult animals that may be caught only once and moved on, and animals that remained within the population and subsequently classed as "last" or "previous". The "last" category are the core individuals that have all or most of their home-range with the trapping area. In both the continuous habitat and fragmented habitat, new individuals were caught during almost every trapping trip. These individuals comprised both adult animals and juveniles born several months before. Most individuals that were "previous" were caught on the edge of the grid and therefore are likely to have only a small part of their home-range within the trapping grid, and are therefore only caught occasionally.

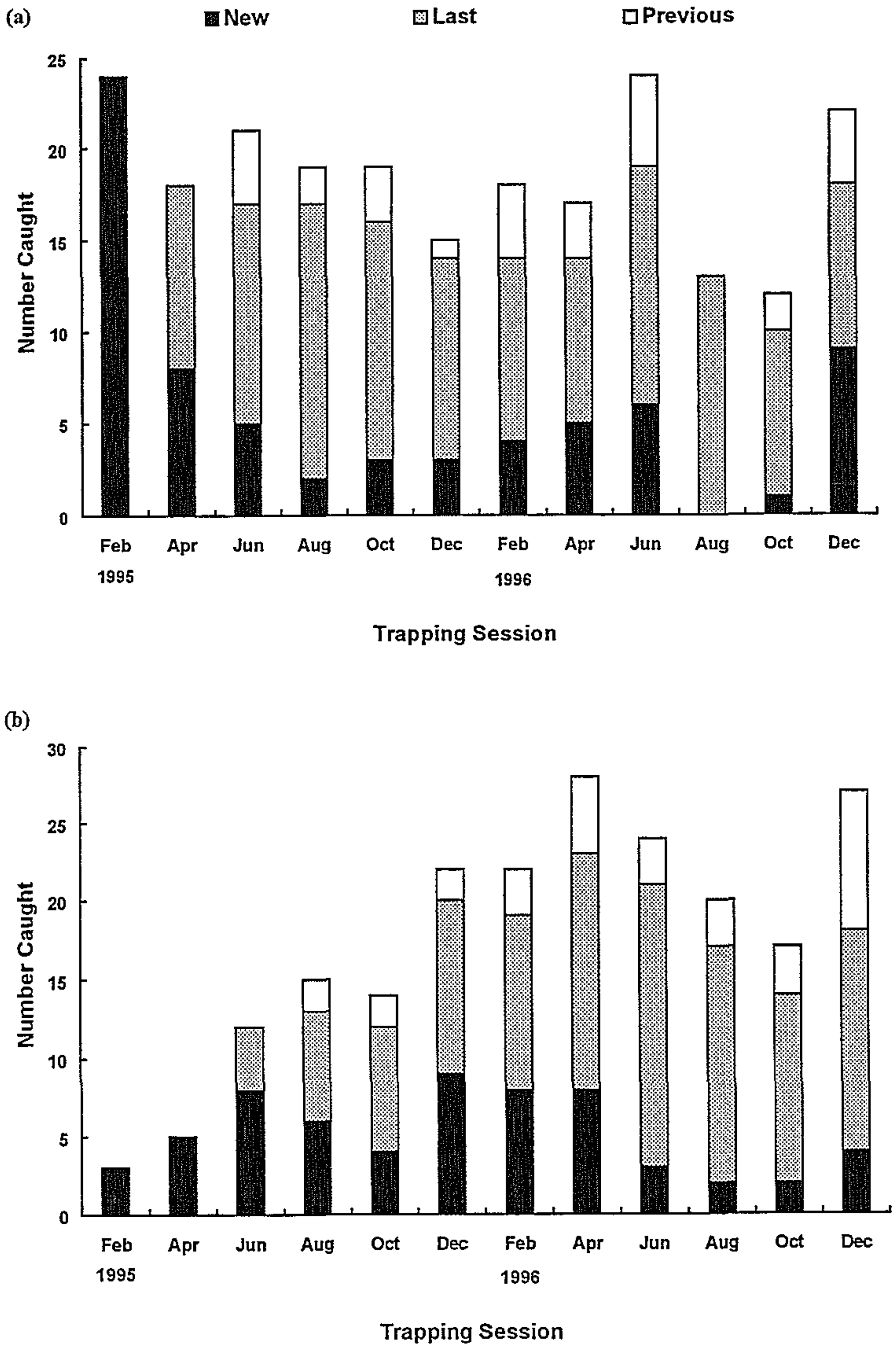
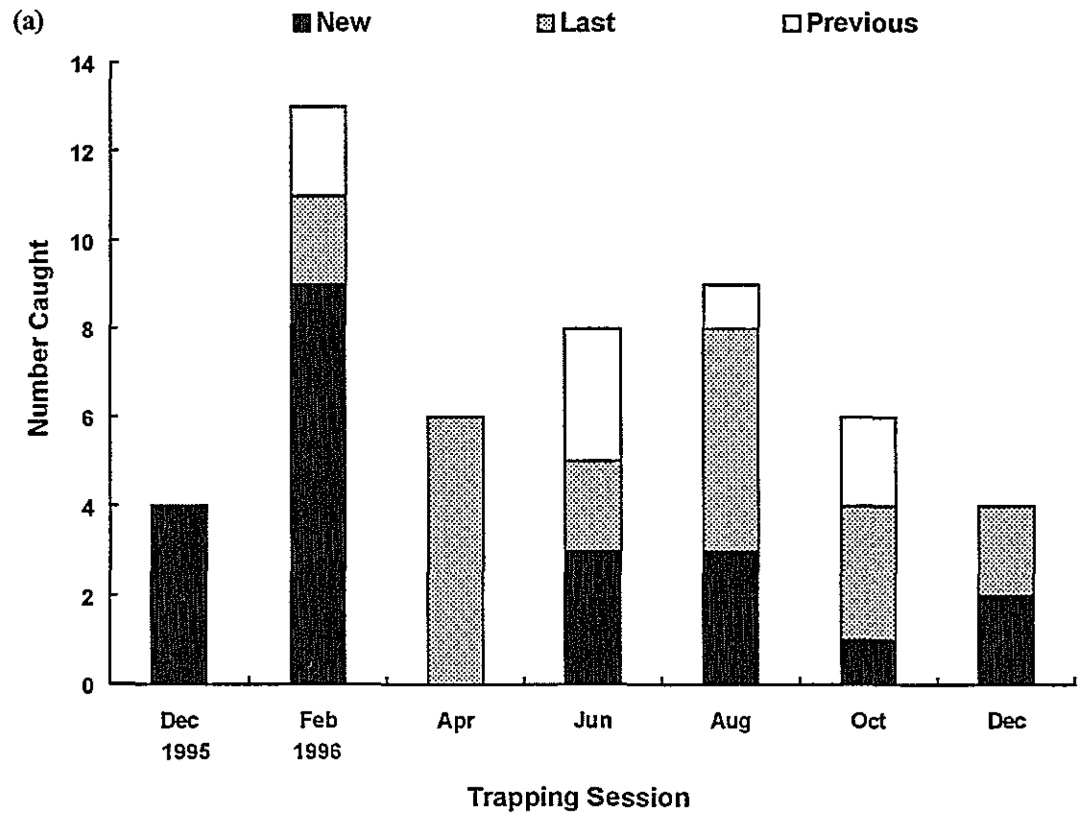


Figure 3.1. Capture type for (a) mahogany gliders and (b) sugar gliders in the continuous habitat at Mullers Creek between February 1995 and December 1996.



Note - the 2 'previous' in February were animals previously caught in the Mullers Creek area.

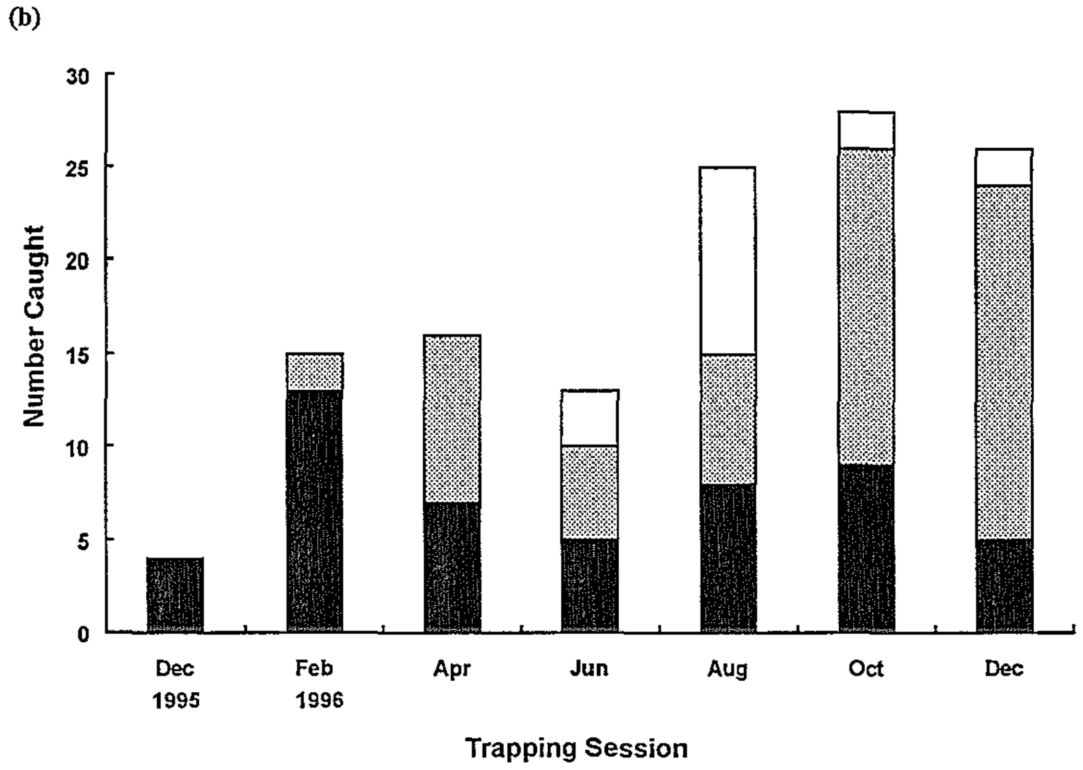


Figure 3.2. Capture type for (a) mahogany gliders and (b) sugar gliders in the fragmented habitat at Porters Creek from December 1995 to December 1996.

3.3.2 Population Size, Density and Trappability

Within the trapping area of continuous habitat at Mullers Creek, the average population size for the mahogany glider was 22.36 and 23.47 using the MNKTBA and the modified Petersen estimate respectively, resulting in an average density of 0.23 and 0.24 ha^{-1} (Fig. 3.3a). The sugar glider population averaged 23.09 using the MNKTBA and 23.79 using the modified Petersen estimates. The number of sugar gliders caught was initially very small and steadily increased from February 1995 until April 1996. The MNKTBA increased from 6 to 33 where it plateaus. The density of sugar gliders was 0.23 and 0.30 ha^{-1} for the MNKTBA and modified Petersen estimates respectively. The lower density of sugar gliders using the MNKTBA is because of the low numbers of sugar gliders caught initially.

In the fragmented habitat at Porters Creek a much lower density of mahogany gliders compared to the continuous area at Mullers Creek was observed with densities of 0.15 and 0.16 ha^{-1} using the MNKTBA and modified Petersen estimates respectively (Fig. 3.3b). In contrast to the mahogany glider, the density of sugar gliders in the fragmented habitat at Porters Creek was much higher than the sugar glider population in the continuous habitat at Mullers Creek, with a density of 0.43 and 0.48 ha^{-1} for the MNKTBA and modified Petersen estimates respectively. The higher density of sugar gliders at Porters Creek appears to be because of a larger proportion of closed acacia habitat compared to the continuous area at Mullers Creek (See Chapter 4). The similar results obtained using both the MNKTBA and the modified Petersen estimates suggest that the modified Petersen estimate was a good indicator of the population size.

Glider trappability was determined by dividing the number of gliders caught during a trapping census by the MNKTBA at that time and multiplying by 100. The trappability of mahogany gliders at Mullers Creek was high for both males and females, averaging 80.9% (range 71-100%) and 76.2% (range 56-100%) respectively (Fig. 3.4a). The trappability of male and female sugar gliders was also high with a trappability of males being 84.2% (range 60-100%) and females 70.2% (range 50-83%)(Fig. 3.4b). In the fragmented area at Porters Creek, the trappability of both male and female mahogany gliders and sugar gliders was similar to that observed at

Mullers Creek (Fig. 3.5). The low trappability recorded for both the mahogany glider and sugar glider at both sites during several trapping sessions, is largely a result of the smaller sample sizes collected (See Table 3.3 for values).

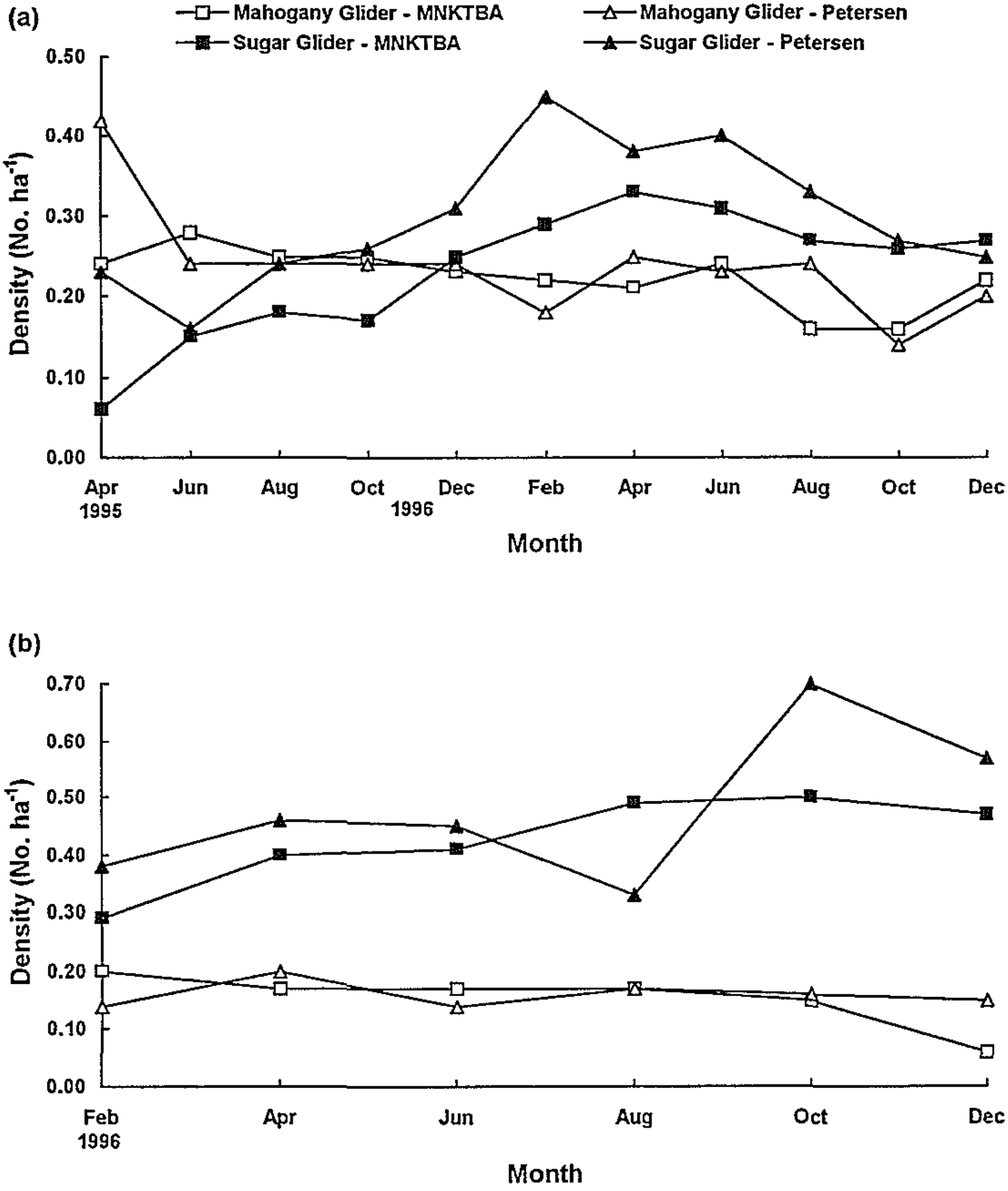


Figure 3.3. Density of mahogany gliders and sugar gliders in (a) the continuous area of habitat at Mullers Creek and (b) the fragmented area of habitat at Porters Creek using Petersen estimates of population size and MNKTBA.

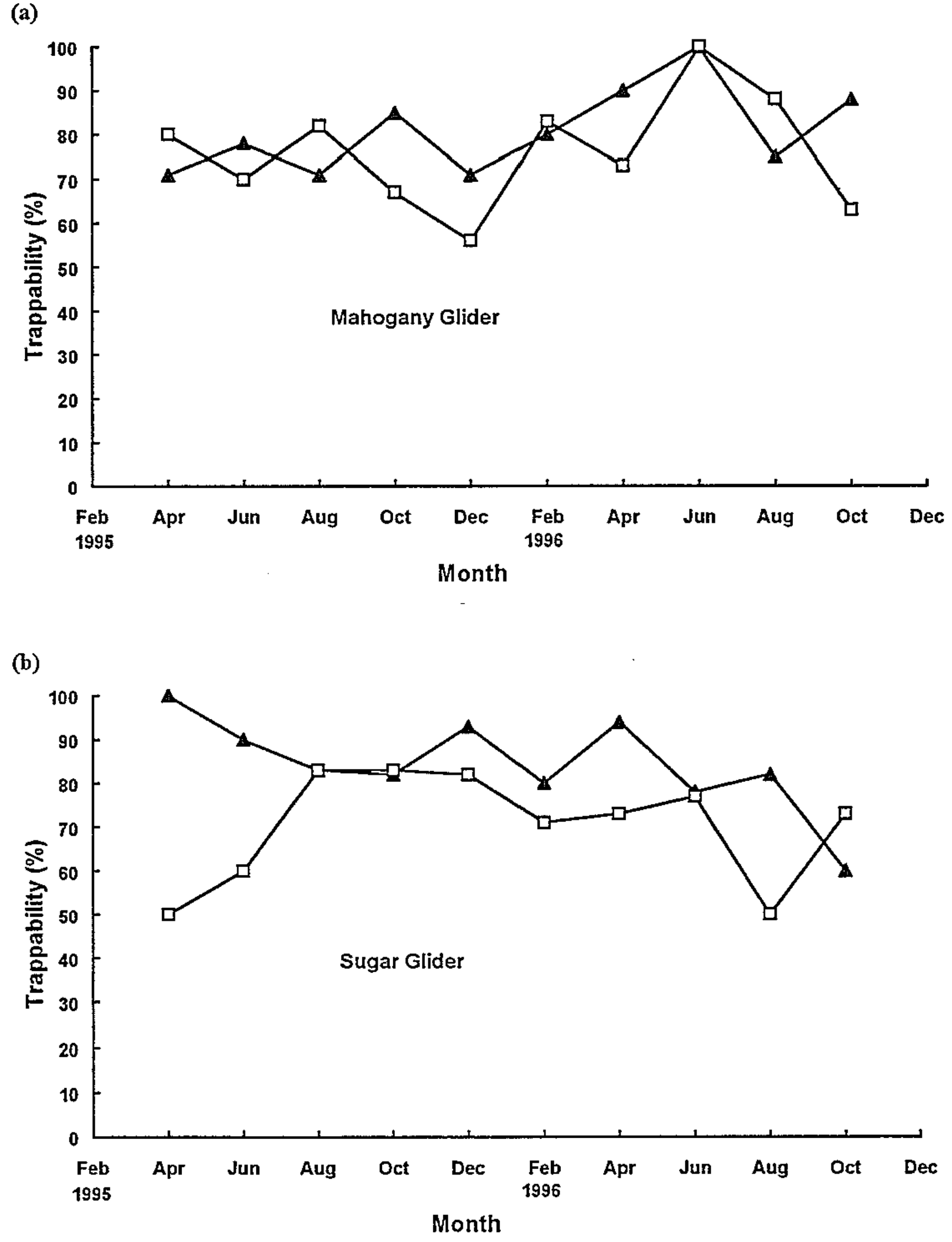


Figure 3.4. The percentage trappability of (a) mahogany gliders and (b) sugar gliders during censuses in the continuous habitat at Mullers Creek from February 1995 to December 1996 (▲ males and ☐ females). Trappability is equal to the number of individuals trapped during a census divided by the MNKTBA for that census, and multiplied by 100.

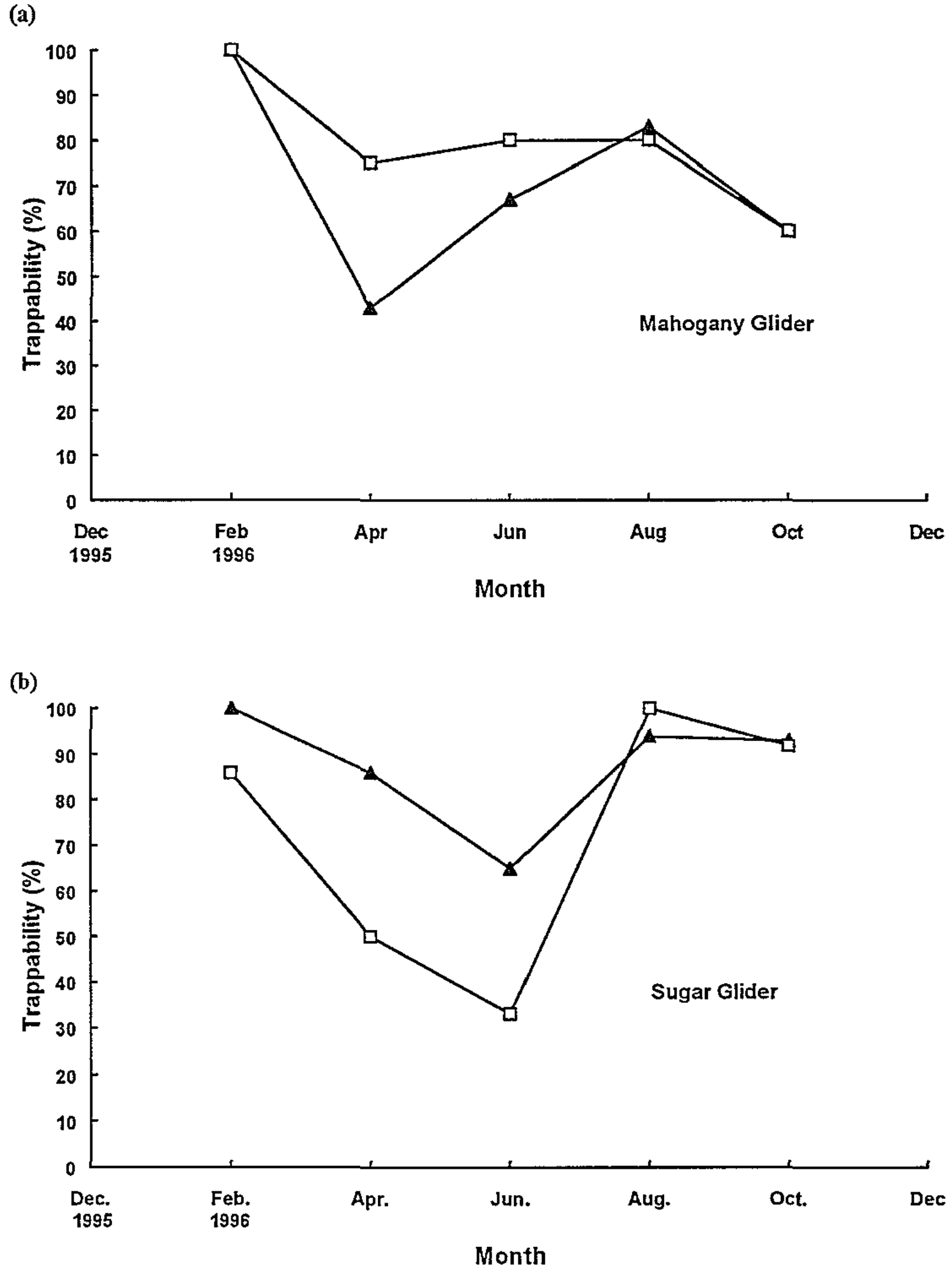


Figure 3.5. The percentage trappability of (a) mahogany gliders and (b) sugar gliders during censuses in the fragmented habitat at Porters Creek from December 1995 to December 1996 (▲ males and □ females). Trappability is equal to the number of individuals trapped during a census divided by the MNKTBA for that census, and multiplied by 100.

3.3.3 Sex Ratio and Population Structure

In both 1995 and 1996, the overall sex ratio of mahogany gliders was male biased; however the only age group which was significantly different was adults in 1996 ($\chi^2 = 6.61$, d.f. = 1, $P < 0.05$; Table 3.4). In comparison, pouch young, juvenile and adult sugar gliders had no significant difference in the numbers of males and females.

Table 3.4. Sex ratio (M:F) of all pouch young, juveniles and adult mahogany and sugar gliders during 1995 and 1996. Actual numbers of gliders are in brackets under the ratio.

Month	Mahogany gliders			Sugar gliders		
	Pouch Young	Juvenile (<1)	Adult	Pouch Young	Juvenile (<1)	Adult
1995	1: 1.20 (10:12)	1:1 (3:3)	1.26:1 (24:19)	1:1.29 (7:9)	1.67:1 (5:3)	1.58:1 (19:12)
1996	1.36:1 (15:11)	1:2.2 (5:11)	2.27:1 (34:15)	1.41:1 (31:22 (6?))	1.90:1 (19:10)	1.22:1 (39:32)

The population structure of the mahogany glider in the continuous habitat at Mullers Creek (Fig. 3.6a) was somewhat evenly aged, however in the fragmented habitat at Porters Creek, the population was largely made up of animals more than 3 years of age (Fig. 3.7a).

The sugar glider population at Mullers Creek was evenly aged with a marked increase in the number of juveniles (<1 year) from October as they entered the population (Fig. 3.6b). In contrast to the continuous habitat at Mullers Creek site, the population structure of sugar gliders in the fragmented habitat at Porters Creek was dominated by animals between 1-2 years of age (Fig. 3.7b). Similar to the continuous habitat at Mullers Creek there was an increase in juvenile animals from October.

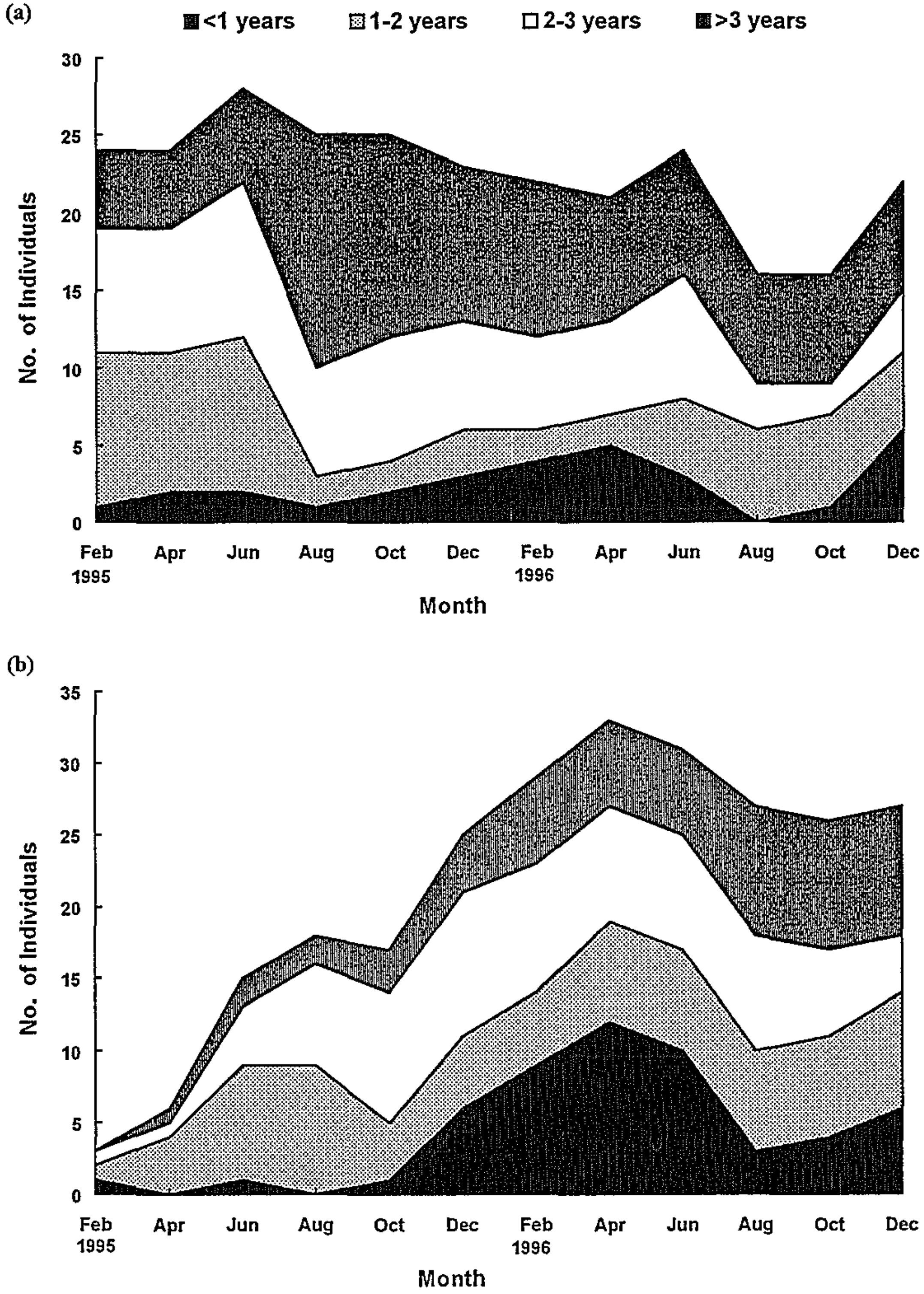


Figure 3.6. Population age structure for (a) mahogany gliders and (b) sugar gliders in the continuous habitat at Mullers Creek from February 1995 to December 1996 using the MNKTBA.

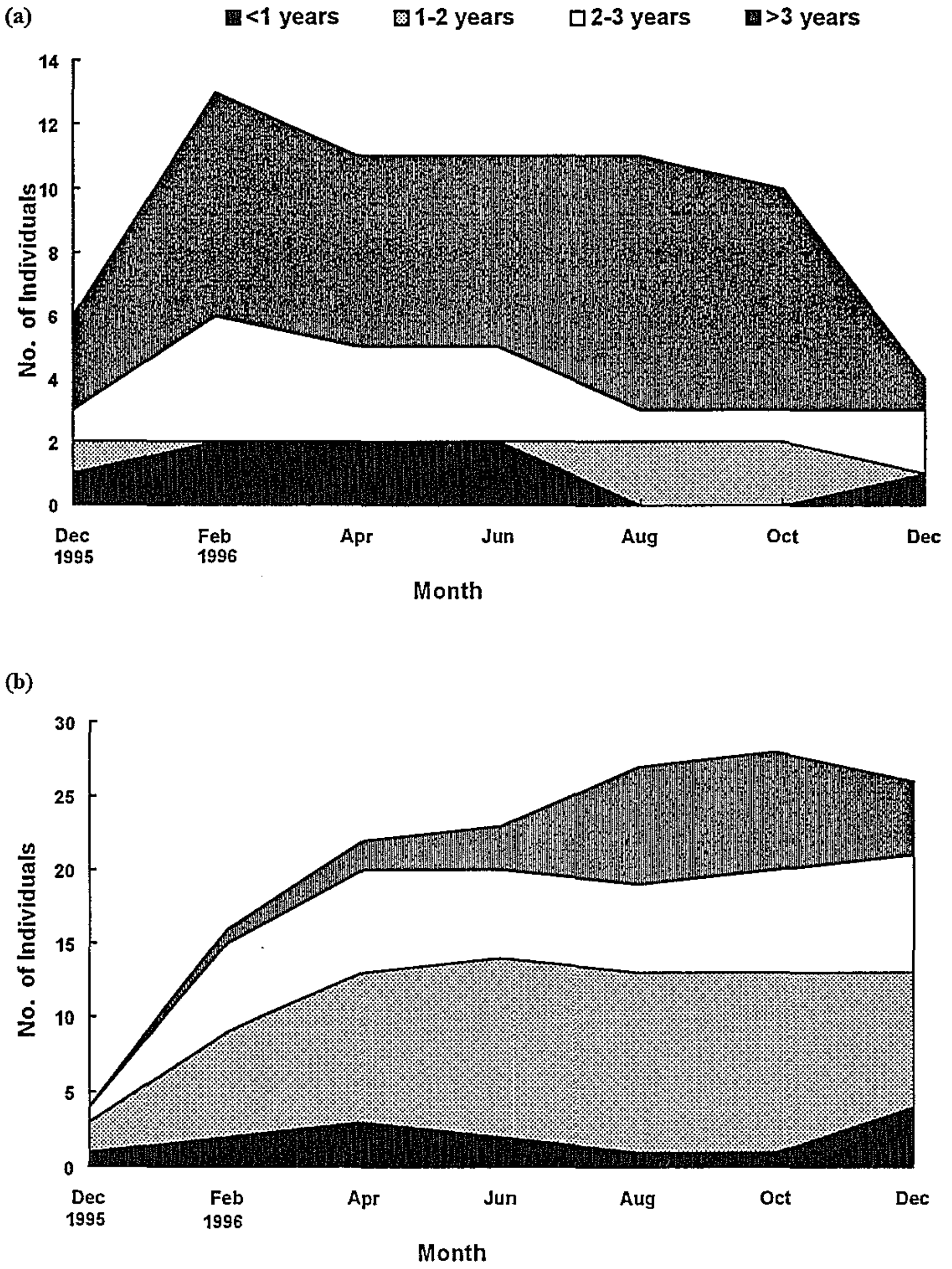


Figure 3.7. Population age structure for (a) mahogany gliders and (b) sugar gliders in the fragmented habitat at Porters Creek from December 1995 to December 1996 using the MNKTBA.

3.3.4 Transients

Of the 18 individuals trapped only once at the continuous area at Mullers Creek, 14 were caught on the edge (ie. within 200m of the edge), and of these 5 were also less than two years of age and so may have been dispersing sub-adults. The remaining 4 individuals caught only once were all less than 2 years of age. Similarly in the fragmented area at Porters Creek, 5 of the 7 individuals caught only once were less than 2 years of age with the other 2 being near the edge. Therefore it appears that all transients were dispersing sub-adults.

Sugar gliders showed a similar pattern to that of the mahogany glider with 16 of 17 individuals caught only once in the continuous area being on the edge. Fourteen of these were less than two years of age and potentially dispersing from the grid. In the fragmented area at Porters Creek all 15 animals caught only once were near the ends of the transects, with 9 of these also being less than two years of age. When the edge sugar gliders and those that are potentially dispersing (<2 years of age) are not included only one animal was potentially a transient.

3.3.5 Body Measurements, Weight and Condition Index

Sexual dimorphism was observed in the mahogany glider with males being significantly heavier, having a longer snout-vent length, head length and head width (Table 3.5). Although females had an average tail length longer than males, this difference was not significant. This was however reflected in females having a significantly larger tail length to body length ratio to males. In the sugar glider, males were also significantly heavier than females, and had significantly longer and wider heads, and longer tibias than females (Table 3.6). Unlike the mahogany glider, no significant difference was observed with body length or tail to body ratios between males and females.

Table 3.5. Weights and measurements of all adult mahogany gliders during 1995 and 1996. * = t; P>0.05, ** = t; P>0.01, NS = not significant.

Measurement (mm)	Males (n = 36)		Females (n = 22)		Significance
	Mean (±SD)	Range	Mean (±SD)	Range	t test
Weight (g)	407.1 (33.9)	337-500	365.2 (30.9)	310-454	**
Snout-tail-tip	624.6 (19.6)	590-660	624.3 (21.2)	585-660	NS
Vent-tail-tip (VT)	370.1 (15.4)	340-395	376.8 (17.4)	345-405	NS
Snout-vent (SV)	254.6 (11.8)	230-275	248.0 (12.4)	225-270	*
Ratio VT:SV	1.46 (0.09)	1.30-1.65	1.52 (0.10)	1.38-1.72	*
Head length	57.3 (3.6)	51-68	55.0 (2.23)	52-62	**
Head width	35.2 (1.2)	32-41	33.7 (1.2)	30-37	**
Length - right tibia	71.3 (2.6)	61-77	71.3 (2.4)	66-75	NS
Length pes	38.1 (2.9)	32-45	36.9 (2.8)	33-42	NS
Length testis	5.5 (1.1)	4-9	-	-	-
Width of scrotum	10.9 (1.5)	9-15	-	-	-

Table 3.6. Weights and measurements of all adult sugar gliders during 1995 and 1996. * = t; P>0.05, ** = t; P>0.01, NS = not significant.

Measurement (mm)	Males (n = 49)		Females (n = 34)		Significance
	Mean (±SD)	Range	Mean (±SD)	Range	t test
Weight (g)	90.2 (8.8)	68-115	80.3 (9.9)	60-104	**
Snout-tail-tip	313.8 (10.0)	300-345	316.6 (10.3)	290-335	NS
Vent-tail-tip (VT)	176.1 (9.4)	160-200	176.3 (7.6)	160-190	NS
Snout-vent (SV)	142.7 (6.3)	130-160	140.4 (6.7)	115-150	NS
Ratio VT:SV	1.25 (0.09)	1.10-1.43	1.26 (0.08)	1.13-1.57	NS
Head length	38.1 (1.53)	35-44	36.7 (2.2)	23-47	**
Head width	24.8 (1.4)	21-36	24.0 (1.6)	21-36	**
Length - right tibia	41.5 (1.6)	32-45	40.8 (1.5)	37-45	**
Length pes	22.8 (1.4)	20-25	22.41 (1.3)	20-25	NS
Length testis	4.3 (0.7)	3-6	-	-	-
Width of scrotum	9.0 (1.2)	6-11	-	-	-

The average body weight of adult male and female mahogany gliders fluctuated throughout the year with no detected pattern (Fig. 3.8a). The mahogany glider increased in weight during April, and decreased in weight in June. This was reflected in the condition indices of the mahogany glider (Fig. 3.8b). The condition indices were determined using head width as it had the best relationship with body weight for both male ($F_{1,42} = 8.85$, $P < 0.01$) and female ($F_{1,18} = 6.37$, $P < 0.05$) mahogany gliders. Body condition varied significantly between months ($F_{11,173} = 3.009$, $P < 0.05$), with no interaction between sex and month ($F_{11,184} = 0.764$, $P > 0.05$).

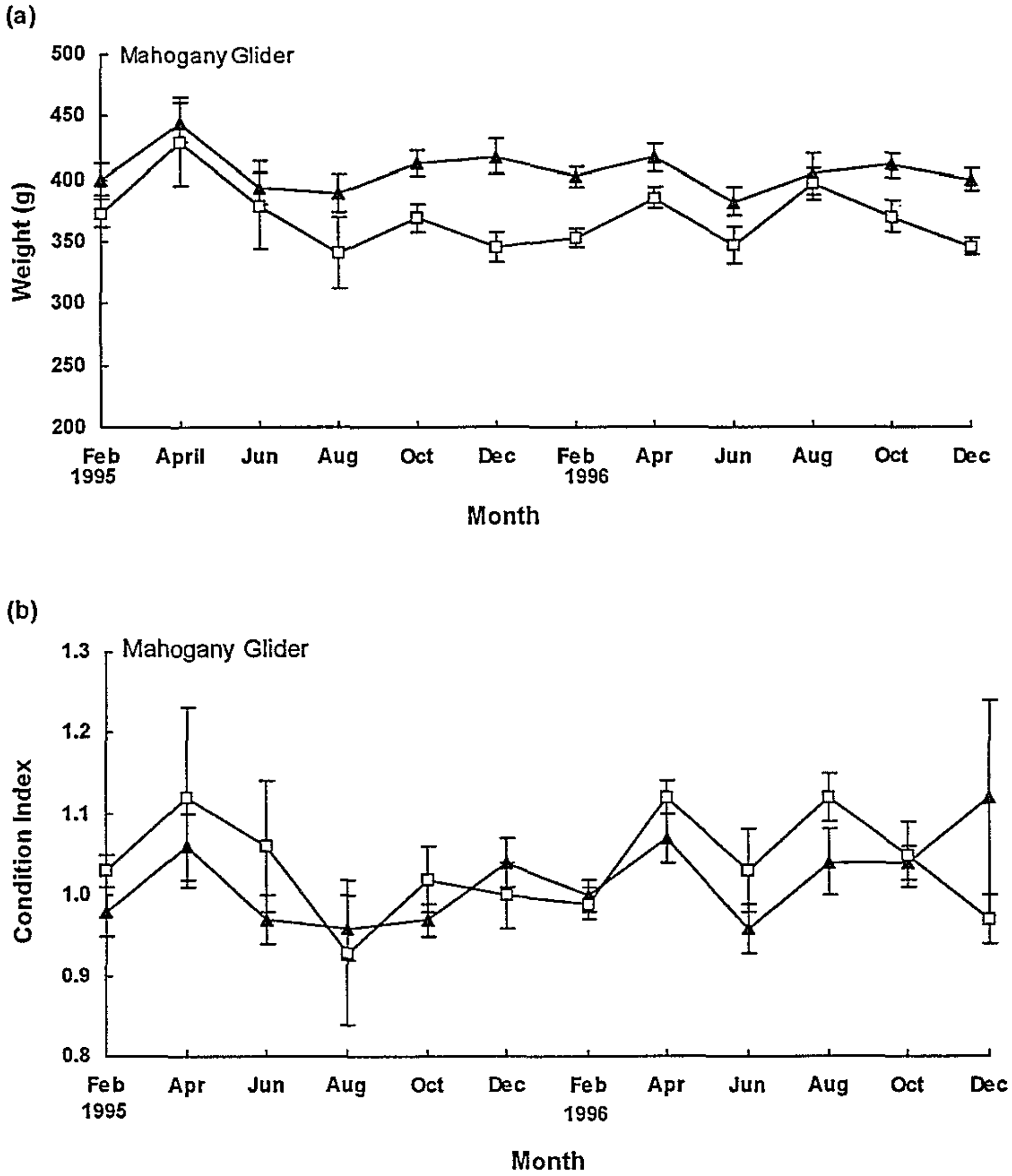
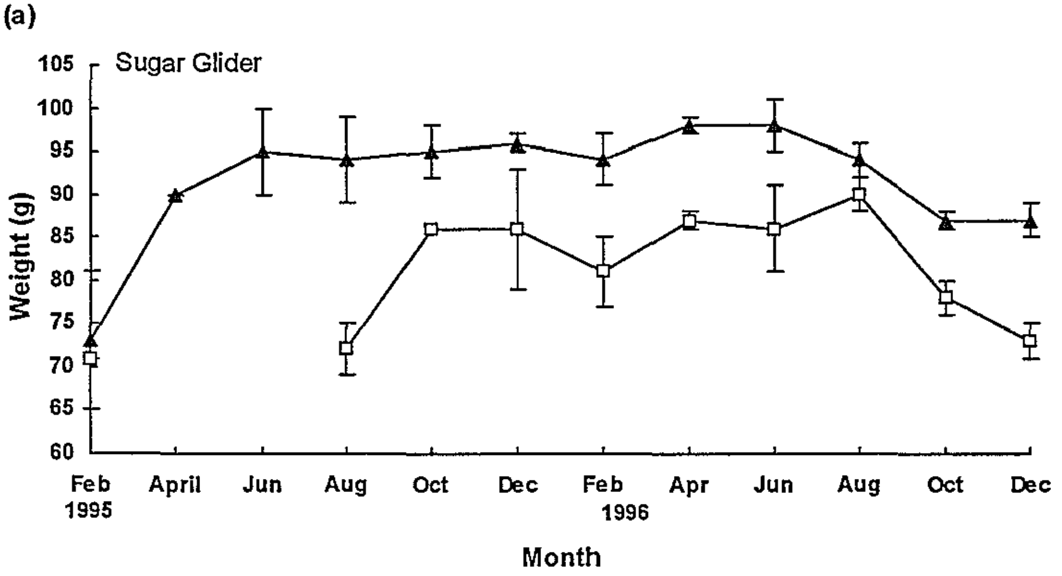


Figure 3.8. Yearly variation in (a) mean body weight and (b) condition index of adult male and female mahogany gliders during 1995 and 1996. (▲ males and □ females). Standard errors are shown.

Similarly no consistent pattern was observed in the average body weight of sugar gliders in either males or females (Fig. 3.9a). This is most probably a result of the low numbers trapped during most of 1995, which included several trapping sessions where no females or only a single female was caught (April & June 1995). Head width was the linear measurement that best correlated with weight for adult male sugar gliders ($F_{1,45} = 5.87$, $P < 0.05$), however head length was the best predictor of weight of adult females ($F_{1,31} = 7.09$, $P < 0.05$). Body condition varied significantly between months ($F_{11,184} = 7.391$, $P < 0.05$), with no interaction between sex and month ($F_{9,184} = 1.285$, $P > 0.05$). During 1995 when few sugar gliders were caught, the condition indices were very erratic, however during 1996, when larger numbers of sugar gliders were caught, the condition indices of both male and female sugar gliders closely mirrored each other with a decrease in condition in wet season and higher condition scores in dry season (Fig. 3.9b).



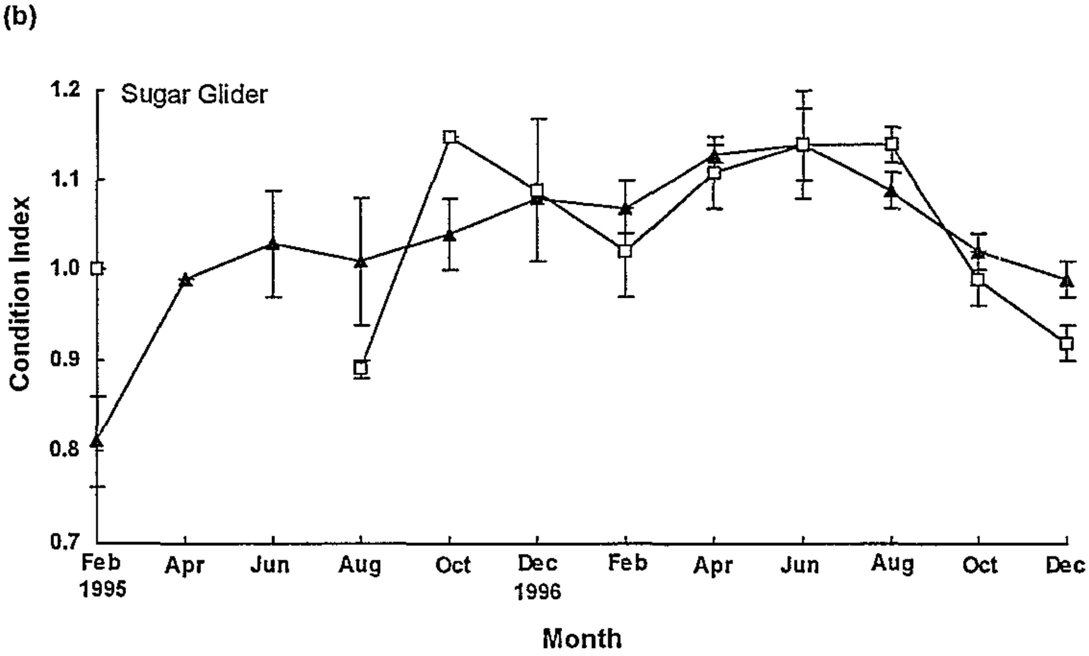


Figure 3.9. Yearly variation in (a) mean body weight and (b) condition index of adult male and female sugar gliders during 1995 and 1996. (▲ males and □ females). Standard errors are shown.

3.3.6 Reproduction

The mahogany glider had a distinct breeding season with pouch young present only between April and October, except for a single observation in December 1996 (Fig. 3.10a). Births were calculated to have occurred from April to September in 1995 and April to October in 1996 (Fig. 3.11a). The peak birth time appears to be from April to August/September. The time to weaning is estimated to be approximately 4-5 months for the mahogany glider based on the presence of young in the pouch and the occurrence of young in the trapped population. After weaning both sexes appeared to disperse from their parents' home-range within a year. In both areas recruitment into the trappable population was observed from October each year as young (<1 year) from that breeding season entered the population.

The sugar glider, in contrast, had pouch young present during all months of the year with a peak from August to October (Fig. 3.10b). Births were calculated to have occurred during all months except February and April (Fig. 3.11b) with a peak from June to September. Of the adult female mahogany and sugar gliders caught more than 2-3 times, 100% were found to have bred during both 1995 and 1996 as all had bred by 24 months. A number of sub-adult (age <1) mahogany and sugar gliders were caught, however none were found to have pouch young. Therefore the age of first breeding appears to be approximately 12-18 months in the mahogany glider and the sugar glider.

In both the mahogany glider and the sugar glider, litters of 1-2 were recorded with the interval between successive trapping sessions being greater than pouch-life. Of the total of 31 mahogany glider litters recorded during the study, 17 were twins and 14 were single young. It appears that female mahogany gliders will produce a second litter if the first litter is lost within a given year, suggesting they enter lactational anoestrous. For the sugar glider, 41 litters were recorded, of which 34 were twins and 7 were single young. The sugar glider was able to produce more than one litter per year. Several female sugar gliders were observed to have two enlarged lactating teats suggesting young back in the den, and had young in the pouch. The sex ratio of all mahogany glider and sugar glider pouch young over the two years was 25:23 (males:females) and 38:31 (6 unknown sex) respectively. For both the mahogany glider and sugar glider there did not appear to be a change in sex ration of the pouch young with age or litter size Table 3.7. A reproductive summary of female mahogany and sugar gliders can be found in Table 3.8.

When the condition index was determined for all adult female mahogany gliders and sugar gliders at each reproductive stage throughout the two year period, there was a clear trend in the condition index (Fig. 3.12). The condition index of mahogany gliders was high when pregnant and during the early stages of lactation, then deceased during late lactation and weaning. There was significant variation in condition index with reproductive stage ($F_{4,62} = 3.99$, $P < 0.01$), with the difference being significant between early (stage 4) and late lactation (stage 5)(Tukey's test; 0.05). A similar result was observed for the sugar glider, except that pregnant females had a very low condition index. This may be a result of the low sample size (4) and potentially error in determining if they were pregnant. A significant difference was also observed between reproductive stage and condition index ($F_{4,64} = 3.81$, $P < 0.01$) with the difference being significant between pregnant females (stage 3) and early lactation (stage 4), and between early lactation and late lactation (Tukeys test; 0.05).

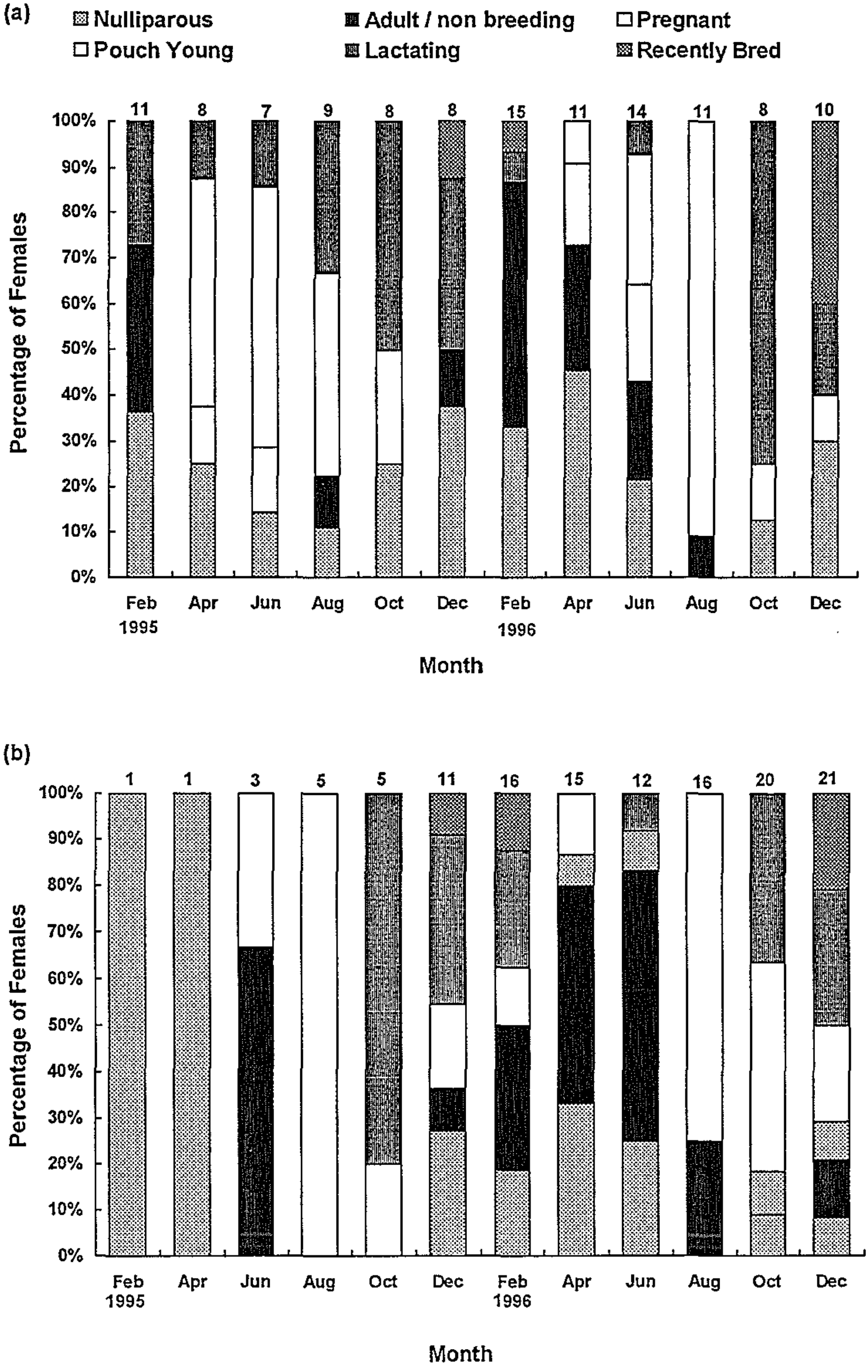
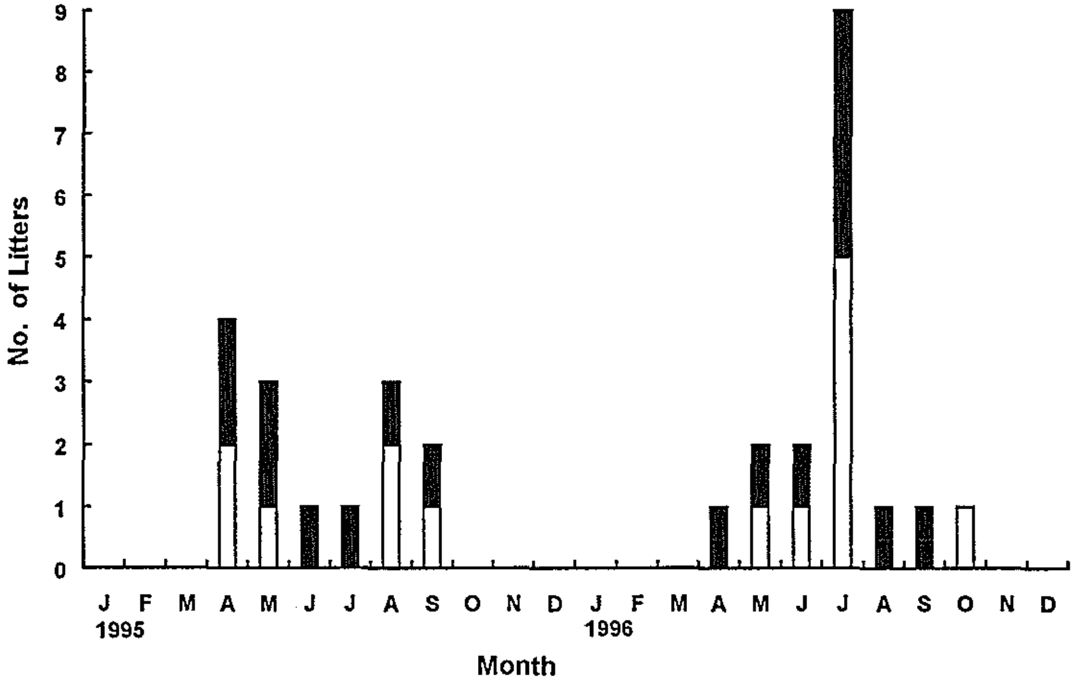


Figure 3.10. Seasonal variation in reproductive condition of all adult female (a) mahogany gliders and (b) sugar glider during 1995 and 1996. The number of individuals is at the top of the column.

(a)



(b)

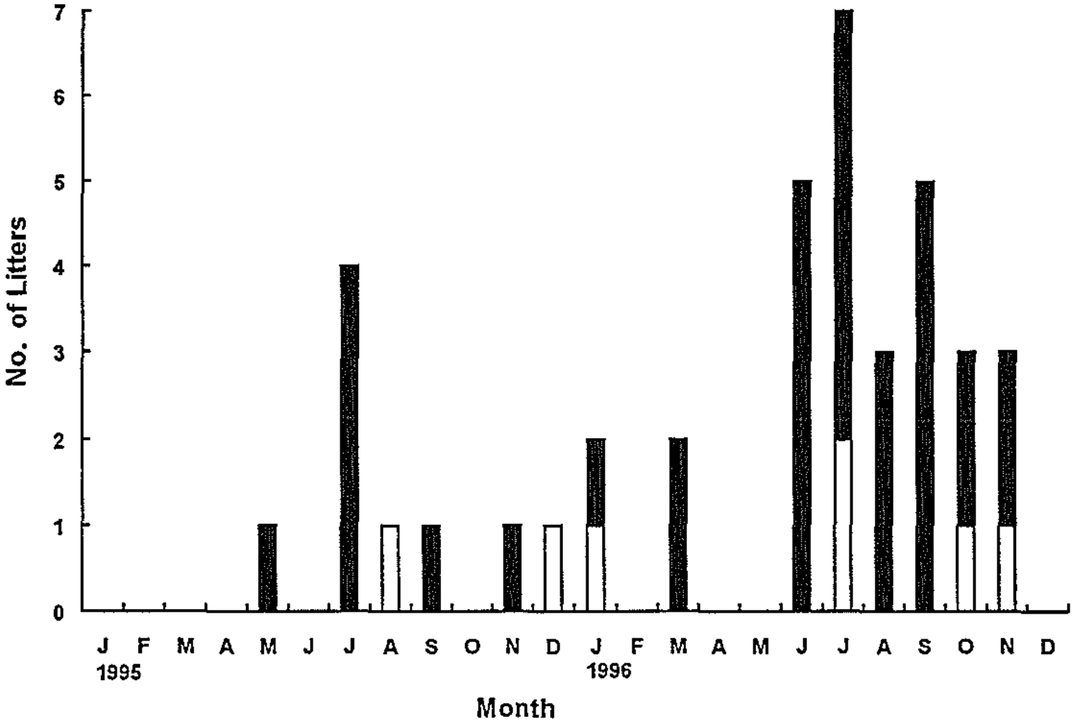


Figure 3.11. Estimated months of all recorded births of (a) mahogany gliders and (b) sugar gliders during 1995 and 1996. Solid bars represent litters of two, clear bars represent litters of one.

Table 3.7. Reproductive output of adult female mahogany gliders and sugar gliders during 1995 and 1996 in relation to age class.

	Age Class		
Sex Ratio	1-2	2-3	>3
Mahogany Glider			
2:0	1	1	1
1:1	5	3	3
0:2	1	2	0
1:0	1	5	2
0:1	0	3	3
Total	8	14	9
Sugar Glider			
2:0	4	2	3
1:1	7	5	5
0:2	2	1	2
1:0	1	1	1
0:1	2	2	0
2? unknown sex		2	1
Total	16	13	12

Table 3.8. Reproductive summary for all adult female mahogany and sugar gliders during 1995 and 1996. It is assumed that females with lactating teats and large pouches had bred during that year.

Parameter	Mullers Creek	Mullers Creek	Porters Creek	
	1995	1996		Total
		Mahogany glider		
No. of adult females	12	8	5	23
Females breeding (%)	100	100	100	100
Litter size - 1	6	4	4	14
Litter size - 2	8	7	2	17
Total litters	14	11	6	31
Total young	22	18	8	48
Sex ratio of pouch young	10:12	9:9	6:2	25:23
Mean litter size	1.57	1.64	1.33	1.55
Natality rate	1.83	2.25	1.60	2.09
		Sugar glider		
No. of adult females	11	12	12	35
Females breeding (%)	100	100	100	100
Litter size - 1	2	3	2	7
Litter size - 2	7	14	13	34
Total litters	11	17	15	41
Total young	16	31	28	75
Sex ratio of pouch young	7:9	14:13 (4?)	17:9 (2?)	38:31 (6?)
Mean litter size	1.78	1.82	1.87	1.83
Natality rate	1.45	2.58	2.33	2.14

Note - only females caught at least 2-3 times were counted unless they had pouch young or were lactating as they may have bred during the year but were not observed to at the time of capture. Number in brackets were individuals too small to sex.

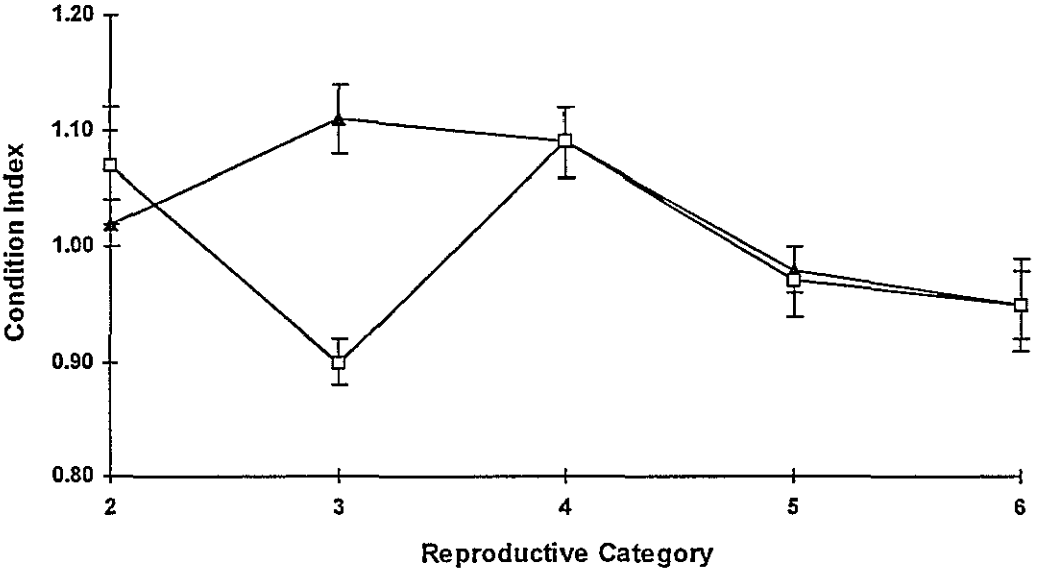


Figure 3.12. Condition indices of all adult female mahogany gliders (▲) and sugar gliders (□) in relation to reproductive condition. 2 (adult non-breeding), 3 (pregnant), 4 (pouch young present), 5 (lactating with no pouch young), 6 (teat regressing).

3.4 Discussion

3.4.1 Density

The density of mahogany gliders in the continuous habitat at Mullers Creek (0.23-0.24 ha^{-1}) and particularly in the fragmented area at Porters Creek (0.15-0.16 ha^{-1}) was less than recorded for the closely related squirrel glider (0.89-1.54 ha^{-1}) at Limeburners Creek in New South Wales (Quin 1995). The density of sugar gliders in the continuous habitat at Mullers Creek (0.23-0.30 ha^{-1}) was similar to those recorded at Limeburners Creek in NSW (0.24-0.54 ha^{-1})(Quin 1995). However it was much less than other studies at Glengary in eastern Victoria (1.1-2.2 ha^{-1})(Henry 1985) and Willung in south-east Victoria (2.9-6.1 ha^{-1})(Suckling 1984). In the fragmented habitat at Porters Creek the density of sugar gliders (0.43-0.48 ha^{-1}), was still greatly less than found by Henry (1985) and Suckling (1984). The yellow-bellied glider however has densities much lower than the mahogany glider, being recorded at 0.05-0.06ha^{-1} in Victoria by Henry and Craig (1984) and 0.10-0.14ha^{-1} in New South Wales by Kavanagh (1984).

The very low numbers of sugar gliders caught initially within the Mullers Creek area may have been caused by initial trap shyness or could reflect an increasing population from immigration and breeding after a population crash (eg. caused by intense predation or disease). An increasing population size suggests the body condition of individuals is high, which is relatively consistent with the condition indices observed, although this should be interpreted with caution because of natural seasonal changes in body condition and initial small sample sizes.

3.4.2 Longevity

Several individuals of both species that were classed as being >3 at the beginning of the study were still present at the end of two years trapping, making them at least 5 years of age. As this study was conducted over a two year period, longevity could not be accurately determined for individual mahogany or sugar gliders. These longevity's are similar to observations of the squirrel and the sugar glider living up to 5-6 years (Suckling 1984; Henry 1985; Quin 1995), although sugar gliders as old as 7 years have been recorded by Suckling (1984), and up to 9 years by Klettenheimer *et al.* (1997). A longevity of at least 6 years was suggested for the yellow-bellied glider *Petaurus australis* by Russell (1984) and Goldingay and Kavanagh (1990).

Direct predation on the mahogany glider by the scrub python *Morelia amethistina* was observed on three occasions, plus an observation of one python curled around a trap which contained a mahogany glider. Several other species of python occur in the area, including carpet pythons *Morelia spilota* which are also potential predators. Bird predators include rufous owls *Ninox rufa*, barking owls *Ninox connivens*, masked owls *Tyto novaehollandiae*, and lesser sooty owls *Tyto multipunctata* (J. Young pers. comm.). The skull of a mahogany glider was found which appeared to have been eaten by an owl. There are also several records of predation by cats (K. Smith, pers. comm.). Elsewhere cats have been known to prey upon both squirrel gliders and sugars glider (D. Storch, pers. comm.).

3.4.3 Reproduction

The apparent age at first breeding for the mahogany glider and the sugar glider during this study (12-18months) is consistent with the age of first breeding in other petaurids which ranges from 12 months for Leadbeater's possum (Smith 1984b), 8-15 months for the sugar glider (Schultze-Westrum 1965; Smith 1979) to 18-24 months for the yellow-bellied glider (Russell 1984).

The timing of births recorded for the mahogany glider during this study is generally compatible with observations by Van Dyck (1993), who found two adult female mahogany gliders caught in August with hairless pouch young. The observed timing of births is, however, complicated by Van Dyck's (1993) observation of a hairless mahogany glider pouch young in mid February and an observed September mating, suggesting some variation in the timing of births outside that observed at this site and from year to year. However, unlike the well defined April-May breeding observed at this site, Van Dyck (1993) suggested that births occur in August-September.

The April-October birth season for the mahogany glider differs from the timing of birth observations in the closely related squirrel glider for several captive colonies (Table 3.9) and observations by Quin (1995) who observed births in all months except May, October and December at Limeburners Creek in northern New South Wales. The peak birth period observed by Quin (1995) for squirrel gliders was in April and June to August, which is similar to that found in the mahogany glider. It is at present unknown if the breeding season of squirrel gliders at the same latitude as the mahogany glider have a similar breeding season to those in New South Wales and Victoria or if they are similar to the mahogany glider.

Table 3.9. A comparison of the recorded timing of births of the mahogany glider with studies on the squirrel glider.

Location	Months of Births	Reference	Species
Mullers and Porters Creek, north Qld.	Apr.-Oct.	This study	*P. gracilis*
Limeburners Creek, northern NSW.	All months recorded except May, Oct., and Dec.	Quin 1995	*P. norfolcensis*
Captive, Canberra.	May.-Jan. (except Dec.)	Smith 1979	*P. norfolcensis*
Captive, London Zoo	Feb.-Oct. (except May).	Zuckerman 1953	*P. norfolcensis*

The average litter size and natality rate of the mahogany glider was less than the squirrel glider at Limeburners Creek with litter sizes of 1.6 and 1.8 respectively and natality rates of 2.1 and 2.4 respectively. The natality rate for the mahogany glider observed at this site is expected to be lower than observed, as several females were observed to have young in successive trapping trips, suggesting that second litters were produced following the loss of the first litter, as no female mahogany glider was observed to raise a second litter within a single breeding season. Nonetheless these results show that the mahogany glider is polyoestrous (within one season) and can therefore mate again if pouch young are lost. Potentially, females may experience higher pouch losses during their first reproductive season. This is consistent with observations by Suckling (1984) who suggested that in sugar gliders, female breeding rate does not peak until the second year of age when most individuals have reached full adult body weight.

In contrast to the distinct breeding season in mahogany gliders, the sugar glider was quite variable in its timing of births, with births occurring in most months of the year. The birth season for the sugar glider at Mullers and Porters Creeks is similar to several studies in southern Australia (Table 3.10). Females of both species bred in successive years.

Table 3.10. A comparison of the timing of births of the sugar glider during this study, with studies on the sugar glider in southern Australia. Peak birth times are in brackets.

Location	Month of Births	Litter size	Natality	Reference
Mullers/Porters Creeks, North Qld.	Apr., Jun.-Dec. (Apr., Aug.)	1.8	1.9	This study
Rosedale, Victoria	Sep.-Nov.	not known	not known	Smith 1980
Willung, SE Victoria	Aug.-Jan. (Sep.)	1.8	1.7-2.5	Suckling 1984
Glengarry, E Victoria	Jun.-Jan. (Aug.)	1.8	1.6-1.8	Henry 1985
Limeburners Creek, northern NSW	Variable, Apr., June-Aug. (Jun.)	1.9	2.3	Quin 1995

Potentially, mahogany gliders may be able to raise second litters (within one season) if they first breed at the beginning of the breeding season. This is supported by Van Dyck (1993) who observed a female, known to have two pouch young, mating in September. The major constraint on whether a species expresses polyoestry is the length of lactation, which in turn is closely related to body size (Russell 1982;

Tyndale-Biscoe & Renfree 1987). Within the Petauridae, the largest species, the yellow-bellied glider, has a comparatively long lactation period and is limited to producing only one young per year, while the smallest petaurids, such as the sugar glider and Leadbeater's possum *Gymnobelideus leadbeateri*, which have shorter lactation periods, are able to produce more than one litter per year (see Quin 1995 for a summary of reproductive parameters). It appears the mahogany glider may fall between these limits in its fecundity.

Chapter 4

Habitat Relationships of the Mahogany Glider and the Sugar Glider.

4.1 Introduction

The ecological niche a species occupies is the sum of all the environmental factors acting on the organism within its habitat (Hutchinson 1978; Schoener 1989). When two or more species fill similar niches and live in a habitat where resources are limited, competition can occur with one organism interfering with or inhibiting another, resulting in a mutual reduction in fitness (Pianka 1981). Competition is sometimes direct, as in interspecific territoriality, where direct antagonism between species occurs (termed interference competition); or competition may be indirect resulting from the joint use of the same limited resources (termed exploitation competition)(Pianka 1981).

Differences in the sizes of ecologically similar species may provide or reflect differences in their niches sufficient to permit coexistence (Brown & Wilson 1956). The limits to the similarity that can occur between sympatric and ecologically similar species before they effectively have the same niche has been examined by various authors including Wilson (1975), Horn and May (1977), Lewin (1983) and Tonkyn and Cole (1986), and may include differences in dietary requirements and habitat occupied. Hutchinson (1959) proposed that the average difference between typical linear dimensions (eg head length) of two sympatric species necessary to prevent them from occupying the same niche is a ratio of approximately 1.3, or a doubling in weight. More recent analysis, however, has suggested the constant proposed by Hutchinson (1959) is an artefact of the lognormal distribution of animal sizes in nature (Horn & May 1977; Maiorana 1978; Boecklen & NeSmith 1985; Eadie *et al.* 1987).

Throughout its distribution, the mahogany glider *Petaurus gracilis* lives sympatrically with the smaller sugar glider *Petaurus breviceps*. As early as 1859, Darwin noted that species of the same genus usually have many similarities in habits and constitution, and always in structure. As a result Darwin (1859) suggested the struggle will generally be more severe between them if they come into competition with each other than with species of different genera.

Competition can be reduced by partitioning resources and habitats so that species inhabit different realised niches (Lee & Cockburn 1985). Members of the Petauridae do not appear to specialise on any food items (although the proportions and species utilised may vary) and are generalist exudate and insect eaters, suggesting that there is no reason to suspect that dietary resource partitioning is apparent between the different species of petaurids (Quin 1993). Habitat partitioning (or habitat segregation) has been suggested to be a more important mechanism of resource partitioning during times of food shortage for closely related dietary generalists, such as members of the Petauridae, allowing them to coexist (Rosenzweig 1981; Quin 1993).

This chapter has two aims. First, to identify the habitat characteristics that determine the local distribution of both mahogany and sugar gliders, as the use of different habitat types has important implications in managing the habitat of the endangered mahogany glider. Second, to compare the preferred habitat used by the mahogany glider to that used by the sugar glider when both species occur in sympatry.

4.2 Methods

4.2.1 Trapping Records

Trapping records were totalled for each trap locality for the mahogany glider and sugar glider from the 10 transects within the continuous habitat at Mullers Creek over a two- year period, and the five transects within the adjacent fragmented habitat at Porters Creek over a fourteen-month period as part of the study on population biology (Chapter 3). Trap localities which were not trapped for the full trapping period were not included. The relative frequency of animal captures at a particular location was therefore used to suggest the species' preference for a particular habitat type.

4.2.2 Habitat Description

Each trapping area contained several distinct habitat types (riparian forest along creeklines, open woodland and *Melaleuca viridiflora* swamps) with variations observed within these major habitat types with respect to plant species diversity and abundance. At each trapping site, a number of vegetation attributes were recorded within a 20m radius around the trap tree. Each tree or understorey species greater than 1m in height within the area was recorded and classed into one of three 'diameter at breast height' (DBH) categories (0-10cm, 11-30cm and >30cm). These three DBH categories were then collapsed into one variable for the multivariate analysis by multiplying the number of stems in the 0-10cm class by one, those in the 11-30cm class by two, and those >30cm by three, and then taking the sum of these figures. The number of stems for each size category was recorded for a total of 15 species which were potential food for both the mahogany glider and the sugar glider, including bloodwoods, eucalypts, lophostemons, melaleucas, acacias and *Albizia procera*. The total number of species which supply food at each trap location was also included. Other understorey species and rainforest species were grouped separately as additional categories. In addition to the number of trees being recorded, the average grass cover and height was estimated, and the number of grass trees *Xanthorrhoea johnsonii* was counted. Canopy cover was also estimated for the mid canopy and upper canopy using the procedure of McDonald *et al.* (1990) which uses a series of shaded silhouettes to estimate canopy cover.

4.2.3 Analysis

Because of the different structures of the fragmented habitat at Porters Creek and continuous habitat at Mullers Creek they were treated both separately and together in order to examine if there was a difference between the two. Habitat attributes that were most associated with the abundance of the mahogany glider and sugar glider were determined by principal components analysis (PCA) and correlations (Pearson's coefficients). The significance of the Pearson's correlations was adjusted using a Bonferroni correction for 23 simultaneous tests which gave an adjusted significance of 0.0022 (using an initial P value at 0.05).

The examination of any separation of habitat utilisation between sugar gliders and mahogany gliders in the continuous habitat at Mullers Creek and the fragmented habitat at Porters Creek was done using canonical correlation analysis. This used the vegetation variables recorded at each trap point and the number of mahogany gliders and sugar gliders caught to examine the linear relationships between these two sets of variables. The canonical correlation analysis was also used to show which tree species were most likely to have resulted in any observed separation. Miller's test (McArdle 1994) was used to calculate an F statistic for the canonical correlations, to determine if there was a significant relationship between the habitat variables and the number of mahogany gliders and sugar gliders caught at each trap point. The Miller's test calculation of the F statistic was determined from the following formula:

$F = (D^2/(1-D^2))(N-p-1)q/pq$. Which approximates $F_{pq,\,(N-p-1)q}$

Where:
D^2 = Total variation explained by habitat variables.
p = Number of animal species (2).
q = Number of habitat variables (23).
N = Number of trap sites (80 in continuous forest and 44 in fragmented forest).

4.3 Results

4.3.1 Number of Gliders Caught at Each Trap Point

A ratio of 2:1 in mahogany glider to sugar glider captures was used to separate trap locations that clearly favoured either mahogany gliders or sugar gliders (Fig. 4.1). The mahogany glider was favoured at 43 of 124 locations (38 in continuous forest and 5 in fragmented forest), with the sugar glider dominant at 46 locations (18 in continuous forest and 28 in fragmented forest). The remaining 27 trap locations in which gliders were caught did not favour either species (having a trap success ratio of less than 2:1 for mahogany gliders to sugar gliders), with a further eight trap locations within riparian rainforest producing no captures of either species.

In the continuous habitat at Mullers Creek the mahogany glider was clearly more commonly trapped (Fig. 4.2). Within the fragmented habitat at Porters Creek there was an even greater difference in the number of mahogany gliders and sugar gliders caught, with this habitat clearly favouring sugar gliders (Fig. 4.3). Figures 4.2 and 4.3 show a clear picture of the differential trappability at each trapping location, and therefore reflects the differential habitat usage of the two species over both study grids.

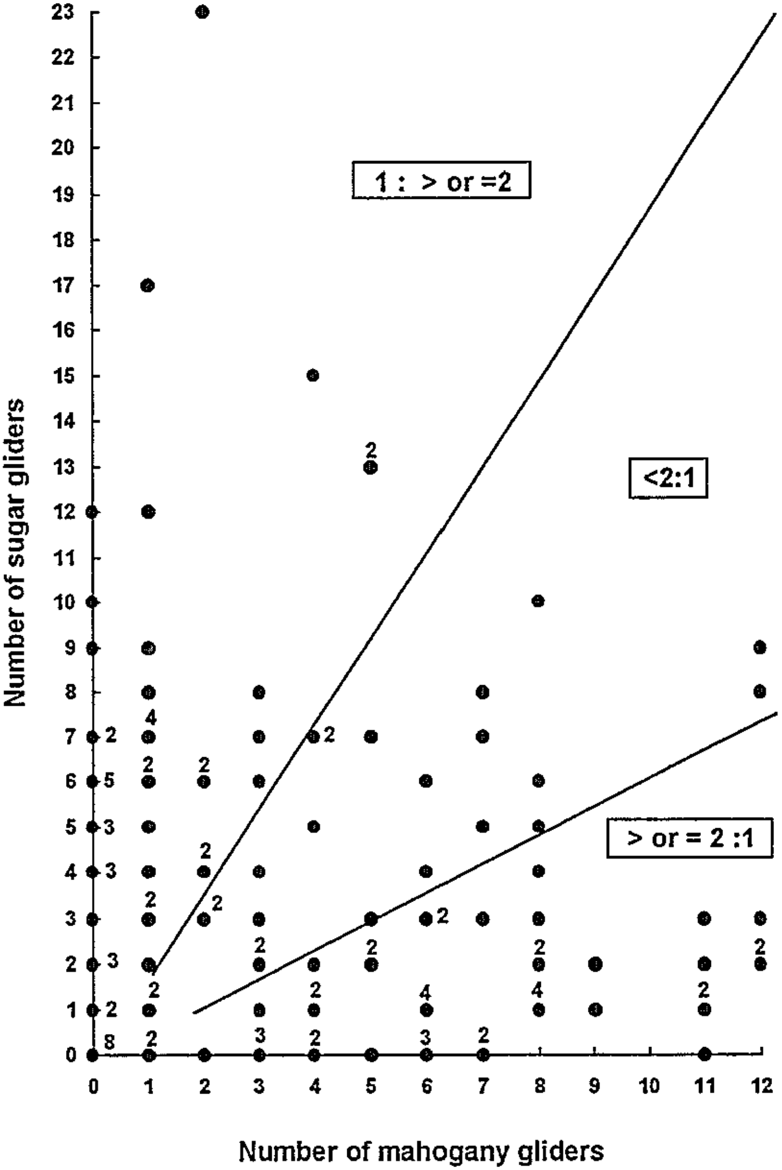
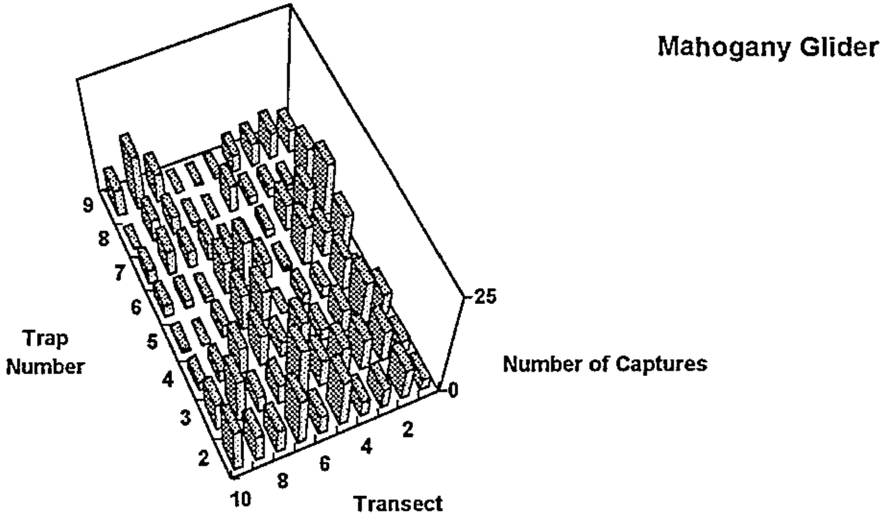


Figure 4.1. A comparison of the number of captures of mahogany gliders and sugar gliders at each trap location for the entire study area. The lines separate trap localities with a ratio >2:1 with those <2:1. The numbers next to the dots mean that the ratio occurred more than once.

(a)



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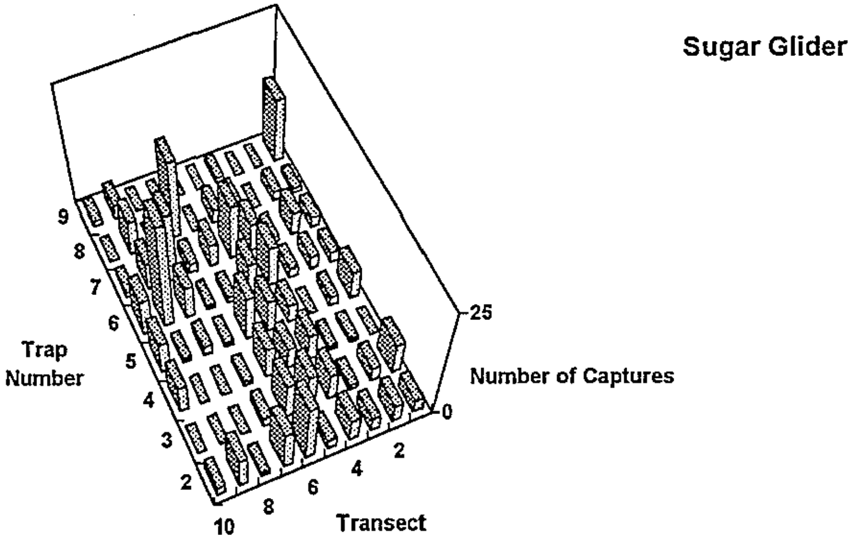


Figure 4.2. Number of (a) mahogany gliders and (b) sugar gliders trapped at each trap point in the continuous habitat at Mullers Creek.

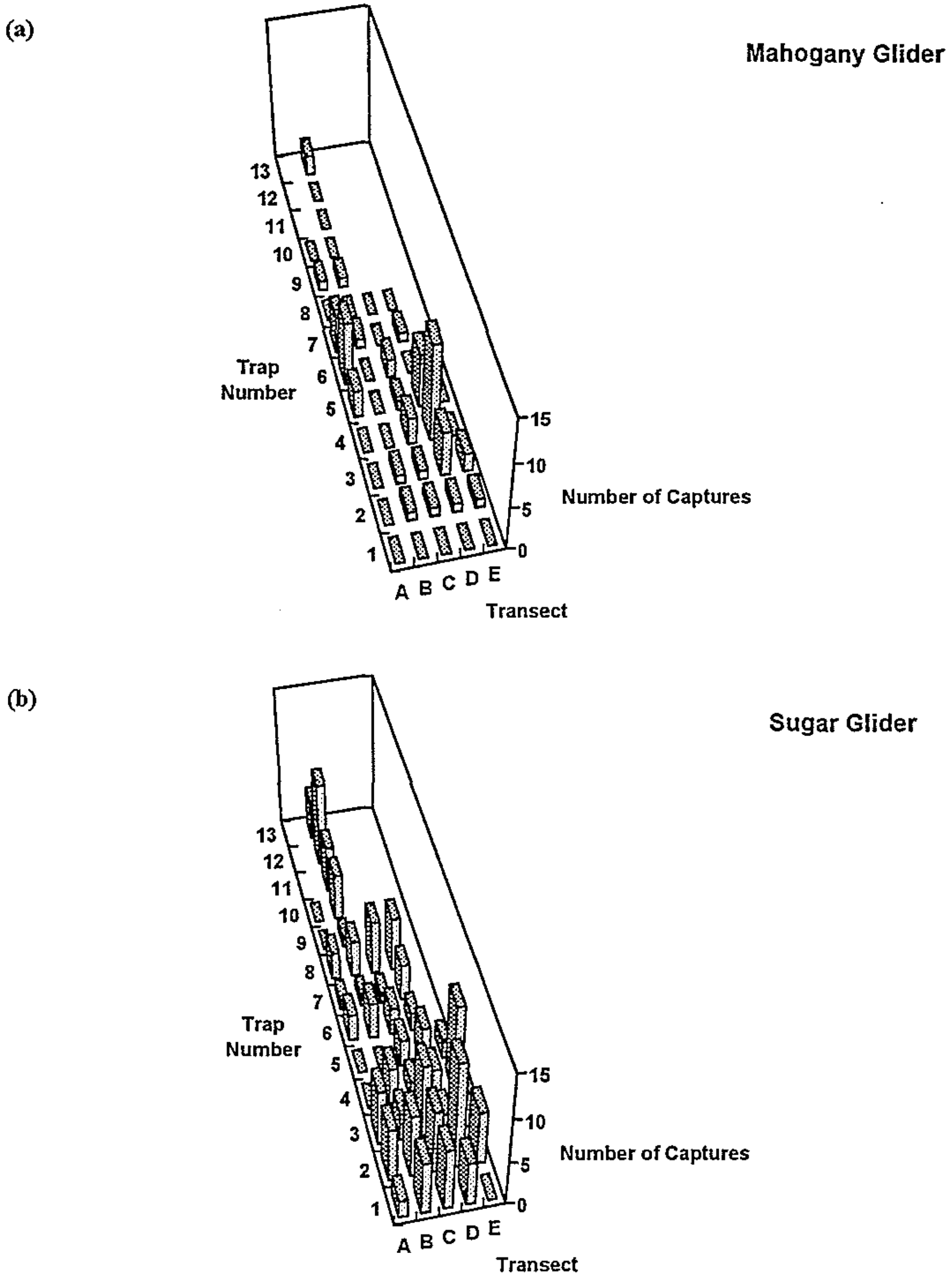


Figure 4.3. Number of (a) mahogany gliders and (b) sugar gliders trapped at each trap point in the fragmented habitat at Porters Creek.

4.3.2 Habitat Preference of the Mahogany Glider and Sugar Glider

The abundance of the mahogany glider was significantly correlated with the abundance of *Corymbia clarksoniana* and *Eucalyptus platyphylla*, the absence of *Corymbia intermedia* and *Acacia mangium*, and a small mid and upper canopy cover (Table 4.1). When only the continuous area was examined, *E. platyphylla* was the only significantly correlated tree species, with a high grass cover (caused by an open canopy) and a small mid and upper canopy cover being significantly correlated with the abundance of mahogany gliders. When the fragmented habitat is considered by itself, there was no significant correlation with any eucalypts or bloodwoods with only *Melaleuca viridiflora* and *Xanthorrhoea johnsonii* being significantly correlated with abundance of mahogany gliders. These two species generally occurred together as a ditypic assemblage and represented the only large areas with an open canopy within the fragmented habitat. The lack of a positive correlation with eucalypts, bloodwoods, acacias or canopy cover appears to be caused by the high proportion of these species throughout the entire fragmented habitat (except where *M. viridiflora* and *X. johnsonii* occur).

The abundance of the sugar glider was best correlated with a large number of other stems and the absence of *Eucalyptus tereticornis* (Table 4.2). When only the continuous habitat was considered *Acacia flavescens*, *Acacia mangium* and other stems were significantly positively correlated with the abundance of sugar gliders. As mentioned above, the lack of a significant relationship with these species in the fragmented habitat appears to be caused by the high density of trees and canopy cover throughout the entire fragmented area. The ordinated habitat data using PCA showed that none of the principle components were more strongly correlated with mahogany gliders or sugar gliders than derived from Pearson correlations.

Table 4.1. Pearson correlations of mahogany gliders with individual habitat variables. * indicates significance at 0.05 using the Bonferroni adjusted level of 0.0022. Non-food stems - the number of stems of non food species, not including rainforest stems. Rainforest stems - all rainforest non-food species stems.

	Total	Continuous	Fragmented
Corymbia clarksoniana	0.338*	0.228	0.236
Corymbia intermedia	-0.366*	-0.231	-0.287
Corymbia tessellaris	-0.009	0.126	-0.194
Eucalyptus pellita	-0.200	-0.243	-0.082
Eucalyptus platyphylla	0.366*	0.338*	-0.153
Eucalyptus tereticornis	-0.026	-0.039	-0.105
Lophostemon suaveolens	-0.110	0.025	-0.220
Melaleuca dealbata	0.177	0.196	0.085
Melaleuca leucodendra	0.214	0.204	-0.084
Melaleuca viridiflora	0.162	0.003	0.526*
Acacia crassicarpa	0.208	0.127	0.136
Acacia flavescens	-0.257	-0.152	-0.173
Acacia leptocarpa	0.030	0.177	0.006
Acacia mangium	-0.432*	-0.299	-0.271
Albizia procera	0.211	0.129	-0.103
Xanthorrhoea johnsonii	-0.029	-0.077	0.478*
Total No. Food Species	-0.175	-0.039	-0.200
Non-Food Stems	-0.209	-0.103	-0.126
Rainforest Stems	-0.258	-0.318	-0.215
Grass Cover	0.152	0.356*	0.271
Grass Height	0.116	0.276	0.115
Mid Canopy Cover	-0.548*	-0.464*	-0.373
Upper Canopy Cover	-0.472*	-0.477*	-0.242

Table 4.2. Pearson correlations of sugar gliders with individual habitat variables. * indicates significance at 0.05 using the Bonferroni adjusted level of 0.0022.

	Total	Continuous	Fragmented
Corymbia clarksoniana	0.027	0.060	-0.101
Corymbia intermedia	-0.011	-0.010	-0.003
Corymbia tessellaris	-0.073	-0.080	-0.070
Eucalyptus pellita	-0.076	-0.041	-0.184
Eucalyptus platyphylla	0.064	0.100	-0.103
Eucalyptus tereticornis	-0.306*	-0.330	-0.233
Lophostemon suaveolens	0.146	0.148	0.170
Melaleuca dealbata	-0.020	-0.045	0.150
Melaleuca leucodendra	0.063	0.070	-0.026
Melaleuca viridiflora	-0.003	-0.021	0.073
Acacia crassicarpa	-0.008	0.023	-0.169
Acacia flavescens	0.198	0.341*	0.007
Acacia leptocarpa	-0.003	-0.163	0.274
Acacia mangium	0.265	0.416*	-0.005
Albizia procera	-0.195	-0.214	-0.208
Xanthorrhoea johnsonii	0.145	0.205	0.086
Total No. Food Species	0.180	0.187	0.193
Non-Food Stems	0.352*	0.446*	0.281
Rainforest Stems	-0.133	-0.128	-0.165
Grass Cover	-0.107	-0.174	0.040
Grass Height	0.039	0.021	0.114
Mid Canopy Cover	0.128	0.256	-0.147
Upper Canopy Cover	0.062	0.127	-0.148

4.3.3 Habitat Partitioning Between the Mahogany Glider and Sugar Glider

When the abundance of the mahogany glider is compared to the sugar glider with respect to habitat variables for the entire study area, the first two canonical variates showed significant correlation between the number of mahogany gliders and sugar gliders present and the habitat variables, with canonical correlations of 0.800 and 0.602 respectively (Wilk's test. $\lambda = 0.230$, d.f. = 46, $P < 0.01$ and $\lambda = 0.638$, d.f. = 22, $P < 0.01$ respectively). The canonical coefficients showed a good separation between mahogany gliders and sugar gliders on the first axis, but little separation on the second axis (Table 4.3). The abundance of the mahogany glider was negatively correlated with the first axis and separated from that of the sugar glider by the abundance of *C. clarksoniana*, *Eucalyptus pellita*, *E. platyphylla*, *Lophostemon suaveolens*, *Melaleuca dealbata* and a reduced lower and upper canopy cover that is reflected in high grass height (Table 4.4). The abundance of the sugar glider was not well correlated with the first axis although most associated with *C. intermedia*, *A. mangium*, a larger number of potential food species, rainforest species, a high grass cover and a dense mid and upper canopy cover. The sugar glider was highly correlated with the second axis, although as the mahogany glider also had a positive coefficient it was difficult to determine with which species of glider the habitat variables were most correlated. The first two canonical variates were a good summary of the two sets of variables, with fifty-four percent of the variation in the number of animals caught at each trap location being explained by the first two canonical variates (Miller's test. $F_{46, 2783} = 62.22$, $P < 0.01$).

When only the continuous habitat at Mullers Creek is considered, the first two canonical variates were significantly correlated with the number of mahogany gliders and sugar gliders present, with canonical correlations of 0.781 and 0.721 respectively (Wilk's test. $\lambda = 0.187$, d.f. = 46, $P < 0.01$ and $\lambda = 0.480$, d.f. = 22, $P < 0.01$ respectively). The canonical coefficients showed a good separation between mahogany gliders and the sugar glider on the first axis, but little separation on the second axis (Table 4.3). The first axis was positively associated with mahogany gliders and negatively associated with sugar gliders. Using the first axis, the distribution of mahogany gliders was best explained by the abundance of *C. clarksoniana*, *Corymbia tessellaris*, *E. pellita*, *E. platyphylla*, *E. tereticornis*, *M.*

dealbata, an absence of other stems and a greatly reduced mid canopy cover, which is reflected in high grass height (Table 4.4). The abundance of the sugar glider was best correlated with *C. intermedia*, *A. mangium*, *A. flavescens*, a high number of food plant species, other stems and a dense mid canopy cover. Fifty-four percent of the variation in the number of animals caught at each trap location was explained by the two canonical variates (Miller's test. $F_{46, 1771} = 51.66$, $P < 0.01$).

When only the fragmented habitat at Porters Creek is considered, the first two canonical variates were again found to have high canonical coefficients (0.790 and 0.665 respectively). In contrast to the Mullers Creek site, the first canonical variate contained all significant correlations, with no further correlations being significant (significance of remaining axis using Wilk's test $\lambda = 0.209$, d.f. = 46, $P > 0.05$ for the first correlation and Wilk's test $\lambda = 0.557$, d.f. = 22, $P > 0.05$ for the second correlation). Again the canonical coefficients showed a good separation between the mahogany gliders and the sugar gliders on the first axis with a less distinct difference on the second axis (Table 4.3). Similar to the overall habitat, the first axis was negatively associated with mahogany gliders and positively associated with sugar gliders. Using the first axis, the distribution of the mahogany glider best correlated with *C. clarksoniana*, *E. pellita*, *E. tereticornis*, *M. viridiflora*, *A. crassicarpa*, *A. procera*, other stems and high grass height which reflects the poorly developed upper canopy cover (Table 4.4). The sugar glider was most highly correlated with *C. intermedia*, *A. mangium*, *A. flavescens*, *Acacia leptocarpa*, *X. johnsonii*, the number of food tree species, rainforest plants, and a highly developed upper storey. The dense understorey which the sugar glider was associated with in the continuous habitat was not well correlated with either the sugar glider or mahogany glider in the fragmented habitat. Fifty-four percent of the variation in the number of animals caught at each trap location was explained by the two canonical variates (Miller's test. $F_{46, 943} = 24.26$, $P < 0.01$).

Table 4.3. Standardised canonical coefficients for the mahogany glider and the sugar glider in the continuous habitat at Mullers Creek and the fragmented habitat at Porters Creek.

	Total Area		Continuous		Fragmented	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Mahogany Glider	-0.985	0.222	0.728	-0.707	-0.933	0.398
Sugar Glider	0.085	1.006	-0.574	-0.837	0.239	0.985

Table 4.4. Standardised canonical coefficients for the habitat variables in the continuous habitat at Mullers Creek and the fragmented habitat at Porters Creek. Non-food stems - the number of stems of non food species, not including rainforest stems. Rainforest stems - all rainforest non-food species stems.

	Total Area		Continuous		Fragmented	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Corymbia clarksoniana	-0.207	-0.109	0.249	-0.017	-0.385	-0.622
Corymbia intermedia	0.145	-0.366	-0.304	0.086	0.139	-0.544
Corymbia tessellaris	-0.098	0.053	0.169	-0.193	0.050	-0.200
Eucalyptus pellita	-0.320	-0.070	0.451	-0.169	-0.411	-0.242
Eucalyptus platyphylla	-0.298	0.228	0.364	-0.180	0.081	-0.226
Eucalyptus tereticornis	-0.073	-0.548	0.216	0.410	-0.274	-0.163
Lophostemon suaveolens	-0.148	0.231	0.064	-0.524	0.050	-0.148
Melaleuca dealbata	-0.223	0.023	0.239	-0.173	-0.125	0.483
Melaleuca leucodendra	-0.116	0.153	-0.002	-0.252	0.048	-0.034
Melaleuca viridiflora	-0.123	0.224	0.068	-0.039	-0.852	0.096
Acacia crassicarpa	0.046	-0.249	-0.094	0.176	-0.326	-0.100
Acacia flavescens	0.034	0.168	-0.149	-0.112	0.163	-0.032
Acacia leptocarpa	0.125	0.061	0.041	0.079	0.439	0.321
Acacia mangium	0.301	0.255	-0.494	-0.241	0.915	0.110
Albizia procera	-0.051	-0.230	0.089	0.280	-0.582	-0.714
Xanthorrhoea johnsonii	-0.036	0.157	0.043	-0.207	0.749	0.150
Total No. Food Species	0.439	-0.035	-0.262	0.534	0.427	0.208
Non-Food Stems	-0.023	0.368	-0.158	-0.342	-0.200	0.393
Rainforest Stems	0.200	-0.161	-0.074	0.274	0.202	0.092
Grass Cover	0.162	-0.547	-0.048	0.129	0.042	-0.076
Grass Height	-0.198	0.219	0.191	-0.272	-0.208	0.225
Mid Canopy Cover	0.398	-0.066	-0.525	-0.085	0.053	-0.010
Upper Canopy Cover	0.189	-0.214	0.121	0.704	0.693	0.358

4.4 Discussion

4.4.1 Habitat Use by the Mahogany Glider and Sugar Glider

Although there was significant overlap in the habitat utilised by the mahogany glider and the sugar glider, a preference for different habitat types was revealed by multivariate analysis. The fine scale distribution of the mahogany glider was associated with an open canopy, poorly developed understorey and the dominance of Myrtaceae species including *C. clarksoniana* and *E. platyphylla*. The preference for open habitat by the mahogany glider is similar to that of the closely related squirrel glider *Petaurus norfolcensis*, with records as early as 1846 showing them to prefer more open and grassy portions, rather than thick forest (Waterhouse 1846).

In contrast, the sugar glider favoured habitat with a more developed mid storey and dominated by species such as *C. intermedia*, *A. mangium* and *A. flavescens*. The preference of sugar gliders for habitat with a closed mid canopy has been observed by Davey (1984) who found them to spend most of their foraging time in the lower stratum, while the squirrel glider prefers to forage in higher strata. The sugar glider's preference for habitat containing acacias has been observed previously by Smith (1982a), Braithwaite *et al.* (1983), Davey (1984) and Suckling (1984) who have found them across a range of floristic communities containing *Acacia* trees.

The density of the mahogany glider in the fragmented habitat at Porters Creek is only two-thirds that in the continuous forest at Mullers Creek (0.16 *c.f.* 0.24ha^{-1}; See Chapter 3) and appears to be a result of the much greater proportion of closed habitat associated with species such as *A. flavescens* and *A. mangium*. This in turn favours the sugar glider whose density in the fragmented habitat was much greater than in the continuous habitat (0.48 *c.f.* 0.30ha^{-1}). Similarly, Suckling (1984) found the sugar glider to be highly successful in roadside strips and fragmented forest habitat although he found much higher densities (2.9-6.1ha^{-1}) than in this study.

4.4.2 Movements of Gliders in Open and Closed Habitats

The preference for open habitat by the mahogany glider and closed habitat by the sugar glider is also supported by theories related to their movement within their habitat and their gliding ability (Chapter 7). Although both gliders do make short glides, measured glides revealed the mahogany glider to launch and land significantly higher in trees, and to make significantly longer glides than the sugar glider, even though there was no significant difference in their gliding efficiency (Chapter 7, Table 7.1). From the perspective of locomotion, open habitat has greater air turbulence and therefore favours the larger body size of the mahogany glider, which allows them to launch higher and therefore make longer glides than smaller species such as the sugar glider. Their large body size however means they have a decreased ability to steer, which favours open habitat (Chapter 7). In contrast, a closed understorey has less air turbulence and favours the smaller body size of the sugar glider. The closed canopy also favours shorter glides and the ability to make tighter turns.

4.4.3 Sympatry in the Australian Petauridae

There is a high degree of overlap in the diet between the species of Petauridae, with all species occupying the exudivorous/insectivorous dietary niche, feeding on insects, insect exudates such as honeydew, and plant exudates such as nectar, pollen, manna and sap (Smith 1982a, 1984a; Craig 1985; Goldingay 1986, 1990; Menkhorst & Collier 1988; Summers 1988; Van Dyck 1993; Handasyde & Martin 1996; pers. obs.). Quin (1993) noted that with the exception of Leadbeater's possum *Gymnobelideus leadbeateri* and the sugar glider, the exudivorous/insectivorous possums differ markedly in body size, but are otherwise remarkably similar in diet and morphology.

As diet in the Petauridae varies little between species, differential body weight and habitat selection may be important mechanisms permitting these closely related species to co-exist where resources are limiting, with the degree of habitat selectivity (and overlap) related to the degree of specialisation of each species in the community (Brown & Wilson 1956; Hutchinson 1959; Schoener 1965, 1974a, 1974b; Quin 1993). Wilson (1975) noted the role of body size in competition and in promoting niche difference, with larger species being able to exclude smaller species and establishing a competitive gradient. Where species are sympatric, the dominant species is usually considered to exclude the subordinate species from optimal habitat through some form of territorial defence (Rosenzweig 1981; Dueser & Hallet 1980; Hallet *et al.* 1983; pers. obs). The subordinate species is usually assumed to possess lower fitness because of the occupancy of sub-optimal habitats (Quin 1993). However, if the subordinate species is more efficient at exploiting the lower quality patches (has higher foraging efficiency), its fitness may not necessarily be lower than that of the dominant species (Abramsky *et al.* 1991, 1992).

A comparison of the body length ratios of the Australian Petauridae shows no significant difference between broadly sympatric and allopatric species ($t_{13} = 2.16$; $P > 0.05$) (Table 4.5). A more detailed examination of the sympatry between Australian petaurids suggests habitat partitioning occurs on a local scale between species, and is discussed further below.

Table 4.5. Similarity ratios of the Australian Petauridae using body length. Measurements from Strahan 1995. Species which are broadly sympatric in at least part of their geographic range are shaded.

	Leadbeater's possum	Sugar glider	Squirrel glider	Mahogany glider	Striped Possum	Yellow-bellied glider
Leadbeater's possum	-	-	-	-	-	-
Sugar glider	1.06	-	-	-	-	-
Squirrel glider	1.31	1.24	-	-	-	-
Mahogany glider	1.56	1.47	1.19	-	-	-
Striped possum	1.64	1.54	1.25	1.05	-	-
Yellow-bellied glider	1.75	1.64	1.33	1.12	1.06	-

The sugar glider is broadly sympatric with Leadbeater's possum in the mountain ash forests of Victoria. As a result of their similar body size and niche they should face significant competition, and therefore should have difficulty coexisting unless there is a high degree of resource partitioning. Although both species have very similar diets, feeding on arthropods, *Acacia* sap, manna and honeydew, the sugar glider also feeds on eucalypt sap, nectar and pollen (Smith 1982a; Smith 1984a; Howard 1989; pers. obs). Despite a high degree of overlap in the height of foraging, Leadbeater's possum is most often observed at 10-15m above the ground, while the sugar glider is most often observed at 15-20m above the ground (Davey 1984; Lindenmayer 1997). Macfarlane (1988) found that sugar gliders occurred in the same areas as Leadbeater's possums, however they were less common in mountain ash forests than in more open mixed eucalypt forest where Leadbeater's possum was not recorded. The preference of sugar gliders for more open habitat than Leadbeater's possum is suggested to be a result of its ability to glide, whereas Leadbeater's possum requires extremely dense vegetation with interlocking branches and scrub in the middle and lower storey of the forest for locomotion (Smith 1978; Macfarlane 1988). These observations are supported by Lindenmayer *et al.* (1990a) who found that Leadbeater's possum and the sugar glider never co-occupied the same trees, whereas they did share trees with other species of mammals. Indeed Lindenmayer (1997) found differences in habitat, characteristics of trees selected for nesting, height of the entrance to the nest and method of locomotion (gliding vs non volant) and suggested that these differences may enable them to co-exist in mountain ash forests. In contrast to Macfarlane (1988), Smith *et al.* (1985) proposed that in the central highlands of Victoria, Leadbeater's possum excludes the sugar glider, as the sugar glider was only found in areas where Leadbeater's possum was absent. Unlike Leadbeater's possum which has an extremely narrow habitat niche, being restricted to the central highlands of Victoria, the sugar glider has a very broad habitat niche, being able to exist in rainforest, tall open forest and eucalypt woodland (Winter 1997) and to co-exist with the larger squirrel glider, mahogany glider and yellow-bellied glider (Russell 1981; Quin 1993; Winter 1997; pers. obs.).

When considering the larger petaurids, current records indicate the distribution of the squirrel glider in north Queensland surrounds that of the mahogany glider with no known overlap, with records showing them to occur within 25 km (Chapter 8). It is suggested that these two species would find it difficult to coexist unless character displacement occurred, and it appears that the squirrel glider replaces the mahogany glider outside its limited distribution (*sensu* Brown & Wilson 1956; Grant 1972). The distribution of the squirrel glider and the yellow-bellied glider do not appear to overlap, as Winter (1997) found the yellow-bellied glider to occupy an extremely narrow habitat niche in the wet sclerophyll forest on the western boundary of the wet tropics rainforest in north Queensland, with the squirrel glider having a slightly broader habitat niche, occupying drier areas immediately adjacent to the yellow-bellied glider.

The striped possum *Dactylopsila trivirgata*, yellow-bellied glider and mahogany glider are similar in body size, and although the striped possum lives in close proximately to both of these species over part of its range, it appears to overlap little them. The striped possum occurs in tropical rainforest, gallery forest and adjacent woodlands (Handasyde and Martin 1996), whereas the yellow-bellied glider occurs in wet sclerophyll forest, in North Queensland (Winter 1997), and the mahogany glider occurs in open woodland (Van Dyck 1993). Although all of these species consume insects (Handasyde and Martin 1996; Henry and Craig 1984; Smith and Russell 1982; Van Dyck 1993; Chapter 5), the striped possum appears to consume more insects and has specialised cranial morphology and an elongated fourth finger for feeding on wood-boring insects, so it appears to be able to consume insects unavailable to the other two species. As the striped possum lacks a patagium and therefore does not glide, it would further enable them to co-exist due to different movement, and therefore utilisation, patterns of their habitat.

The limits to similarity that allow co-existence appear to be quite conservative among the petaurids as even species with large differences in body size, and which appear to be sympatric, show habitat separation, as shown by the mahogany glider and the sugar glider, and between the yellow-bellied glider and squirrel glider in north Queensland. The habitat partitioning observed by Menkhorst *et al.* (1988) for the squirrel glider and the sugar glider appears to be far more severe than that observed between the mahogany glider and the sugar glider. Although the sugar glider and the squirrel glider are broadly sympatric, Menkhorst *et al.* (1988) found them to be syntopic at only one site and suggested that habitat partitioning was occurring. In contrast Traill and Lill (1997) observed considerable interspecific overlap in the use of hollows and nest-boxes by sugar gliders and squirrel gliders, with both preferring hollows and nest boxes with narrow entrances (<50mm diameter). The sugar glider preferred nest boxes and possibly natural tree hollows with entrances too narrow for the larger squirrel glider (Traill & Lill 1997). Trail and Lill (1997) found an increase and then a decrease in sugar glider numbers when nest boxes were added and then removed, suggesting that the larger squirrel gliders monopolise the best available hollows. They concluded that sugar glider numbers may have been limited by a lack of suitable hollows.

In contrast to the sugar glider which has a broad habitat niche, the mahogany glider, yellow-bellied glider, the non-gliding Leadbeater's possum and striped possum, and to a lesser degree the squirrel glider, are far more specialised and therefore restricted in the habitat niche they can occupy.

4.4.4 Management Implications of Habitat Preference of the Mahogany Glider

The preference for open habitat shown by the mahogany glider has several major implications for the management of this species' habitat, particularly along corridors provided for the mahogany glider to move between fragments of habitat. As corridors are generally only narrow strips of habitat, they have a high tendency to have a well developed understorey compared to areas in larger patches of forest. This is caused by edge effects, as exotic and some native plant species (such as *A. flavescens*) favour the disturbed habitat along the edge of fragments resulting in an increased mid-storey canopy cover (pers. obs.). As corridors are generally along creeklines which invariably have at least a partial riparian rainforest component, the corridors are further vulnerable to rainforest invasion and even further increases in the density of both the understorey and upperstorey. If rainforest covers the complete width of the corridor, then the use of this habitat as a corridor is likely to be drastically reduced or stopped. The use of fire to control the understorey and rainforest expansion along key corridors, and potentially some areas of closed forest within continuous habitat needs to be examined to successfully manage the habitat of the mahogany glider.

Chapter 5

Foraging Behaviour and Food Availability of the Mahogany Glider.

5.1 Introduction

Information on the diet of the mahogany glider *Petaurus gracilis*, has been limited primarily to a preliminary study by Van Dyck (1993) and casual observations (Lyon 1993; Eyre 1993). Although none of these observations have been extensive enough to examine seasonal trends in diet, or relate diet to food availability, they do suggest the importance of nectar and pollen in the diet of the mahogany glider. Observations of other members of the Petauridae, Burramyidae, Acrobatidae and Tarsipedidae also show the importance of nectar and pollen (Smith 1982b; Turner 1984a & 1984b; Richardson *et al.* 1986; Menkhorst & Collier 1988; Howard 1989; Goldingay 1990; Quin *et. al.* 1996a).

In order to understand exudate-feeding species, it is important not only to monitor the diet, but also the timing of the availability of food resources during the year. Biological events in plants, such as flowering, fruiting, shedding of bark and the production of new leaves occur at various, yet specific times during the year. Therefore, with the exception of sap, plant food items utilised by the mahogany glider such as nectar and pollen, and *Acacia* arils are generally available for only a limited time with different species being available during the year. Other non-plant food items are also available as a result of different plants' events, including lerps and honeydew which are generally associated with new leaf production, and insects which are generally more available when bark is cracking and shedding, as the bark provides cover for them (Kavanagh 1987).

The timing of phenology has also been suggested to affect life history processes such as the timing of reproduction, the time and energy that gliders invest in searching for food and the distance required to travel between food resources (Smith & Lee 1984; Kavanagh 1987; Goldingay 1990). Consequently this determines how large a home range is required to adequately fulfil an animals needs (McNab 1983; Goldingay & Kavanagh 1990; Goldingay 1992).

The aims of this chapter were to: (1) determine the diet of the mahogany glider and examine how it changes seasonally; and (2) examine the timing and success of flowering for species of trees which are utilised by the mahogany glider, and the potential availability of insects.

5.2 Methods

5.2.1 Feeding Observations

5.2.1.1 Observation Sessions

Mahogany gliders were observed over a 5-11 night period every two months from March 1995 until November 1996, except for March 1996 when as a result of poor weather (Tropical Cyclone 'Ethel'), predation by an amethystine python and the failure of the radio receiver aerial, only 3 full nights were completed. Field trips initially involved following individual animals from their emergence from their den until approximately 2:30-3:00am with one night per trip involving observation during the entire night. From September 1995, all animals were followed for the entire night to allow the full nights activities to be recorded and to increase the sample size. Gliders were followed, using a 30W spotlight and a red filter to reduce the light intensity. It was not possible to follow the animals continuously so they were relocated with the use of radio collars previously attached during trapping trips. Feeding activities were recorded every 30 seconds on a tape recorder.

5.2.1.2 Feeding Behaviours

Feeding behaviours were allocated to one of the following six categories.

Nectar and Pollen Feeding - Gliders were recorded as harvesting nectar and pollen when licking flowers.

Sap Feeding - Identified by the behaviour of incising and licking the trunk or smaller branches of acacias or *Albizia procera* (Mimosaceae).

Arthropod Feeding - This behaviour consisted of the mahogany glider catching and feeding insects. Insects were sometimes caught in the air, or squashed on the trunk with the use of a flattened manus. On other occasions gliders were observed to lunge into a group of leaves and retrieve an insect. Small parts of the insects such as wings were often discarded, allowing confirmation of insect-eating. Mahogany gliders were occasionally observed to incise dead branches or pull apart bark. Although they often appeared to closely inspect the bark of eucalypts and bloodwoods this behaviour was not included as feeding on arthropods.

Lerp and Honeydew Feeding - Identified by the behaviour of licking leaves of *Eucalyptus platyphylla* and *Corymbia clarksoniana.* Lerps are the coverings or testa excreted by the nymphs of psyllids, under which they shelter and feed and which enlarge as they develop. The adult then emerges from the lerp and lives a free existence (Hockings 1980; CSIRO 1991). Honeydew is the sugary waste excreted by psyllids on the leaves and other parts of the plant on which they feed. This causes the growth of a black fungus called sooty mould (Hockings 1980).

Fruit Feeding - Gliders were considered to be feeding on fruit when in a mistletoe plant. This behaviour was confirmed by the retrieval of partly eaten fruit (the fruit coat, often showing incisor marks, and seeds) discarded while the glider was observed in this plant.

Acacia Aril Feeding - Arils are short attachments that connect the ovule to the carpel wall during seed development in many acacias and are high in lipids (O'Dowd & Gill 1986). Gliders were considered to be feeding on the arils when pulling apart the seed pods of acacias. This activity was quite noisy and easily distinguished.

5.2.2 Forest Phenology

5.2.2.1 Tree Choice

To assess plant phenology, 250 trees were chosen by selecting 10 trees from 25 evenly spaced localities throughout the study grid (see Chapter 2). All of the trees chosen were from the family Myrtaceae as this family was already known to be the major source of nectar and pollen for the mahogany glider (pers. obs.; Van Dyck 1993) and other members of the genus *Petaurus* (Smith 1982b; Goldingay 1986, 1990; Howard 1989; Quin 1993; Sharpe & Goldingay 1998). The ten trees at each of the grid points were chosen by standing next to the grid point tree and choosing two trees, within a radius of 30m, from each of four quadrants surrounding that tree, with a further two trees selected at random from these four quadrants. The diversity and number of species chosen therefore reflected their natural abundance throughout the study area. This procedure was used to select trees for two reasons: (1) it reflects the patchy food sources (single trees and clumps of trees) the mahogany glider feeds on; and (2) it reflects the total food available to mahogany gliders. To facilitate finding each of these trees at a later stage, each tree was spray painted with a number from one to ten and given a coordinate (distance and angle) from the central grid point tree. The use of coordinates was particularly important for smooth barked species when they shed their bark (and hence their number). For each tree that was chosen for phenology assessment, the height was recorded with a clinometer, the diameter at breast height (DBH) of the trunk was recorded and the cross sectional area calculated. Plant phenology was recorded every two months during trapping sessions from December 1994 until December 1996.

5.2.2.2 Flowering Phenology

Plant phenology is the study of the timing of biological events in plants such as flowering, bark shedding and new leaf growth, and their relationship to seasonal climatic changes (Leith 1974). The number of plants with flowers present was expected to provide an indication of the quantity of nectar and pollen available (Kavanagh 1987). To assess the flowering phenology, the presence or absence of flowers was recorded for each tree selected for each of nine species of Myrtaceae trees (Table 5.1).

5.2.2.3 Flowering Index

As the 250 trees chosen for phenological study were selected according to their species relative abundance, a flowering index was calculated in order to measure the relative abundance of nectar during any given period. The flowering index was calculated by multiplying the proportion that each species formed of the 250 phenology trees, by the percentage of trees of that species flowering during any particular trapping session. The sum of all species' indices during any particular trapping period gave a total flowering index. This index only considers the number of plants in flower and does not include the number of flowers within each plant or between species, which can vary greatly.

5.2.2.4 Bark Shedding

Invertebrates have been found to be more abundant under loose bark than on foliage (Smith 1982b; Henry & Craig 1984). Therefore bark shedding has been suggested to indicate when arboreal bark-dwelling arthropods might be more or less available (Kavanagh 1987). Three species of smooth barked eucalypts occur in the Mullers Creek area (*Corymbia tessellaris*, *E. platyphylla* and *Eucalyptus tereticornis*). Bark shedding from these species may indicate periods when higher numbers of insects would be available (Kavanagh 1987). The bark of the three species of smooth barked trees was classified into one of four stages: (1) bark intact, (2) bark cracking, (3) bark peeling, and (4) some old bark hanging on.

5.3 Results

5.3.1 Feeding Behaviour

A total of 439.68 hours was spent observing mahogany gliders, of which 222.43 hours of feeding behaviour was observed. During the year the foraging behaviour (searching, finding and eating food) of the mahogany glider suggested that nectar and pollen were clearly the most important food items, comprising between 37.7 and 97.8% of the observed feeding time when available (Fig. 5.1). In November 1995, no nectar or pollen feeding was observed as the individuals followed did not appear to have access to any plants in flower. Of all the species of plants observed to be utilised by mahogany gliders the only rainforest species used was the cadagi *Corymbia torrelliana* which was used for nectar and pollen. Although a member of the Myrtaceae, this species is generally confined to rainforest. This proved to be an important species during November 1996 when not much else was in flower, and several mahogany gliders left normal foraging ranges to feed on it. Casual observations of a number of faecal samples (pers. obs.) showed that Myrtaceae pollen was abundant, and that approximately 80% of pollen grains of all genera consumed are digested, suggesting pollen was a major source of protein.

Sap from *A. procera* was consumed during all times of the year. A fawn-footed melomys *Melomys cervinipes* and a sugar glider *Petaurus breviceps* were also observed to feed on the sap of *A. procera.* Apart from the sap of *A. procera*, the only species of plant utilised for sap for any length of time was *Acacia mangium* which was observed to be used on only three occasions during the entire observational period (66 minutes in May, 92 minutes in September, and 13 minutes in November 1996).

During November to early January the arils from different species of *Acacia* were available and readily consumed. Fruit and nectar from mistletoes was also observed to be eaten on five occasions during the year. When mahogany gliders were feeding on mistletoe fruit, they appeared to eat only the sticky flesh and discard both the fruit coat and the seed. Insects were eaten during most of the year with a peak during the warmer months.

Species observed to be utilised were all Myrtaceae or Mimosaceae, although the casual examination of a number of faecal samples showed several to contain pollen of either *Grevillea* or *Hakea* flowers. As the only Proteaceae observed in the area were *Grevillea parallela* and *Grevillea pteridifolia* it is highly likely to be one or both of these species. In obtaining these different food types the mahogany glider relied on complex seasonal cycles of food availability with a high species diversity of plants, with each species having distinct periods of availability (Fig. 5.2).

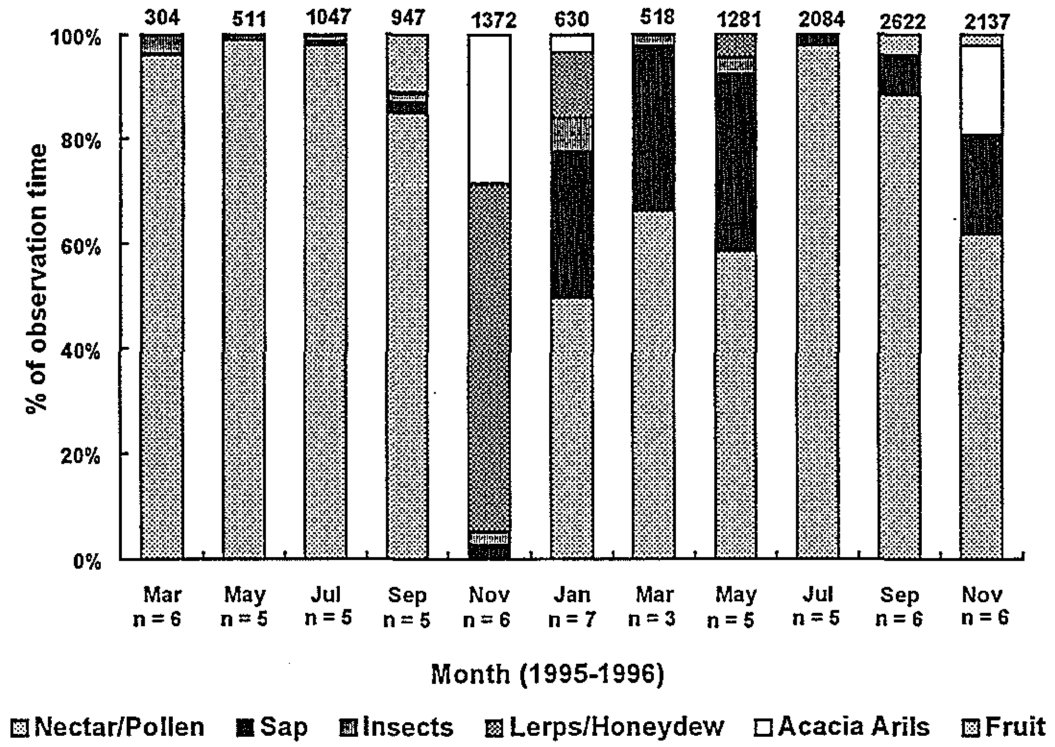


Figure 5.1. Monthly feeding observations of the mahogany glider during 1995 and 1996. Total time (minutes) animals were observed feeding during each month is above each column. n = number of individuals observed feeding.

5.3.2 Flowering Times, Intensity and Duration

Within the Mullers Creek area, flowering plants were available at all times of the year (with a few brief exceptions) (Fig. 5.3). The peak periods, taking into account number of trees available, were during April to October with the continuous succession of a large number of plants in flower. During the wet season, less nectar and pollen appears to be available as there were few *Corymbia intermedia* and *C. tessellaris* (which also had a high flowering failure rate) available (Table 5.1). It is during this period that other food items such as acacia arils become available, sap from *A. procera* was increasingly utilised, and other food such as lerps, honeydew and insects were abundant.

The proportion of individual trees flowering during both 1995 and 1996 was generally low for species that had large numbers of individuals (Table 5.1). With the exception of *C. tessellaris*, the two most abundant species of trees, *C. clarksoniana* and *E. platyphylla*, had the lowest flowering rates, whilst species such as *C. intermedia*, *Eucalyptus pellita*, *E. tereticornis* and *Melaleuca dealbata* and *M. viridiflora* had fewer individuals, but had a much higher flowering success for individual trees between years.

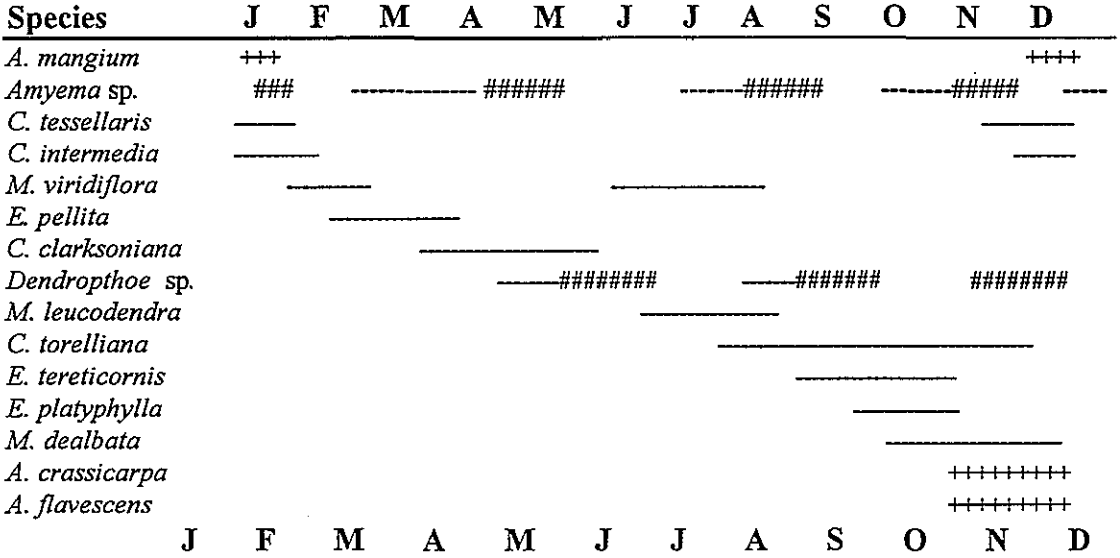
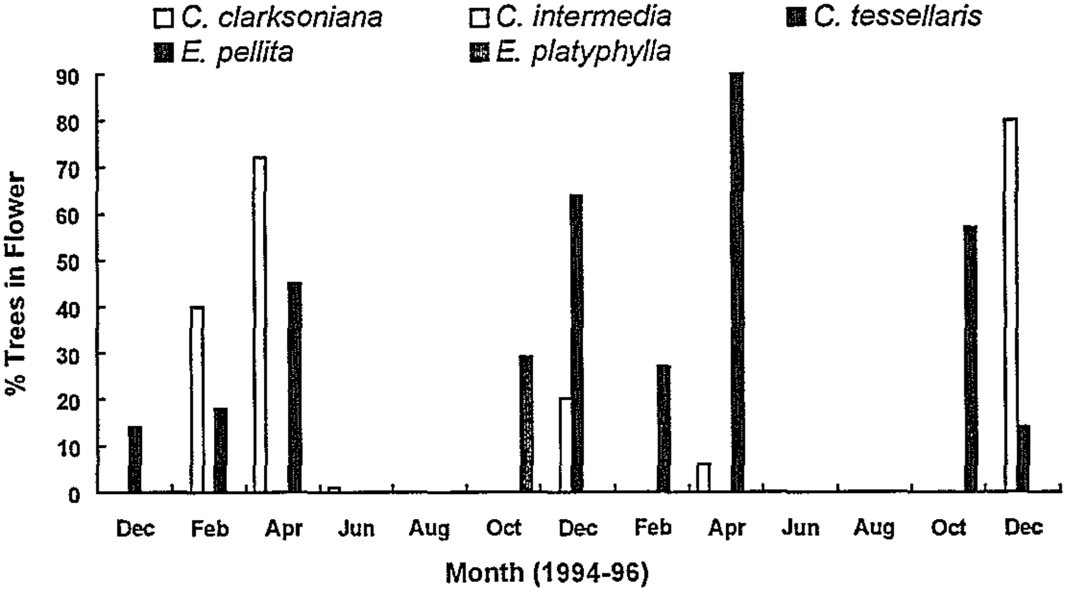


Figure 5.2. Timetable of flowering phenology of food trees utilised by the mahogany glider. - nectar and pollen availability (flowering); # timing of fruit production; + *Acacia* arils.

Table 5.1. Flowering success of marked trees at Mullers Creek from December 1994 to December 1996.

Species	Number	% Flowering During Study	% Flowering in both 1995 and 1996
Corymbia clarksoniana	79	73	6
Corymbia intermedia	5	100	80
Corymbia tessellaris	14	64	14
Eucalyptus pellita	11	91	45
Eucalyptus platyphylla	58	62	24
Eucalyptus tereticornis	19	95	84
Lophostemon suaveolens	31	87	52
Melaleuca dealbata	10	100	90
Melaleuca viridiflora	23	100	70
Total	250		



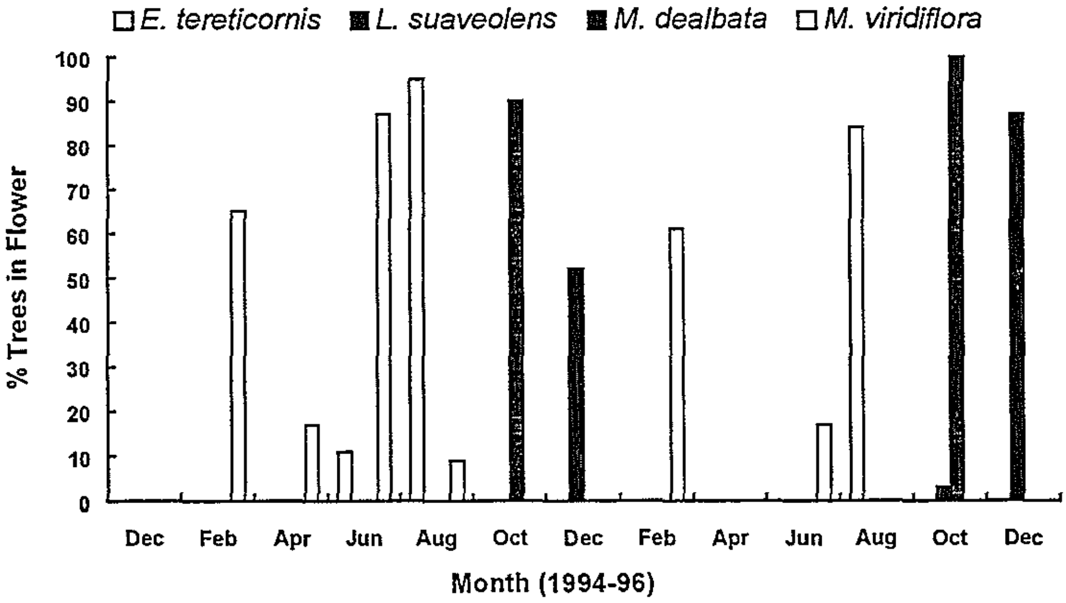


Figure 5.3. Flowering phenology of trees at Mullers Creek, based on the percentage of marked trees.

5.3.3 Flowering Index

The flowering index (Fig. 5.4) showed a peak in abundance of trees flowering during April in 1995 and October 1996, with the least food available from this source during December 1994 and June 1996. A comparison of the proportion of feeding time observed and flowering index (Fig. 5.5) showed a general trend of increased nectar use with increased nectar availability with a correlation of 0.128, although this was not significant ($F_{1,9} = 1.51$; $P = 0.25$). The lack of correlation can potentially be explained by the high utilisation mahogany gliders can make of only a few individual trees. Therefore the flowering index may be low, however the utilisation of the available nectar and pollen can still be very high on the few trees that are in flower. Additionally even though there may be several species of trees that were recorded in flower, some individuals may not have access to these trees within their home range (pers. obs).

5.3.4 Bark Shedding

Bark shedding in both *C. tessellaris* and *E. tereticornis* clearly peaked during the wet season, occurring from October to April (Fig. 5.6a & c). In contrast to the highly seasonal shedding of these species, *E. platyphylla* (Fig. 5.6b) was observed to shed bark continuously throughout the year, with a peak in shedding during April to October. The availability of shedding bark coincided with warmer weather and increased insect consumption.

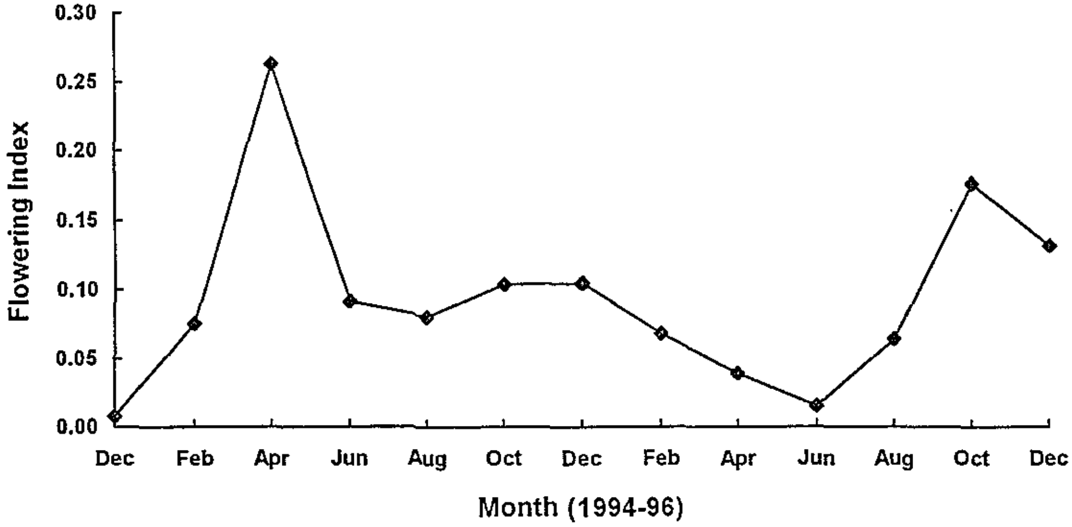


Figure 5.4. Flowering index of plants based on the proportion of each tree used in phenology and their flowering success.

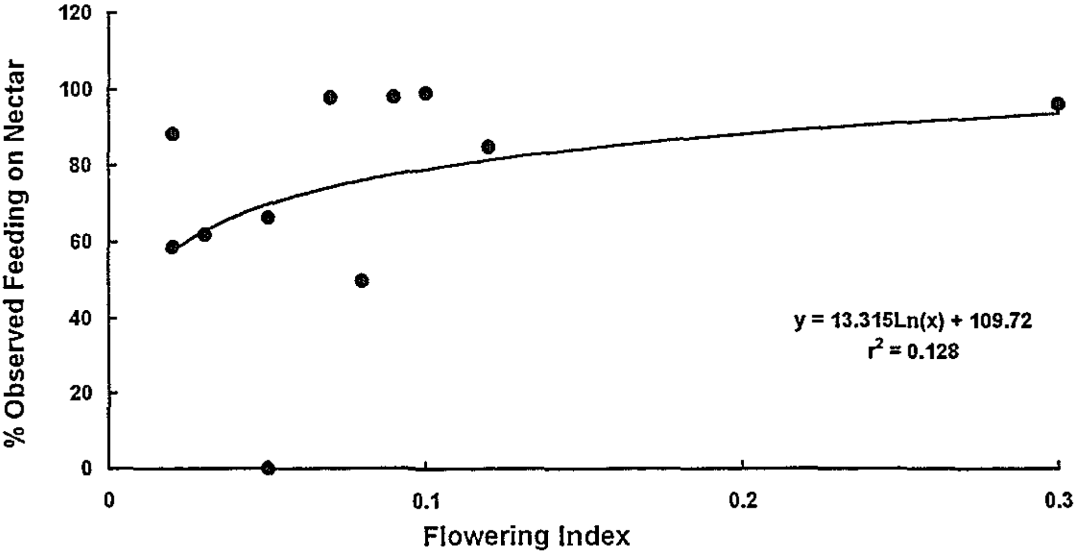


Figure 5.5. The relationship between flowering index (nectar availability) and the percentage of nectar feeding observed.

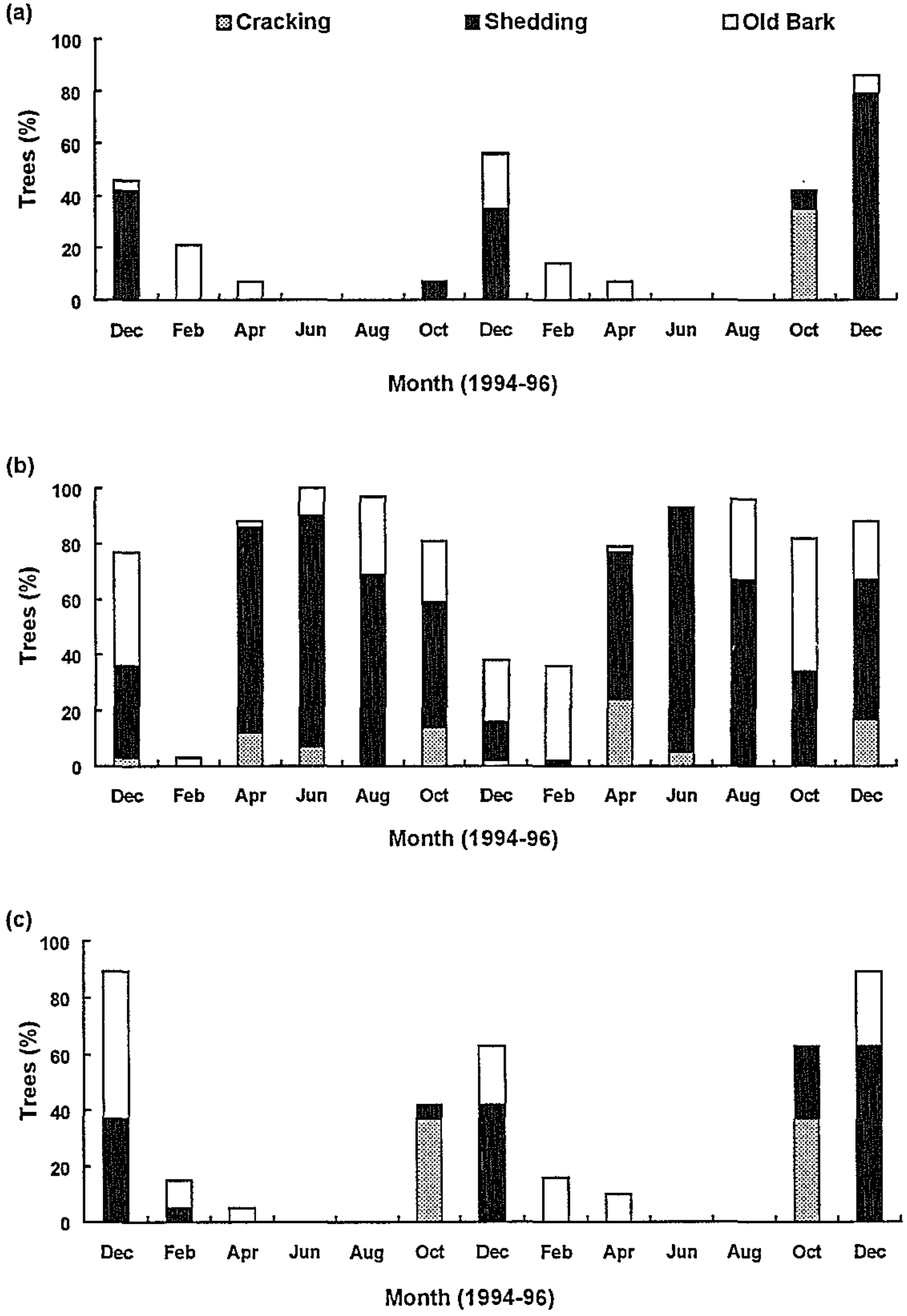


Figure 5.6. Bark-shedding patterns of (a) *C. tessellaris*, (b) *E. platyphylla* and (c) *E. tereticornis* at Mullers Creek between December 1994 and December 1996.

5.4 Discussion

5.4.1 The Importance of Nectar and Pollen

The mahogany glider relies on complex seasonal cycles of food availability, where each food type has its own cycle of food availability during the year. Of the food types consumed, nectar and pollen are clearly the most important when available. However when nectar was less available the importance of sap from *A. procera* increased.

In agreement with Smith and Russell (1982), it is suggested that, because of their larger size, species such as the mahogany glider and the yellow-bellied glider *Petaurus australis* must rely more on exudates and pollen compared to smaller exudivores such as the sugar glider. This may be because their larger body size does not increase their ability to harvest insects (as they do not move proportionally faster than smaller species such as the sugar glider) as they do not feed primarily on social insects.

The importance of nectar to the mahogany glider is supported by Lyon (1993) who found sightings were strongly correlated with flowering upper storey species. Although the diet of the mahogany glider is largely similar to that of other members of the Petauridae (Smith 1982b; Menkhorst & Collier 1988; Howard 1989; Goldingay 1990; Quin *et. al.* 1996a), the mahogany glider appears to be the only species for which nectar is available, and consumed, at almost all times of the year. Because of the large numbers of flowers visited by mahogany gliders while foraging (pers. obs.) they are likely to be significant pollinators, as has been found of other non-flying mammals (Turner 1982; Goldingay *et al.* 1987; Goldingay *et al.* 1991).

Although Van Dyck (1993) observed a mahogany glider to lick the flowers of an *Acacia crassicarpa* (which produce little or no nectar), the deliberate feeding of only pollen was never observed despite numerous opportunities, suggesting that nectar is the primary target of feeding behaviour in flowers. Nonetheless pollen is a major source of protein for the members of the Petauridae, Burramyidae, Acrobatidae and Tarsipedidae along with other food items such as insects and spiders (Table 5.2).

Table 5.2. Sources of Protein in the Petauridae, Burramyidae, Acrobatidae and Tarsipedidae.

Species	Protein Source	Ref.
Dactylopsila trivirgata	insects	1,2,3,4,5
Gymnobelideus leadbeateri	tree crickets, beetles, moths, spiders	6
Petaurus breviceps	pollen, moths, scarabaeid beetles.	7,8.
Petaurus australis	pollen, arthropods, tree crickets, beetles, caterpillars, spiders, moths.	9,10.
Petaurus gracilis	pollen, green ants, spiders, other invertebrates.	11,12
Petaurus norfolcensis	pollen, caterpillars, beetles, eggs, occasionally birds.	13,14
Burramys parvus	moths, worms, beetles, spiders, grasshoppers, fruits, flowers, seeds.	15,16.
Cercartetus lepidus	pollen, insects.	17
Cercartetus nanus	pollen, seeds, insects.	18,19
Acrobates pygmaeus	pollen, seeds.	20,21
Tarsipes rostratus	pollen only?	17,22,23

References: 1 Strahan 1995; 2 Rand 1937; 3 Fleay 1942; 4 Smith 1982a; 5 Handasyde & Martin 1996; 6 Smith 1984a; 7 Howard 1989; 8 Smith 1982b; 9 Henry & Craig 1984; 10 Smith & Russell 1982; 11 this study; 12 Van Dyck 1993; 13 Menkhorst & Collier 1988; 14 Winter 1966; 15 Mansergh & Broome 1994; 16 Mansergh *et al.* 1990; 17 Ward 1988; 18 Turner 1984a; 19 Arnould 1986; 20 Turner 1984b; 21 Huang *et al.* 1987; 22 Richardson *et al.* 1986; 23 Vose 1973.

Stanley (1971) showed that pollen is high in protein and contains a complete complement of essential amino acids. Therefore animals such as the petaurids can greatly benefit from the contents of pollen. Despite the outer coat, or exine, of pollen grains generally being considered highly resistant to degradation by digestive enzymes (Heslop-Harrison 1971; Stanley & Linskens 1974), high levels of digestion of pollen grains (50-100%) have been observed in the sugar glider (Goldingay *et. al.* 1987), yellow-bellied glider (Goldingay 1990; Quin *et al.* 1996a), eastern pygmy possum *Cercartetus nanus* and the honey possum *Tarsipes rostratus* (Turner 1984a; Richardson *et. al.* 1986) and the feathertail glider *Acrobates pygmaeus* (Turner 1984b). Turner (1984a) suggested that pollen from very few *Banksia* inflorescences may satisfy the minimum daily protein requirements of the eastern pygmy possum and the honey possum. Similarly the importance of pollen as a major source of protein appears to be high for the mahogany glider, as casual observations of a number of faecal samples suggested that approximately 80% of pollen grains were digested. It appears the mahogany glider can sustain itself on a diet of almost exclusively nectar and pollen when this is abundant. This is supported by Smith and Green (1987) who showed the sugar glider to be able to sustain itself on only honey and pollen.

The fecundity of the mahogany glider (Chapter 3) appears to be intermediate between the smaller sugar and squirrel glider *Petaurus norfolcensis* (Quin 1995) and the yellow-bellied glider, which produces only one young at a time (Craig 1986). It was proposed by Smith and Russell (1982) that the restricted availability of protein for the yellow-bellied glider may help to explain its low fecundity compared to the other smaller petaurids. Therefore the mahogany glider's fecundity may reflect its intermediate body size and therefore protein requirements which are greater than the smaller sugar and squirrel glider, but less than the heavier yellow-bellied glider.

5.4.2 Consumption of Fruit

Within the Mullers Creek area and throughout the distribution of the mahogany glider, a number of tree species produce fruit which could potentially be utilised (Table 5.3). *Nauclea orientalis* produces a large number of large fruit while several species of figs, including *Ficus congesta*, *Ficus hispida*, *Ficus opposita*, *Ficus racemosa* and *Ficus variegata* produce fruit year round. Other plants that could potentially provide fruit are in the genera *Amyema*, *Carallia*, *Diploglottis*, *Elaeocarpus*, *Euroschinus*, *Melicope*, *Planchonia*, *Randia*, *Syzygium* and *Terminalia*.

Despite a number of species of trees providing fruit within the home ranges of the mahogany glider, the only fruit consumed was that of several species of mistletoe (families Loranthaceae and Viscaceae). The consumption of mistletoe fruit has also been observed in squirrel gliders (Sharpe & Goldingay 1998), and the yellow-bellied glider may also eat fruit, as mistletoe pollen has been found in their diet (Seebeck pers. comm.; Quin *et al.* 1996a). A list of all mistletoe species likely to occur within the distribution of the mahogany glider can be found in Table 5.5 (See also Appendix 1). Although not observed to feed on any other types of fruit, the mahogany glider is capable of digesting a wide variety of fruit, as several hand-raised mahogany gliders readily ate a number of types of fruit and vegetables. The sugar glider and the squirrel glider also feed on a variety of fruit and vegetables in captivity (pers. obs.). In New Guinea, the sugar glider frequently occurs in closed rainforest where it has been found to eat the fruits of plants such as figs *Ficus* spp. Similarly the northern glider *Petaurus abidi* is restricted to closed rainforest on Mount Somoro in New Guinea where it eats the fruit of *Syzigium* spp. and *Ficus* spp (Hide *et al.* 1984; Flannery 1995b).

5.4.3 Timing of Reproduction

With births occurring from April to October in the mahogany glider at Mullers and Porters Creeks (Chapter 3), and with a time until weaning of approximately 4-5 months (Chapter 3; Smith & Lee 1984), juveniles would be expected to be weaned from August until the following February. It has been suggested that when food is seasonally abundant, births are generally timed so that the period of late lactation or weaning corresponds with the period of maximum food abundance (Tyndale-Biscoe 1979). Smith (1982b) also proposed that if protein is only seasonally abundant, it may influence the timing of reproduction for petaurid marsupials. Smith (1982b) suggested that as protein requirements of the mother and young are likely to be greatest during late lactation, the timing of reproduction is likely to make use of the most abundant period of insect availability for late lactation. Similarly, Goldingay & Kavanagh (1990) proposed that the yellow-bellied glider breeding pattern ensures that young are able to make use of the high numbers of insects during the wet season and allow the young to be foraging independently before the ensuing dry season. Therefore the mahogany glider may also time its reproduction (with weaning occurring during the end on the dry season and into the wet season) so that late lactation coincides with the peak availability of insects as suggested by the bark shedding.

At Mullers and Porters Creeks the mahogany glider relies on complex seasonal cycles of food availability, where each species of tree has a distinct period of food production. They therefore require a high species diversity to provide food during the year. From August to October, nectar and pollen are available from flowering *E. tereticornis*, *E. platyphylla* and *M. dealbata*. During November and December nectar from *E. tessellaris* is available as well as acacia arils which are high in lipids from *Acacia crassicarpa*, *Acacia flavescens* and *A. mangium* (O'Dowd & Gill 1986). Lerps and honeydew on the leaves of *E. platyphylla* and *C. clarksoniana* appear to be particularly abundant at this time based of feeding observations. During end of the dry season and in the wet season the number of insects, and therefore protein, (although not quantified) increases greatly with cicadas and various other insects becoming abundant. During January and February nectar from *M. viridiflora*, *E. pellita* and *C. clarksoniana* become available. Sap from *A. procera* is available all year and is often utilised during the wet season. Despite the very limited distribution of the mahogany glider there is variation in the abundance of different species, and therefore food, throughout its' distribution. Therefore there may be some degree of local variation in birth and weaning times in different areas to coincide with peak food availability. This may partly explain the variation in reproduction observed by Van Dyck (1993) at Barrett's Lagoon (where he observed a pouch young present in February) which is near the northern limit of the distribution of the mahogany glider.

In addition to food availability, the timing of weaning may also be influenced by the wet season that occurs in January and February. Heavy rain significantly reduces activity (pers. obs.) so that individuals would find it more difficult to obtain food especially if in late lactation when energy demands are likely to be at their highest. The limited foraging allowed would also be compounded by a dilution of nectar and sap, further reducing food availability. Therefore it would be advantageous to be weaned before the onset of the wet season. It is presently not known if young born later in the breeding season (September and October) have a lower chance of survival because of being weaned during the following wet season.

5.4.4 Competitors

The mahogany glider has several nocturnal competitors that also consume nectar. Feathertail gliders were frequently observed feeding in the same trees as mahogany gliders, while large quantities of nectar and pollen are also consumed by the sugar glider, black flying-fox *Pteropus alecto*, spectacled flying-fox *Pteropus conspicillatus*, and little red flying-fox *Pteropus scapulatus*.

Mahogany gliders are clearly dominant over the sugar glider and feathertail gliders, as although I saw mahogany gliders and these two species co-occurring in the same tree on several occasions, on each of these the smaller species left the tree. On one occasion a sugar glider was chased out of the tree by a mahogany glider. Mahogany gliders are however subordinate to the different species of flying fox that occur in the area. Fruit bats in particular, compete in four ways: (1) they reduce nectar availability by feeding on nectar and pollen; (2) they waste large numbers of flowers by knocking down branches full of flowers or buds; (3) they crash land on or near gliders disrupting them from feeding, or knocking them out of the tree; and (4) they physically chase and vocalise towards mahogany gliders, which rarely retaliate. Similar observations of antagonism between fruit bats and yellow-bellied gliders, sugar gliders, and greater gliders have been made by Russell (1981) and Boorsboom (1982). In contrast Goldingay (1990) observed that yellow-bellied gliders were not aggressively excluded from flowering trees by fruit bats.

5.4.5 Variation in Flowering Times

Overall, the timing of flowering was quite consistent during 1995 and 1996 with only small variations observed. The most notable difference in flowering times during the study period was with *C. clarksoniana* which showed a delayed flowering time in 1996 with a peak in April/May as opposed to a peak in March/April in 1995.

Casual observations throughout the distribution of the mahogany glider showed the number of trees flowering and flowering times to be similar to those in the Mullers Creek area. In many areas the species composition of trees is different to that at Mullers Creek, with a number of species that are present at Mullers Creek not found in other areas within the mahogany glider distribution. In cases such as these they are often replaced by species not at Mullers Creek such as *Corymbia dallachiana*, *Eucalyptus acmenoides*, *Eucalyptus drepanophylla*, *Melaleuca nervosa* and *Melaleuca quinquenervia*. In some cases tree species such as *Melaleuca leucadendra*, *C. intermedia* and *C. tessellaris* are more common in other areas than in the Mullers Creek and Porters Creek area.

In addition to direct observations, the plant collection at James Cook University, Townsville, texts and over 1100 records from the Queensland Herbarium (Herbrecs) were used to determine variation in flowering and fruiting times within the distribution of the mahogany glider (Table 5.3). Wherever possible, only records from within the region from Townsville to Cairns were used, because of potential regional variation in flowering and fruiting. Only fruits of plant species that were considered potential food items are included. This provides important information in understanding what other species may be utilised by the mahogany glider and when they become available.

Table 5.3. List of all known and potential food trees within the range of the mahogany glider and their flowering and fruiting times. N = nectar and pollen, P = pollen only, F = fruit, S = sap, A = acacia arils, H = honeydew and lerps. * = known to eat that food type. Each species has been classed as occurring in either woodland (W) or riparian (R) to distinguish species that are more likely to be found along creek lines. When a species is found in both habitat types, the major habitat type where the species occurs is put first.

Species	Family	Flowering/Fruiting Time	Habitat	Ref.
Euroschinus falcata (N)(F)	Anacardiaceae	Sep.-Jan. (flowers) Nov.-Feb. (fruit)	R,W	1,2,3,4 5
Scheffera actinophylla (N)	Ariliaceae	Nov.-Mar. (flowers)	R	4,6
Deplanchea tetraphylla (N)*	Bignoniaceae	Aug.-Nov. (flowers)	R	1,4,7,8.
Canarium australianum (N)	Burseraceae	Jan.-Mar. (flowers)	R,W	9
Terminalia muelleri (N)(F)	Combretaceae	Nov.-Apr. (flowers) Jan.-Jun (fruit)	R	4,9. 4,5.
Terminalia sericocarpa (N)(F)	Combretaceae	Nov.-Jan. (flowers) Apr.-Aug. (fruit) Nov.-May. (fruit)	R	1. 9. 5.
Dillenia alata (N)(F)	Dilleniaceae	Jul.-Dec. (flowers) Sep.-Feb. (fruit)	R	1,4,6,7. 4,5.
Elaeocarpus angustifolius (N)(F)	Elaeocarpaceae	May. (flowers) Any month (fruit)	R	1. 5.
Erythrina vespertilio (N)	Fabaceae	Jul.-Oct. (flowers)	R,W	1,4,7.
Planchonia careya (N)(F)	Lecythidaceae	Oct.-Nov. (flowers) Dec.-Jan. (fruit)	R,W	1,4,6,7. 5.
Amyema sanguineum (N)(F)	Loranthaceae	Feb.-Mar (flowers) Apr. (fruit). Jul. (flowers)(Aug. fruits). Sep.-Oct. (flowers) (Nov. fruit) Dec. (flowers) Jan (fruit).	W	2,6.
Dendrophthoe falcata? (N)*(F)*	Loranthaceae	Apr.-May (flowers) Aug.-Sep. (fruits) Sep.-Oct. (flowers) Nov. (fruits)	W	6.
Dendrophthoe glabrescens (N)(F)	Loranthaceae	Apr.-Jun. (flowers) Jun.-Jul. (fruit) Aug.-Sep(flowers) Oct.(fruit)	W	4
Dendrophthoe homoplastica (N)(F)	Loranthaceae	Apr. (flowers) May-Jun. (fruit) Nov.-Jan. (flowers) Feb.-Mar. (fruit)	W	4
Dendrophthoe vitellina (N)(F)	Loranthaceae	Mar.-Apr. (flowers) Apr.-May (fruit) Jun.-Jul.(flowers) Aug.-Sep. (fruit)	W	4
Acacia aulacocarpa (P)(A)(S)	Mimosaceae	Dec.-Aug. (flowers) Jun.-Dec. (arils)	W	4,10. 4,9.
Acacia crassicarpa (P)*(A)*(S)*	Mimosaceae	May-Jun. (flowers) Apr.-Jul. (flowers) Oct.-Dec. (arils)	W	4,6,8. 1. 1,6,8.
Acacia flavescens (P)(A)*(S)	Mimosaceae	Mar.-Jun. (flowers) Oct.-Nov. (arils)	W	1,4,6. 1,6.
Acacia holosericea (P)(A)(S)	Mimosaceae	Apr.-Aug. (flowers) May.-Oct. (arils)	W,R	4,11. 4,11.
Acacia leptocarpa (P)(A)(S)	Mimosaceae	May-Aug. (flowers) Oct.-Nov. (arils)	W	1,6. 1,6.
Acacia mangium (P)(A)*(S)*	Mimosaceae	Apr.-May (flowers) Oct.-Jan. (arils)	W	4,6. 1,4,6.
Albizia procera (S)*	Mimosaceae	All year (sap) - old trees.	W,R	6.
Ficus congesta (F)	Moraceae	All year.	R	5.
Ficus hispida (F)	Moraceae	All year	R	4,5.
Ficus opposita (F)	Moraceae	All year.	R,W	1,2,4,6.
Ficus racemosa (F)	Moraceae	All year	R	1,5,7.
Ficus variegata (F)	Moraceae	All year.	R	2,3,5.
Callistemon viminalis (N)	Myrtaceae	Jun.-Dec. (flowers)	R	1,4.
Corymbia clarksoniana (N)*(H)*(S)* = *E. clarksoniana* (part)	Myrtaceae	Mar.-May (flowers)	W	1,4,6,8 12,13,.
Corymbia dallachiana (N)(H)(S) = *Eucalyptus tessellaris var. dallachyana* = *E. papuana* (part)	Myrtaceae	Nov.-Apr. (flowers)	W	1,4,12.

Table 5.3 Continued

Corymbia intermedia (N)*(H)*(S)*	Myrtaceae	Nov.-Apr. (flowers)	W,R	4,6,8,12,
= *E. intermedia*				13,14
Corymbia tessellaris (N)*(H)(S)	Myrtaceae	Nov.-Jan. (flowers)	W,R	1,6,8,12,13
Corymbia torelliana (N)*(H)(S)	Myrtaceae	Aug.-Nov. (flowers)	R	6,12,13
Eucalyptus acmenoides (N)(H)	Myrtaceae	Oct.-Feb. (flowers)	W	1,3,4,6,
				13,14.
Eucalyptus cloeziana (N)(H)(S)	Myrtaceae	Jan.-May (flowers)	W	4,6.
Eucalyptus drepanophylla (N)(H)(S)	Myrtaceae	Nov.-Jun. (flowers)	W	4,6.
= *E. creba*		Jul.-Dec. (flowers)		1,14.
		May-Aug. (flowers)		13.
Eucalyptus pellita (N)*(H)*(S)*	Myrtaceae	Jan.-Mar. (flowers)	R	6,8,13.
Eucalyptus platyphylla (N)*(H)*(S)	Myrtaceae	Sep.-Oct. (flowers)	W	1,6,13.
Eucalyptus tereticornis (N)*(H)(S)	Myrtaceae	Jun.-Sep. (flowers)	W,R	6,8.
Lophostemon grandiflora (N)	Myrtaceae	Oct.-Dec. (flowers)	W	1,14.
Lophostemon suaveolens (N)*	Myrtaceae	Sep.-Dec. (flowers)	W	6,8,14.
		Oct.-Mar.(flowers)		1.
Melaleuca dealbata (N)*	Myrtaceae	Sep.-Nov. (flowers)	W,R	1,4,6,8.
Melaleuca leucadendra (N)*	Myrtaceae	Jun.-Jul. (flowers)	R	1,6.
		May-Aug.(flowers)		5,15.
Melaleuca nervosa (N)	Myrtaceae	May-Sep. (flowers)	W	1,2,4,15.
Melaleuca quinquenervia (N)	Myrtaceae	May-Jul. (flowers)	W	1,4.
		Jun.-Aug. (flowers)		15.
Melaleuca viridiflora (N)*	Myrtaceae	Jan.-Feb, May-Jul. (flowers)	W	4,6,15.
Syzygium australe (N)(F)	Myrtaceae	Oct.-Dec. (flowers)	R	1,4.
		Nov.-Feb. (fruit)		4,5.
Syzygium forte (N)(F)	Myrtaceae	Oct.-Jan. (flowers)	R	4,6,9.
		Nov.-Feb. (fruit)		4,5.
Syzygium tierneyanum (N)(F)	Myrtaceae	Aug.-Jan. (flowers)	R	1,4.
		Jan.-Feb. (fruit)		4,5.
Tristaniopsis exiliflora (N)	Myrtaceae	Aug.-Mar. (flowers)	R	1,4.
Xanthostemon chrysanthus (N)(F)	Myrtaceae	Apr.-Jun. (flowers)	R	1,2,4,6
		Jul.-Nov. (fruit)		4.
Bursaria incana (N)	Pittosporaceae	Jan.-Jul. (flowers)	R	1,3,4.
Banksia aquilonia (N)*	Proteaceae	Aug.-Mar. (flowers)	W	1,4,7,16
Banksia plagiocarpa (N)	Proteaceae	Jun-Aug. (flowers)	W	1,3,4.
Grevillea parallela (N)*	Proteaceae	Jun.-Oct. (flowers)	W	1,4,6,7.
Grevillea pteridifolia (N)*	Proteaceae	May.-Oct. (flowers)	W	1,4,6,7.
Xylomelum scottianum (N)	Proteaceae	Dec.-Jun. (flowers)	W	4
Carallia brachiata (N)(F)	Rhizophoraceae	May.-Sep. (flowers)	R	1,3,4.
		Nov. (fruit)		2.
Nauclea orientalis (N)(F)	Rubiaceae	Oct.-Dec. (flowers)	R	4,7.
		Feb.-May (fruit)		5,6.
Randia fitzalanii (N)(F)	Rubiaceae	Sep.-Dec. (flowers)	R	1,2,4.
		Mar.-Oct. (fruit)		4,5,7.
Timonius timon (N)	Rubiaceae	Jul.-Nov. (flowers)	R	2,4.
Melicope elleryana (N)*(F)	Rutaceae	Oct.-Mar. (flowers)	R	4,8.
		Apr.-Jul. (fruit)		4,5.
Diploglottis diphyllostegia (N)	Sapindaceae	Jun.-Dec. (flowers)	R	4,9.
Xanthorrhoea johnsonii (N)*(S)*	Xanthorrhoeaceae	Apr.-Jun. (sap)	W	6,7,8.
		Jun.-Aug. (nectar).		

1 James Cook University, Townsville plant records; 2 Williams 1984; 3 Williams 1987; 4 Queensland Herbarium records; 5 Cooper & Cooper 1995; 6 Pers. Obs.; 7 Williams 1979; 8 Van Dyck 1993; 9 Jeanette Kemp pers. comm; 10 Anderson 1993; 11 Brock 1993; 12 Hill & Johnson 1995; 13 Brooker & Kleinig 1994; 14 Blake & Roff 1988; 15 Tweddell 1982; 16 Dettmann *et al.* 1995.

5.4.6 Primary Plant Food Types Utilised, or Predicted to be Utilised by the Mahogany Glider

The mahogany glider is somewhat opportunistic in its diet, feeding on a wide variety of plant species (Table 5.3 and Appendix 2). Almost all of the dominant food species utilised by the mahogany glider are in the family Myrtaceae, particularly from the genera *Corymbia*, *Eucalyptus* and *Melaleuca*, which provide many flowers with abundant nectar and pollen. The second most utilised family of plants was the Mimosaceae, in particular *Acacia crassicarpa*, *Acacia flavescens* and *Acacia mangium* that produce arils from October to December. A species in a second genus of Mimosaceae, *Albizia procera*, has proven to be a highly significant species, being utilised exclusively for sap particularly when nectar is not readily available.

Mahogany gliders were not observed to feed on sap or nectar from grass tree *Xanthorrhoea johnsonii* spikes, even though this has been observed by Van Dyck (1993) previously. Footprints and incision marks were often observed on the green spikes during this study, suggesting that both sap and nectar were utilised, although not seen during this study. The failure to observe gliders feeding on grass trees may have been due to a combination of the timing of field trips with their flowering, access to these species by the animals being followed and alternative food sources available. It appears the sap from the flower spikes is only available early in their development before they begin flowering; at this stage they still have a white powder on the surface which often shows the footprints of gliders (pers obs; Van Dyck 1993). Once the spikes begin to flower they become much more woody as a result of a decrease in protein, fat, phosphate and an increase in fibre (Hall 1956).

Although not yet confirmed, a number of plant species are predicted to be primary food sources where they are present. They are all Myrtaceae and include *Corymbia dallachiana*, *Eucalyptus acmenoides*, *Eucalyptus drepanophylla*, *Melaleuca quinquenervia* and *Melaleuca nervosa*. Interestingly, the food sources utilised by other animals may help to provide an indication of which food types are likely to be eaten by the mahogany glider. For example, species of trees utilised by fruit bats for nectar and potentially fruit can be considered as analogous in the diet of the mahogany glider. In addition food sources utilised by sap feeding insects such as cicadas and ants provide a good indication of food sources utilised by the mahogany glider. For example sap feeding insects were used to predict the use of sap in *A. procera* and *A. mangium* before they were later confirmed.

5.4.7 Secondary Plant Food Types utilised, or Predicted to be Utilised by the Mahogany Glider

There are a large number of plant food types that could potentially be utilised by the mahogany glider, several of which have been confirmed (Table 5.3 and Appendix 3). These plant foods are classified as secondary food types because they are either not as common as the primary food sources, produce fewer flowers, have little nectar, or are food types that are not often utilised such as fruit.

Several species of Myrtaceae, all *Syzygium*, may be a secondary food source because of the small number of plants present. Although pollen from *A. crassicarpa* has been observed to be utilised by the mahogany glider (Van Dyck 1993), pollen from acacias is considered a secondary food source. Despite numerous observations of the mahogany glider in this and other species of acacias during flowering, pollen was never observed to be eaten during any nightly observations in this study.

Although the nectar from species such as *Deplanchea tetraphylla* is known to be utilised by the mahogany glider (Van Dyck 1993), this species has a low number of flowers compared to the Myrtaceae. This species is perhaps most likely to be utilised when there is little else flowering. Some species such as *Banksia aquilonia* and particularly *Banksia plagiocarpa* are generally not likely to be widely used because they occur at higher elevations. However, when they do occur in areas which gliders inhabit, they are likely to be a significant food source due to the large amount of nectar they provide, and the long flowering period.

5.4.8 Distribution of Food Trees and the Potential Occurrence of Mahogany Gliders at Higher Altitudes

At present all records of the mahogany glider occur below approximately 500m elevation (with 97% of observations below 200m) in open woodland forests that are dominated by eucalypts, bloodwoods, acacias, melaleucas and swamp mahoganys *Lophostemon suaveolens*. The altitude at which the mahogany glider is present is clearly not uniform, with many areas, particularly on the eastern slopes, containing very low tree species diversity and probably as a result apparently containing few if any mahogany gliders, even at altitudes less than 100m. In some lowland areas there are many sites containing high densities of almost exclusively *X. johnsonii* and *M. viridiflora* (although they can occur independently at usually lower densities) in boggy soil in a ditypic assemblage, which do not appear to support mahogany gliders.

Along the creek lines and gullies on the sides of hills there is often a higher diversity of species of trees which provide food particularly when little else is flowering (Table 5.3). These areas include species that are also located in the open woodland, but are more common in riparian vegetation along creeks and include *C. tessellaris, E. tereticornis* and *M. dealbata.* Other species such as *C. intermedia, Corymbia torelliana, E. pellita, M. leucadendra* and *Syzygium* spp. are found almost exclusively in wetter areas such as in creek lines and gullies. Therefore areas where woodland forest is dominated by only several species of eucalypts or bloodwoods, the presence of creeks and gullies (and the associated higher plant diversity) appears critical in allowing long term persistence of some mahogany glider populations. Despite the need for creeklines and the higher species diversity associated with them, they do not appear be areas which the mahogany glider frequents, because of their high canopy cover (as discussed in Chapter 4) and appear to be used only when not much else is available.

At present, the utilisation of areas of high elevation by the mahogany glider appears to be relatively slight (Van Dyck 1993; pers. obs.). Although a number of eucalypts inhabit higher areas, there are several species of plants that are restricted to higher altitudes and which could be potentially utilised by the mahogany glider in some areas. These include *Eucalyptus cloeziana* which is restricted to the foothills. Several species of banksia are also present up the foothills including *B. aquilonia* and *B. plagiocarpa* which are generally found at quite high elevations.

Chapter 6

Home-Range and Den Use of the Mahogany Glider.

6.1 Introduction

The mahogany glider *Petaurus gracilis* has a varied diet that consists primarily of nectar, pollen, insects, acacia arils, lerps, honeydew, and sap from albizia *Albizia procera*, bloodwoods and grasstrees (Van Dyck 1993; Chapter 5). These dietary items have seasonal cycles, which change during the year in availability, abundance and location throughout the mahogany gliders foraging range. In order to fulfil their dietary requirements and reproduce, individuals must maintain an area that will provide adequate food and shelter throughout the year. The size of a species' home-range is suggested to be inversely proportional to density of animals and resource renewal rate (Ford 1983), with the optimal foraging area needing to be just large enough to yield an adequate food supply, as unnecessarily extensive movements might increase the risk of predation and waste energy (Schoener 1971).

The definition of a home-range area as proposed by Burt (1943) suffers from the lack of a temporal component, which is critical for species that have a patchily distributed food source (Harris *et al.* 1990). Therefore it is important to collect information on the annual use, rather than short term use, of habitat by individual animals. In previous studies of home-range, little attention has been given to distances travelled during nightly feeding, social behaviour, or strategies to facilitate territorial defence, such as the number of nests or dens. In addition, knowledge of the distance individuals move during nightly feeding is critical in understanding their ability to move between patches of habitat for threatened species such as the mahogany glider which has highly fragmented habitat. This information can assist land managers to make informed decisions regarding areas that are required to be set aside as reserves. It can also help to provide an understanding of the role that corridors might play in linking isolated populations that presently occur throughout the distribution of the mahogany glider.

The four objectives of this chapter were to: (1) determine the area of habitat required to supply adequate food and shelter throughout the year with respect to different vegetation types; (2) determine the distance individuals move each night in maintaining their home-range and accessing food; (3) determine the number and location of dens used by the mahogany glider; and (4) interpret the social system.

6.2 Methods

6.2.1 Trapping Technique

Trapping data were obtained from the long-term trapping study in the continuous area from February 1995 every two months until December 1996, and from transects in the buffer strips from December 1995 until December 1996 (See Chapter 3).

There are several limitations of using trapping locations to determine home-ranges. Firstly the presence of the bait could draw animals out of their natural home-ranges. In using trap records it was assumed that the points where gliders were caught were within their natural home-range (Desy *et al.* 1989). Secondly, individuals may have part of their home-range outside the trapping area. This is particularly likely in species which have large home-ranges. Thirdly, trapping might bias estimates to areas close to their dens, if they enter a trap soon after emerging from their dens. Direct observation was used to overcome all of these potential biases.

6.2.2 Radio-Tracking and Estimation of Home-Range Size

Individuals to be fitted with a radio-transmitter were selected if they were thought to have most of their range within the trapping area. Two types of transmitter were used: a single-stage transmitter (Sirtrack, New Zealand), and a 2-stage transmitter (Holohil, Canada). Both types of transmitter were mounted on a leather or rubber collar, weighed approximately 10-12g, and had whip antennas that were 12-15cm long. A three-element hand held yagi antenna (Sirtrack, New Zealand) was used with a receiver operating in the range of 150.700-151.900 Mhz to locate gliders. Gliders were discouraged from chewing collar aerials by the application of cayenne pepper.

During observation sessions, nightly fixes were obtained every 30 minutes, following the emergence of the gliders from their dens at dusk, until their return the following morning. These fixes were marked with pink flagging tape so they could be recorded the following morning. Quin *et al.* (1992) determined previously that this was an adequate time period between fixes for fast moving species of mammals such as the genus *Petaurus*, while Van Dyck (1993) also used 30 minutes as the time period between fixes when he determined the home-range of the mahogany glider. Each individual was followed for a minimum of 5 full nights during different times of the year. The use of the spotlight often resulted in periods of behaviour that were clearly unnatural, when individuals remained stationary and looked at the observer for long periods (up to 4 hours and often greater than 1 hour). This behaviour was frequently associated with long periods of grooming. During these periods, only a single fix was taken so that the fixes were not biased by these periods of unnatural inactivity.

From September 1995 onwards, the end of a hip chain was tied to a tree next to the den and pulled out as the animal was followed to provide a clear path of the nights movements. The following morning, the gliders route was surveyed, and fixes were mapped to provide a path of nightly movements, and the hip chain string and flagging tape were collected. The hip chain also measured the total distance that animals travelled during the nights' foraging and was recorded only for individuals which were considered to behave naturally for the majority of the night.

Home-ranges were calculated using both harmonic mean measure (HMM, Dixon & Chapman 1980) and the minimum convex polygon model (MCP, Southwood 1966). Home-ranges were determined for individual males and females, for male and female pairs, and one juvenile male. All home-range calculations were determined using 95% of fixes (both trapping and radio-tracking locations) with the Ranges V software (Robert Kenward, Institute of Terrestrial Ecology, Wareham, UK). To determine that a sufficient number of locality fixes were obtained, an incremental plot of home-range area against randomly sorted home-range fixes was produced to remove any affects of autocorrelation and checked to make sure it had fully asymptoted.

6.2.3 Vegetation Composition of Home-Ranges

Vegetation types constituting the continuous habitat at Mullers Creek and the fragmented habitat at Porters Creek, were mapped in the field. Four vegetation types were recognised, by Tracey (1982)(TVT), and Cumming and Thomas (1992)(C&T)(Fig. 2.5). The four forest types were:

(1) _Rainforest_. TVT = 1c, C&T = Type 4;

(2) Riparian Forest or gallery rainforest, dominated by rainforest species and Myrtaceae species such as red mahogany *Eucalyptus pellita*, forest red gum *Eucalyptus tereticornis*, pink bloodwood *Corymbia intermedia*, Moreton Bay ash *Corymbia tessellaris* and long-leafed paperbark *Melaleuca leucadendra*. TVT = no equivalent vegetation type, C&T = 5;

(3) Open Eucalypt Forest, dominated by Clarkson's bloodwood *Corymbia clarksoniana*, poplar gum *Eucalyptus platyphylla*, brown salwood *Acacia crassicarpa*, *Acacia flavescens* and swamp mahogany *Lophostemon suaveolens*, with albizia being found occasionally to commonly. TVT = 19, C&T = 14;

(4) Melaleuca Woodland, dominated almost exclusively by broad-leafed tea-tree *Melaleuca viridiflora* (and the occasional forest red gum) with grass trees *Xanthorrhoea johnsonii* being very common underneath. Very limited patches of habitat. TVT = 20, C&T = 18.

The proportion that each vegetation type composed of each home-range was determined by overlaying the home-range areas of each individual with the mapped vegetation types.

6.2.4 Den-Use Index and Den Descriptions

Dens of radio-collared mahogany gliders were located at least once during trapping sessions and several times during observational sessions using radiotelemetry. All dens in which gliders were located by radio tracking were recorded. The location of the tree within the study area, percentage canopy cover, height of tree and diameter at breast height (DBH) was recorded for each den. If the den entrance was known, its height above the ground and aspect were also recorded.

A den-use index was calculated to determine if gliders preferred a particular species of tree for denning. This was done by dividing the proportion that each tree species formed of the total number of dens found by the relative proportion of each tree species at the study site formed of the 250 trees selected for phenology (Chapter 5). The phenology trees were used as they were chosen according to the relative abundance of trees in the study areas.

6.3 Results

6.3.1 Estimates of Home-Range Size

Within the continuous area of habitat at Mullers Creek, home-ranges were estimated over at least a one-year period, for five adult males and four adult females (Table 6.1 & Fig. 6.1). Information gained from trapping suggested that the home-range was determined for all animals within the study grid, although there is no doubt overlap with individuals on the edge of the trapping grids occurs. The number of fixes required for the incremental plot of home-range area of fixes to asymptote was 52.4 (± 20.8) for males and 40.0 (± 15.3) for females. The average home-range was 19.2ha for males and 19.9ha for females using the HMM and 19.3ha and 20.7ha for males and females, respectively, using MCP. A juvenile male had a home-range of 10.90ha (13.1ha and 8.7ha for HMM and MCP respectively). There was a high level of overlap in the home-ranges of particular individual males and females, with an average overlap of 85.9% (Table 6.2), suggesting they form social pairs. This was represented by four male/female pairs and a single male whose partner was thought to have been preyed on by an owl. In contrast, the overlap of males with other females and females with other males was small (8.4% and 10.4% respectively), while the overlap of males with other males and females with other females was similarly low (12.4% and 8.5% respectively). When the male and female den mates were considered as a paired group, the overlap between adjacent groups was also low (13.8%). In suggesting these overlaps, all animals considered to be residents within the trapping grids had transmitters attached to them over the study period. Although a number of other animals were trapped within the study grid these were considered to be either transients or animals that were caught on the edge of the trapping grid, suggesting that only a small part of their home range occurred within the grid (Chapter 3). When males and females were considered as a paired group the average home-range was 23.7ha and 22.6ha for HMM and MCP respectively. There was no significant difference between the estimated areas using either HMM or MCP (Paired t-test: t = 0.239, d.f. = 13, P > 0.05).

Table 6.1. Estimates of long term home-range sizes (ha) for the mahogany glider calculated for 95% isopleths of harmonic mean measure (HMM) and minimum convex polygon (MCP) analysis determined by radiotelemetry and trapping locations. Home-ranges and dens used were also recorded for the paired male and female gliders. The home-ranges for the animals in the buffer strip were adjusted by removing the area of open ground and pine plantation from the home-range area as these were never utilised.

Identification	Fixes	Dens	Fixes to Stabilise	HMM	MCP	Ave. Home Range
Continuous Habitat						
M 5/6	87	4	24	17.5	18.48	18.0
F 147/148	108	3	32	18.6	19.2	18.9
Group	195	6	120	20.7	22.4	21.5
M11/12	101	7	64	23.6	19.8	21.7
F 39/40	66	5	43	14.2	14.5	14.4
Group	167	9	80	22.1	20.2	21.2
M 9/10	91	5	64	25.4	25.1	25.3
F23/24	115	7	25	31.2	33.9	32.5
JM75/76	47	4	34	13.1	8.7	10.9
Group	206	8	100	35.6	30.9	33.2
M 13/14	97	9	73	16.4	17.4	16.9
F 157/158	85	5	60	15.5	15.0	15.3
Group	182	13	48	16.5	17.0	16.8
M 67/68	68	6	37	13.4	15.5	14.4
Male Mean	88.8±12.8	6.2±1.9	52.4±20.8	19.2±5.1	19.3±3.6	19.3±4.3
Female Mean	93.5±22.4	5.0±1.6	40.0±15.3	19.9±7.7	20.7±9.1	20.3±8.4
Group Mean	199.3±37.6	9.0±2.9	87.0±30.7	23.7±8.3	22.6±5.9	23.2±7.1
Fragmented Habitat						
M 17/18	75	7	65	19.7	19.2	19.4
F 209/210	74	2	58	7.9	10.1	9.0
Group	149	7	60	19.0	17.9	18.4
M 247/248	77	4	40	13.1	13.3	13.2
F 195/196	62	5	55	10.2	11.3	10.8
Group	139	6	-	13.3	17.2	15.3
Male Mean	76.0±1.4	5.5±2.1	52.5±17.7	11.1±2.2	11.0±1.8	11.1±2.0
Female Mean	68.0±8.5	3.5±2.1	56.5±2.1	6.0±1.7	7.6±1.0	6.8±1.3
Group Mean	144.0±7.1	6.5±0.7	-	10.9±1.6	12.3±2.0	11.6±0.2

Mahogany gliders were observed to den either solitarily or in pairs, with solitary animals being observed to leave a den on 40 occasions and more than one animal observed to emerge on 21 occasions. Individual males and females used 2 to 9 dens, that varied in their frequency of use (Table 6.1), while pairs utilised approximately 6-13 dens and shared them with any offspring of the previous breeding season.

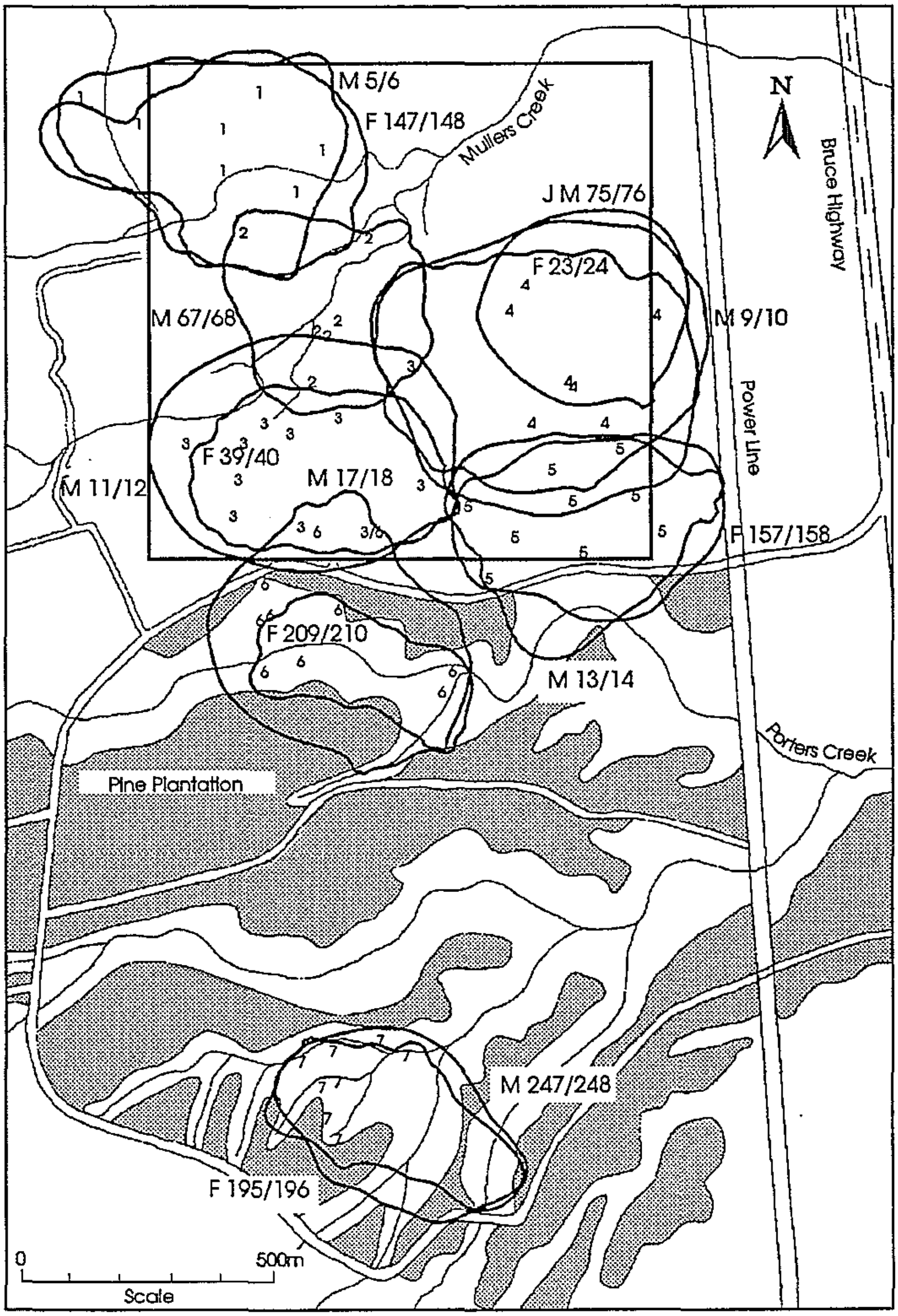


Figure 6.1. Home-ranges and den locations of different mahogany glider individuals and the location of their dens at Mullers Creek and Porters Creek in north Queensland. The 95% HMM isopleth was used in determining home-range estimates. The numbers within home-ranges represent the location of dens used by that glider pair.

Table 6.2. Percentage overlap of adjacent male and female home-ranges using the 95% HMM.

	Mean ± SD	Range
With partner	85.9 ± 11.9	59.9-99.2
With non partner - male with other females	8.4 ± 5.8	0.1-16.8
With non partner - female with other males	10.4 ± 9.5	0.1-31.7
Male with other males	12.4 ± 7.2	0.5-29.6
Female with other females	8.5 ± 11.6	0.2-29.3
Male/female groups with other groups	13.8 ± 9.5	0.9-34.9

Within the fragmented habitat at Porters Creek, the home-ranges of two males and two females (representing 2 pairs) were estimated. The average home-range was 11.1ha for males and 6.0ha for females using HMM and 11.0ha for males and 7.6ha for females using MCP (Table 6.1). When home ranges were calulated for pairs of animals, the average areas were 10.9ha and 12.3ha for HMM and MCP respectively. These home-range figures have been adjusted, as the original home-range sizes included some areas of open ground and pine plantation never utilised by the mahogany glider. The slightly larger size of the male home-range compared to the group home-range for the HMM is a function of the HMM algorithm, which fits a boundary on the basis of modelling of the distribution of points rather than simply enclosing the outermost points. This means that additional fixes can change the model parameters that result in a reduction of home-range area. A two-way analysis of variance of all home-ranges showed no significant difference between the sexes ($F_{1,9}$ = 0.225, $P > 0.05$) and no interaction between habitat type (continuous and fragmented) and sex ($F_{1,9} = 0.597$, $P < 0.459$). A significant difference was observed in the size of home-ranges between continuous and fragmented habitat ($F_{1,9} = 10.035$, $P < 0.05$). Five individuals followed within corridors, or narrow buffer strips, to determine home-range size disappeared before a home-range could be estimated, resulting in the small sample size. It is not known if these individuals died (one was confirmed dead) or if the smaller home-range size (and hence food availability) of the corridor was insufficient for long-term existence, therefore forcing these gliders to move to adjacent continuous habitat. In the continuous habitat, and particularly in the fragmented habitat, several individuals were observed to leave their normal home-range to feed. The movement out of their normal home-range was based on observations of their normal foraging loops and the apparent lack of flowers within their known range.

Both males and females vocalised (a very nasally "na-when"), with individuals generally vocalising on only one occasion per night. Although several calls (approx. 3 seconds apart) were most common, vocalisations ranged from a single call to repeated calls (approximately 3-10 seconds apart) over 8 minutes. Calls from either sex were rarely responded to, with a response being heard on only one occasion. Individual gliders in a pair rarely came together in the same tree at night, although it was suspected they were often not very far apart. When they did come together, the male generally sniffed the cloaca of the female, and occasionally they sat next to each other and groomed. Before and after this interaction, they generally foraged separately in different parts of their paired home-range.

Defence of the home-ranges appeared to be strong with both sexes traversing the edge of their home-range in a 'foraging loop' at least once every 2-3 nights. The foraging loops were traversed (generally quite rapidly and with only limited feeding) either at the beginning of the night prior to the major bout of feeding and/or at the end of the night prior to returning to the den. On one occasion a male was observed to viciously attack a second mahogany glider (thought to be a male). The radio-collared glider rapidly chased the second glider which tried to hide on the opposite side of the trunk as the aggressor moved around. The aggressor lunged and bit the second glider, resulting in both gliders dislodging from the tree they were in. Both landed in the same tree where the animal being radio-tracked continued to quickly chase the second animal until it glided to another tree. The whole sequence of behaviour was completed in almost total silence.

6.3.2 Vegetation Type Composition of Home-Ranges

Throughout the study area, the dominant vegetation type was open woodland, which was reflected in the respective high proportions of glider home-ranges (Table 6.3). The riparian vegetation and the broad-leafed tea-tree swamps were also important components of most mahogany gliders' home-ranges, however gliders clearly spent most of their time with open woodland. These results also show that rainforest is not utilised by the mahogany glider. Interestingly male 9/10 and female 23/24, which had the largest home-ranges (25.4ha and 31.2ha respectively), had no riparian forest within their home-ranges. These larger home-range areas may be the result of the lower diversity of vegetation in the woodland habitat within their home-range compared to individuals which have at least part of their home-range within riparian vegetation and the associated higher diversity of Myrtaceae food species. The composition of each home-range with respect to vegetation type, can be seen in Table 6.3.

Table 6.3. Vegetation composition of the home-ranges of the mahogany glider in the continuous habitat at Mullers Creek and the fragmented habitat at Porters Creek. The values are the percentage of the total area within the home-range (delineated by the 95% HM following Goldingay & Kavanagh 1993) occupied by each forest type. The area (ha) of each forest type is shown in parentheses. A 200m boundary strip was included around the 100ha grid and on the ends of the buffer strip fragments at Porters Creek so as to include all home-ranges.

Animal	Vegetation Type			
ID	**Rainforest**	**Riparian Forest**	**Open Woodland**	***Melaleuca* Woodland**
Continuous Habitat at Mullers Creek				
Total Available	1.13 (1.12)	6.88 (6.81)	81.34 (80.53)	10.65 (10.54)
M 67/68	0	8.13 (1.09)	76.42 (10.21)	15.45 (2.06)
M 9/10	0	0	69.30 (17.57)	30.70 (7.78)
F 23/24	0	0	72.66 (22.63)	27.34 (8.52)
M 75/76	0	0	73.33 (9.60)	26.67 (3.49)
M 11/12	0	6.98 (1.65)	93.02 (21.96)	0
F39/40	0	3.76 (0.54)	96.24 (13.70)	0
M 13/14	0	16.96 (2.78)	64.91 (10.63)	7.02 (1.15)
F 157/158	0	11.64 (1.80)	72.60 (11.22)	7.53 (1.16)
Table 6.3 - Cont.				
M 5/6	0	11.04 (1.93)	67.53 (11.80)	21.43 (3.75)
F 147/148	0	9.71 (1.81)	70.29 (13.09)	20.00 (3.72)
Mean ± SD	0	6.82 ± 5.80	75.63 ± 10.54	15.61 ± 11.39
Fragmented Habitat at Porters Creek				
Total Available	0.00 (0)	30.25 (13.61)	56.02 (25.21)	13.73 (5.91)
M 17/18	0	8.74 (1.72)	54.64 (10.74	0
F 209/210	0	16.30 (1.29)	57.61 (4.57)	0
M 247/248	0	2.84 (0.37)	43.26 (5.67)	27.66 (3.62)
F 195/196	0	5.32 (0.54)	34.04 (3.49)	36.17 (3.70)
Mean ± SD	0	8.30 ± 5.86	47.39 ± 10.84	15.96 ± 18.75

6.3.3 Foraging Distance

Data taken for a total of 46 full nights in which gliders were considered to behave normally were analysed for foraging distance (Fig. 6.2). The average nightly foraging distance was 1506m (range 590-3430m) with no significant difference between male and female gliders in either the continuous or fragmented areas (t_{29} = 1.512, P>0.05 and t_{13} = 0.568; P>0.05 respectively). There was a significant difference in the distance individuals moved during different times of the year ($F_{7,37}$ = 2.586, $P < 0.05$), with a tendency for longer distances during the late dry/ wet season and shorter distances during the early to mid dry season (Fig. 6.3). Mahogany gliders travelled further when there was a high nectar and pollen availability (high flowering index) than when there was a low availability ($t_6 = 7.45$, $P < 0.05$; Fig. 6.4).

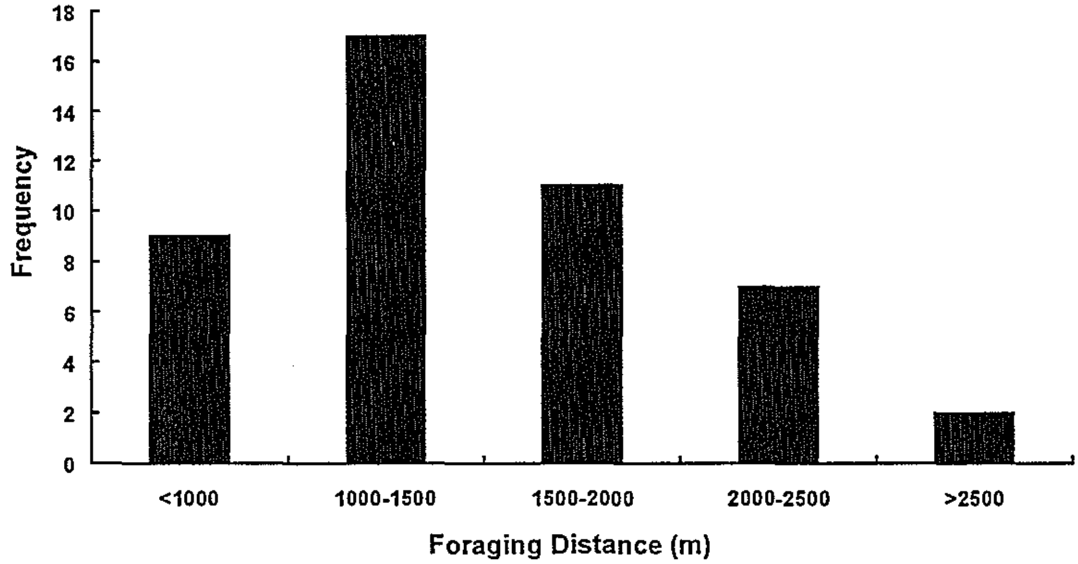


Figure 6.2. Frequency distribution of foraging distances for mahogany gliders moved over 46 full night observations at Mullers Creek and Porters Creek in north Queensland.

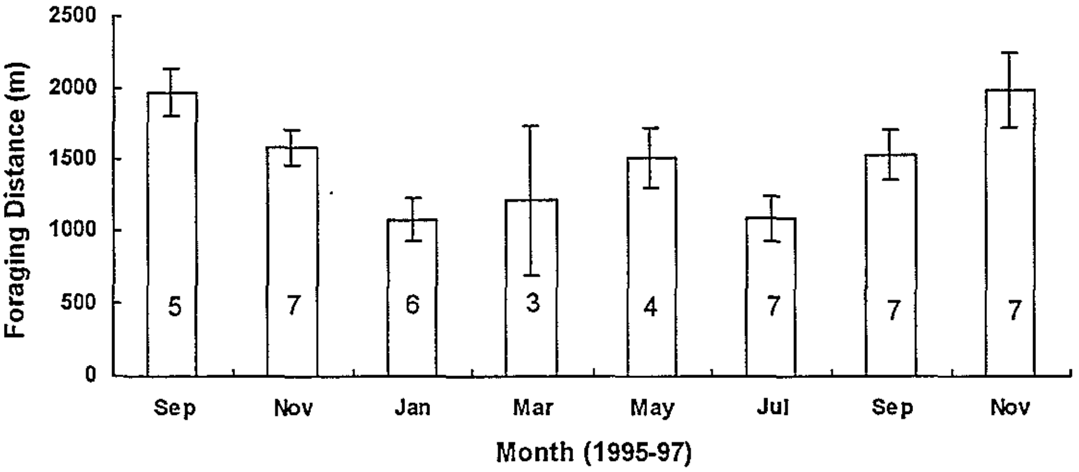


Figure 6.3. Average foraging distance (m) of the mahogany glider, between September 1995 and November 1996. The number of individuals followed is within the column.

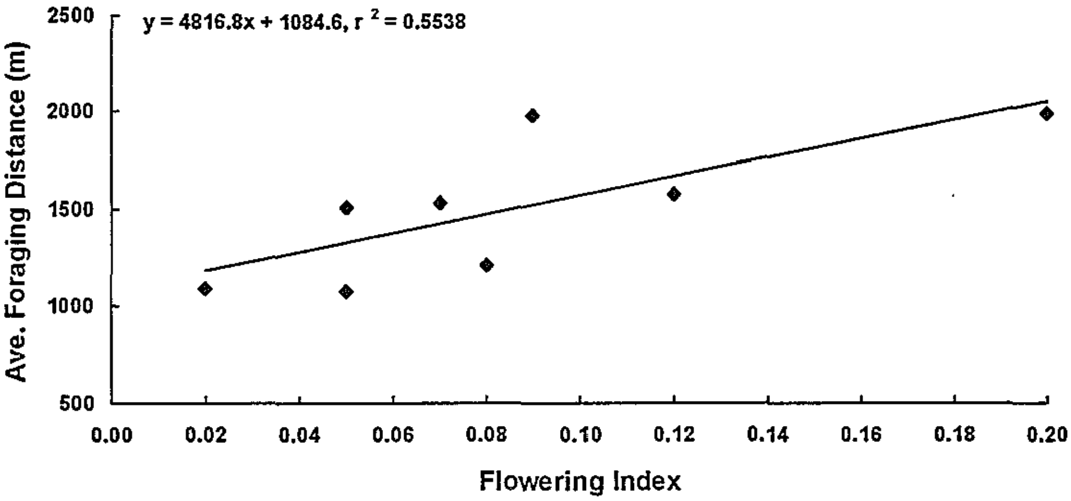


Figure 6.4. Relationship between average foraging distance and flowering index during 1995 and 1996.

6.3.4 Den Tree Occurrence and Characteristics

A total of 83 dens were recorded for the mahogany glider with a significant difference being observed between the predicted and observed utilisation of tree species as den sites ($\chi^2 = 43.22$, d.f = 8, $P < 0.01$)(Table 6.4). Of the tree species utilised as dens, all were in Myrtaceae, with poplar gums and forest red gums being used more than expected, and Clarkson's bloodwood being often used but in proportion to its high availability. Other species such as broad-leafed tea-tree, pink bloodwood and cloudy tea-tree *Melaleuca dealbata* were used on several occasions, with Moreton Bay ash, red mahogany, swamp mahogany and long-leafed paperbark being used only once. Of all the trees utilised as dens, only seven (three of unknown species) were dead. The mean tree characteristics of den trees used more than once are found in Table 6.5. The aspect of the den entrance appeared to be a very important characteristic of den trees with a clear majority facing either west or south (Fig. 6.5). Because poor weather comes from the east to north east, a southern or western den entrance may reduce the risk of rain entering the den.

Table 6.4. The utilisation as dens of each tree species on the study site, based on the relative occurrence of those Myrtaceae species used to monitor phenology. The relative occurrence of each Myrtaceae species is based on the frequencies of tree species determined for the phenology study at Mullers Creek (Chapter 5). The dens in dead trees were not included.

Tree Species	Percentage of the 83 known den trees that were this species.	Percentage of 250 Myrtaceae trees recorded and used as phenology trees.	Den Use Index
E. platyphylla	36.7	23.2	1.58
C. clarksoniana	27.8	31.6	0.88
E. tereticornis	21.5	7.6	2.83
C. intermedia	3.8	2.0	1.90
M. viridiflora	3.8	9.2	0.41
M. dealbata	2.5	4.0	0.63
E. pellita	1.3	4.4	0.30
C. tessellaris	1.3	5.6	0.23
L. suaveolens	1.3	12.4	0.10

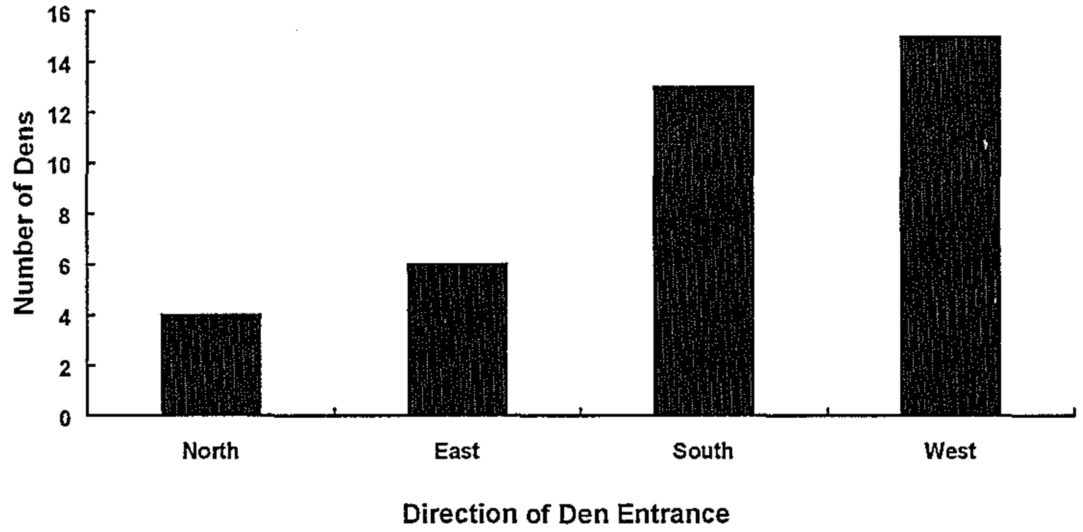


Figure 6.5. The direction of den entrances used by the mahogany glider.

Table 6.5. Mean tree characteristics for den trees utilised by the mahogany glider. The number of individual tree recorded is in brackets after the species name.

	C. clarksoniana (22)		*E. platyphylla* (29)		*E. tereticornis* (17)	
Parameter	**Mean ± SD**	**Range**	**Mean ± SD**	**Range**	**Mean ± SD**	**Range**
Angle of entrance						
North (315-45°)	2	-	2	-	1	-
East (45-135°)	2	-	2	-	0	-
South (135-225°)	1	-	4	-	7	-
West (225-315°)	2	-	6	-	2	-
Height of entrance (m)	11.18 (4.4)	6.6-19.5	14.60 (3.5)	10.7-21.0	22.85 (6.0)	10.1-33.3
No of entrances	1.91 (1.1)	1-5	1.90 (1.1)	1-5	3.06 (1.6)	1-5
% canopy cover	40.34 (10.1)	30-60	37 (14.9)	20-50	42 (8.5)	30-60
DBH of tree (cm)	39.38 (12.7)	20.1-59.2	61.86 (18.7)	35.0-100.3	77.7 (25.7)	44.5-128.9
Height of tree (m)	17.83 (5.8)	6.5-25.6	25.93 (5.81)	9.3-35.8	30.5 (10.0)	15.2-49.2

	C. intermedia (3)		*M. viridiflora* (3)		*M. dealbata* (2)	
Parameter	**Mean ± SD**	**Range**	**Mean ± SD**	**Range**	**Mean ± SD**	**Range**
Angle of entrance						
North (315-45°)	0	-	0	-	0	-
East (45-135°)	0	-	1	-	0	-
South (135-225°)	0	-	1	-	0	-
West (225-315°)	2	-	1	-	0	-
Height of entrance (m)	22.60 (12.7)	13.6-31.6	9.68 (1.5)	8.1-11.0	-	-
No of entrances	2.0 (1.0)	1-3	1.0 (0)	1	3.0 (2.83)	1-5
% canopy cover	45.41 (12.2)	30-60	32.40 (8.2)	20-40	58.76	50-70
DBH of tree (cm)	58.62 (3.6)	54.9-62.1	36.23 (6.6)	28.7-40.6	133.7 (6.8)	128.9-138.5
Height of tree (m)	39.1 (8.28)	22.6-39.1	12.70 (2.4)	9.9-14.4	45.10 (23.3)	28.6-61.6

6.4 Discussion

6.4.1 Mating System

The high degree of overlap between male and female paired animals, the comparatively low overlap with gliders from adjacent groups, the sharing of dens with only one individual of the opposite sex, and the observed aggressive behaviour towards gliders from other groups suggest that the mahogany glider is socially monogamous. The monogamous mating system observed during this study contrasts with Van Dyck's (1993) proposal that the mahogany glider was pseudopolygynous. Emlen and Oring (1977) proposed that the potential for polygyny will be greatest where food resources are concentrated, while monogamy is favoured where food resources are sparse and evenly distributed. In the case of the mahogany glider, food resources are often (though not always) concentrated into patches, suggesting that polygyny may be most advantageous. However, as these patches are widespread, with all patches being defended throughout the year (as suggested from the foraging loops, denning apart and observed aggression), energetically, the situation may be comparable to that where resources are thinly and evenly scattered. Males may be able to defend sufficient resources to attract only one female without reducing their reproductive success. The defence of resources may also help to explain why male and female mahogany gliders often den apart, as this increases their ability to defend their territory (Van Dyck 1993). Goldingay (1992) suggested that abundant arthropods in north Queensland (where Russell (1984) found them to be polygynous) and abundant nectar and pollen availability at Kioloa in southern Australia are responsible for the yellow-bellied glider being polygynous. However despite both high insect availability and very high nectar and pollen availability the mahogany glider appears to be socially monogamous. The sexual dimorphism is body weight is displayed by both the sugar glider *Petaurus breviceps* and the mahogany glider (Chapter 3), also suggesting polygyny (Kleiman 1977), which is largely consistent with the observed behaviour of the sugar glider (Suckling 1984; Henry & Suckling 1984), although not with the observed social system of the mahogany glider.

Although the mahogany glider appears to actively defend its home-range, several individuals were observed to leave their usual area, potentially because there was little food available within their normal home-range. Burt (1943) suggested that occasional excursions outside the home-range, perhaps exploratory in nature, should not be considered as part of the home-range.

Kleiman (1977) suggested that both the male and female of monogamous mammals may exhibit direct aggression toward conspecific intruders. Scent marking is also likely to play an important part in home-range maintenance of the mahogany glider, through urination on branches, and the presence of well developed scent glands on the frontal area of the head and on the chest in male mahogany gliders. It also appears that interspecific competition with the sugar glider is significant, as mahogany gliders were observed to be intolerant of the smaller species, as on several occasions, they actively chased them out of the same tree.

Solitary animals nonetheless do occur, and appear to be primarily males, which is consistent with the trap data which suggest that the adult population is slightly male biased (Chapter 3). Male and female den mates generally forage apart and do not den together every night, as they may spend at least 1-2 days at a time in separate dens in different parts of their home-range. Therefore opportunities for extra pair matings are available. Mating exclusively with a consort is not a dominant feature of socially monogamous species (Kleiman 1977; Wittenberger & Tilson 1980; Carter & Getz 1993). Indeed, Spencer (1996) found that up to 34% of young allied rock-wallabies *Petrogale assimilis*, a species which was considered to be monogamous, were not fathered by the female's socially paired mate. The occurrence of extra-pair matings in the mahogany glider is supported by Van Dyck (1993) who observed a female mahogany glider mating with a male not known to be her den mate.

Smaller species of petaurids, such as the sugar glider and squirrel glider *Petaurus norfolcensis*, are generally considered to be polygynous and have home-ranges, ranging from 1 to 3.7ha (see Quin 1995 for a summary). In contrast, the mahogany glider and the yellow-bellied glider *Petaurus australis* in Victoria and southern New South Wales are considered to be socially monogamous (although the yellow-bellied glider has been found to be polygynous in parts of its range), and have much larger home-ranges, ranging from 10-20 ha for the mahogany glider and 22-85 ha for the yellow-bellied glider (this study; Russell 1984; Craig 1985; Goldingay 1990, 1992; Goldingay & Kavanagh 1993).

Although the sugar glider is generally considered to be polygynous (Suckling 1984; Henry and Suckling 1984), Klettenheimer *et al.* (1997) suggested that only one adult male in a social group of sugar gliders is reproductively active, consisting of a monogamous pair, offspring and occasionally unrelated adult males. Smith (1980) also suggested this situation was apparent in Leadbeater's possum *Gymnobelideus leadbeateri*. These observations, and those of Taggart *et al.* (1997), who found the values of relative testes mass and relative sperm tail length of Leadbeater's possum and the sugar glider to be small for their body mass, suggest that sperm competition, and hence polygyny is unlikely. As the testes of the mahogany glider are relatively very small compared to the sugar glider (Chapter 3), the mahogany glider is likely to be monogamous. However more recent field based studies by Sadler and Ward (*in press*) found very clear evidence that sugar gliders are polygynous and the association between adult males and there putative son by Klettenheimer *et al.* (1997) was an artefact of captivity. The apparent monogamous nature of mahogany gliders contradicts Kleiman (1977) who suggested that sexual dimorphism indicates polygyny.

6.4.2 Vegetation Type Composition of Home-Ranges

The vegetation type composition of home-ranges and the observed diet clearly shows that rainforest is rarely traversed or utilised by the mahogany glider. The only plants observed to be utilised were Myrtaceae or Mimosaceae species, whilst other rainforest species were ignored (Chapter 5). The only rainforest species known to be utilised is nectar and pollen from the cadargi *Corymbia torrelliana* and euodia *Melicope elleryana* on the edge of rainforest and in riparian forest (Van Dyck 1993; Chapter 5).

Consistent with the mahogany glider which made continuous use of a range of vegetation types throughout the year, the yellow-bellied glider also displays highly seasonal utilisation of different forest types within their home-ranges (Goldingay & Kavanagh 1993). However in contrast to mahogany glider which used and defended a range of vegetation types throughout the year, the yellow-bellied glider made successional use of vegetation types throughout the year (Goldingay and Kavanagh 1993). In home-ranges that contain resources that change both spatially and temporally, it may be advantageous for an animal to spend time exploring or being curious to the detriment of immediate foraging efficiency, if the information gained will enable it to switch its behaviour rapidly as conditions change (Pyke *et al.* 1977). This is consistent with this study which found that when food was readily available (higher flowering index), mahogany gliders moved further than when there was less food available, possibly because there was a greater abundance of food to defend. When there was less nectar available, it was probably energetically more efficient to go directly to the few trees in flower. When there are only a few trees in flower within a gliders' home-range, that are often clumped, it may be easier to defend them than those which are more widely spread apart. When there is no nectar and pollen available, other food items such as lerps, honeydew, sap, mistletoe fruit and insects are eaten in greater amounts (Chapter 5), resulting in a greater travelling distance.

Direct observations suggest that both male and female mahogany gliders were observed to traverses around the outer edge of the home range, generally at the beginning or the end of the night, in a 'foraging loop' at least every 2-3 nights. The foraging loop appears to serve two purposes: firstly, it may serve to maintain the defence of their home-range, and secondly, they may serve to locate trees that will soon be in flower or fruiting. As their food is patchily distributed (as even ubiquitous species such as Clarkson's bloodwood and poplar gums have many plants that do not flower; Chapter 5) they can use these foraging loops to find new food sources and remember their location, so that when their current feed trees finish flowering they can move to a new food source. In addition, by foraging solitarily, pairs of gliders can double their exploration potential, increase the defence of their combined home-range and decrease the risk of being preyed upon.

6.4.3 Use of Corridors by the Mahogany Glider

The limited information gained in the fragmented habitat at Porters Creek suggests that the mahogany glider can live within fragmented habitats as long as they are sufficiently wide (approximately 60m), and comprise of adequate food tree species. Throughout this study mahogany gliders were only ever observed to remain within the native vegetation and were never observed traverse through the pine plantation in order to travel between patches, even though this sometimes added several hundred metres to the journey. Instead gliders were always observed to traverse along the length of the linear strip of habitat.

Habitat along creeks offers some advantages with respect to food tree species diversity, with species such as *C. intermedia*, *C. tessellaris*, *L. suaveolens*, *E. tereticornis*, *M. dealbata* and *M. leucadendra* being relatively more common along creek lines than in open areas. There are however, a number of disadvantages for gliders living within wildlife corridors along creeklines. These include: (1) rainforest occurrence and spread; (2) potentially higher predation due to increased exposure to predators such as pythons and owls which occur there in greater abundance; (3) lower number of individuals of each tree species (even though tree species diversity is high) for food and dens due to the smaller area available and competition with rainforest species; (4) higher canopy cover from rainforest species and acacias such as *A. flavescens* which is abundant in disturbed habitat (such as along corridor edges) which favours sugar gliders; (5) lower recruitment of food and den species due to higher canopy cover and competition from weeds; and (6) lower den availability. Therefore long term persistent of mahogany gliders within corridors appears to be difficult, even in areas with fairly wide corridors such as in this study.

When crossing small gaps in habitat, the mahogany glider was observed to use the tallest trees on the edge of the gap to gain the maximum distance from the glide. However, as the mahogany glider is strictly arboreal and appears reluctant to cross open ground, if the gaps between patches of suitable habitat are much greater than that able to be traversed by gliding, they will be unable to disperse from one suitable patch of habitat to the next. Therefore, the mahogany glider (as with other possums) is probably highly sensitive to habitat fragmentation (*sensu* Goldingay & Possingham 1995).

6.4.4 Comparison of Home-Ranges Between Gliding and Non Gliding Exudivores

The size of home-ranges of mahogany glider groups (23.7 ± 8.3ha) and the amount of overlap with adjacent groups (13.8 ± 9.5%) appears to fall between the squirrel glider, which has small home-ranges (2.5-4ha HMM) and a large degree of overlap between groups (Quin 1995), and the yellow-bellied glider which has very large home-ranges (22-85 ha), with no overlap between groups (Russell 1984; Craig 1985; Goldingay 1990, 1992; Goldingay & Kavanagh 1993).

Goldingay and Kavanagh (1993) developed an equation to predict the home-range size given a particular body size, specifically for exudivorous mammals, as the omnivore equation developed by Harestad and Bunnell (1979) included a number of mammals which had diets that were predominantly herbivorous or carnivorous. Consistent with the yellow-bellied glider (Goldingay and Kavanagh 1993), the predicted home-range for the mahogany glider is much greater than expected for an exudivorous mammal of its size using the Harestad and Bunnell (1979) equation, and is intermediate between the small petaurids and the yellow-bellied glider. Since Goldingay and Kavanagh (1993) examined the home-ranges of the exudivores for which home-range estimates were known, estimates of the home-ranges of the mahogany glider and squirrel glider have now been determined. Therefore the species used by Goldingay and Kavanagh (1993) were re-analysed with the addition of estimates determined for these two species and by dividing the exudivores into those that are gliding and non gliding (Fig. 6.6). There was a significant relationship between home-range and body weight for gliding exudivores with the mahogany glider fitting between the larger yellow-bellied glider and the smaller sugar glider and squirrel glider ($F_{1,2} = 44.55$, $P < 0.05$, $r^2 = 0.957$). The non gliding exudivores also showed a significant relationship between home-range and body weight ($F_{1,7} = 15.06$, $P < 0.01$, $r^2 = 0.683$). However, perhaps because of the small sample of gliding mammals, there was no significant difference between the slopes of the gliding and non gliding exudivores ($F_{1,9} = 2.00$, $P > 0.05$). As Goldingay and Kavanagh (1993) found no significant difference between their equation relating body mass to home-range size and that used by Harestad and Bunnell (1979), the Harestad and Bunnell equation for omnivores is still sufficient for specialised gliding omnivores, although the equation produced by Goldingay and Kavanagh (1993) and the one produced here provide more accurate estimates of home-range. In agreement with Goldingay and Kavanagh (1993), it is suggested that the mahogany glider is able to attain its large home-range size and fulfil its dietary niche because of the evolution of gliding, which facilitates movement between its patchily distributed food resources.

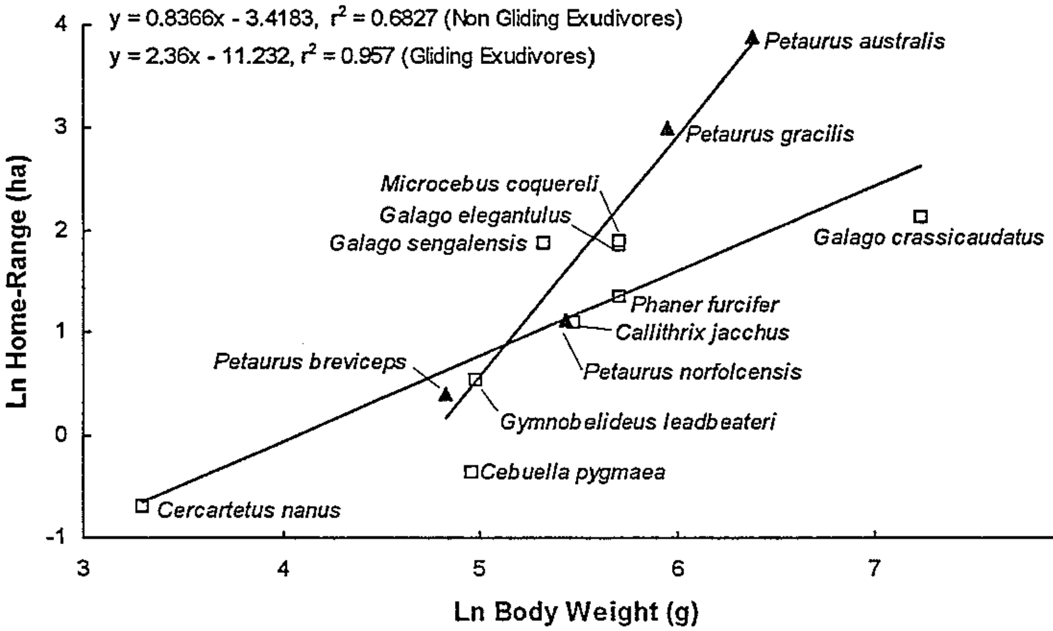


Figure 6.6. Regression of home-range area against body weight using MCP estimates for gliding (closed triangles) and non gliding (open squares) exudivorous mammals. Weights and home-ranges derived from Goldingay & Kavanagh 1993, Strahan 1995, Quin 1995 and this study.

Chapter 7

Gliding Efficiency in the Genus *Petaurus* and a comparison of Gliding with other Gliding Mammals.

7.1 Introduction

Gliding as a means of travel is defined by the Macquarie dictionary (1991) as the movement in air, especially at a downwards angle, by the action of gravity or by virtue of momentum already acquired. Norberg (1990) proposed that species that parachute descend at an angle >45° to the horizontal, while gliders descend at an angle <45°. Pennycuick (1972) suggested that very few animals act as pure parachutes, as most flying animals are not radially symmetrical, therefore gliding animals deflect air flowing past their bodies, so the reaction from it is not parallel to the direction of air flow.

Gliding is utilised in several classes of arboreal vertebrates. It is utilised by reptiles such as *Anolis* sp., the fringed geckos *Ptychozoon* sp. and the East Indian gliding lizard *Draco volans* that has an efficient wing which is composed of a fold of skin on the side of the abdomen and is supported by elongated ribs, that can be folded against the sides of the body when not in use (Oliver 1951; Pennycuick 1972). Even snakes such as *Chrysopelea* sp. and *Dendrelaphis* sp. have developed a form of gliding by flattening and broadening the body, while drawing in the belly so that it forms a concave surface when they leap out of trees (Oliver 1951; Pennycuick 1972). Although often considered to glide, the flying frogs of the genus *Rhacophorus* of Borneo parachute rather than glide by spreading out their large webbed feet (Norberg 1990).

Within the mammals, gliding has evolved independently in six groups. Among eutherians it is utilised by the two species of colugos in the order Dermoptera (*Cynocephalus*: Cynocephalidae); in the order Rodentia in the flying squirrels (Sciuridae: Petauristinae) with fifteen genera and forty-four species; and the African scaly-tailed squirrels (Anomaluridae) with three genera and seven species (although *Zenkerella insignis* does not glide) (Kingdon, 1974; Wilson & Reeder, 1993). Among marsupials, gliding is found in the families Petauridae (6 species of *Petaurus*), Pseudocheiridae (*Petauroides volans*), and Acrobatidae (*Acrobates pygmaeus*) (Flannery 1995a; Flannery 1995b; Strahan 1995). Interestingly, none of the opossums from North and South America have developed the ability to glide.

Within gliding mammals, the gliding membrane or patagium develops from a skin fold on the flanks, between the arms and legs and is under good muscular control so that when the animals are climbing in branches, resting or sleeping, it remains mostly hidden in their flank fur (Parker 1990). The patagium converts the animal's body into an effective airfoil enabling them to ride somewhat on a cushion of air (Norberg 1985; Parker 1990). This allows the animal to travel the greatest possible horizontal distance with the least loss in altitude, so they can make long, sailing flights from tree to tree (Parker 1990). Gliding is an energetically cheap method of movement compared to flight as the muscles do not perform any mechanical work but produce only static forces to keep the gliding membrane on the horizontal plane, opposing the aerodynamic force (Norberg 1985). The lift force produced approximately balances the weight of the animal, with potential energy from the launch being used to overcome the total drag (Norberg 1985).

Gliding has been poorly examined in marsupials, being limited to several papers by Johnson-Murray (1987), Nachtigall *et al.* (1974), Nachtigall (1979a and 1979b) and the occasional mention of approximate gliding distance, with the angle of descent or glide ratio almost never being recorded. The aim of this study was to determine the gliding efficiency of the genus *Petaurus* using the mahogany glider *Petaurus gracilis* and the sugar glider *Petaurus breviceps*, and compare this genus of gliding mammals with other gliding mammals including the greater glider *Petauroides volans*, feathertail glider *Acrobates pygmaeus*, flying squirrels (Petauristinae), scaly-tailed rodents (Anomaluridae) and the colugos (Dermoptera) with respect to their patagium, body size, and gliding techniques.

7.2 Methods

7.2.1 Gliding Distance and Efficiency

Gliding efficiency is considered here to be the glide ratio. This is the distance travelled divided by the net loss in height and was determined for both the mahogany glider and the sugar glider. The glide ratio is directly related to the glide angle, which is the angle of descent to the horizontal, from the point of launch.

To determine the efficiency of glides, the horizontal distance from trunk to trunk was measured to the nearest metre for each glide observed. As noted by Goldingay (1989) this led to a slight overestimate as gliders usually left trees from the outer foliage rather than the trunk. The height of launch and landing were recorded with the use of a clinometer, and the diameter at breast height (DBH) was recorded for the tree in which they landed. Although numerous glides were observed during nightly observations and after releasing captured animals, only full glides observed from animals released after capture were included in the regression analyses as these could be measured more accurately. Additional glides in which only the horizontal distance and the DBH of the landing tree measured, as the exact point of launch and landing were not identified. This provided additional points for the frequency distribution of glides.

Calculations of glide efficiency were derived using the equations of Norberg (1990).

Equation 1 $\alpha = \arctan (N/D)$
Equation 2 $L = Mg \cos \alpha$
Equation 3 $DR = Mg \sin \alpha$
Equation 4 $G = N/\mathrm{Sin}\, \alpha$

Where:-
α = angle of descent (degrees)
N = net height loss (m)
D = distance between trees (m)
L = Lift (N)
Mg = mass (g)
DR = drag (N)
G = glide distance (m)(distance covered in the air), incorporating fall or drop of glide.

7.2.2 Body Proportions and Adaptations of Gliding Marsupials

When preparing to launch, both the mahogany glider and the sugar glider were generally observed to lean from side to side, which has been suggested to be a method of improving triangulation (Scheibe *et al.* 1990; Nowak 1991). Therefore to examine if there has been selection for gliding possums to have eyes further apart than non-gliding possums, the interorbital width and maximum skull width were measured from numerous possum species in the Australian and Queensland Museums, and a ratio of inter-orbital width calculated.

To determine the ratio of tail length to head/body length, measurements were taken from museum study skins. Patagium surface areas were estimated for all species of gliding marsupial by taking the average width and length of the museum specimens in which the patagium was fully extended. The areas listed are products of these two figures and include the areas of the body limbs. Only the area of the plagiopatagium was recorded as the marsupial gliders have only a poorly developed propatagium and uropatagium (Johnson-Murray 1987).

7.2.3 Description of Gliding Behaviour

Details of gliding preparation, manoeuvrability in flight and landing of glides were recorded from both daytime observations and several hundred glides observed during nightly observational periods. In addition video footage was also examined to allow slow motion analysis of gliding behaviour.

7.3 Results

7.3.1 Gliding Distance and Efficiency

The mahogany glider was observed to launch significantly higher than the sugar glider (19.75 ± 1.01m and 11.96 ± 0.48m respectively)(t_{42} = 4.66; $P < 0.01$) and land significantly higher than the sugar glider (4.48 ± 0.31m and 1.95 ± 0.17m respectively)(t_{42} = 4.87; $P<0.01$) suggesting a partitioning in habitat usage. The mahogany glider was also found to have a significantly greater net loss in height between the takeoff and landing points (15.20 ± 1.04m and 10.01 ± 0.51m respectively)(t_{42} = 3.02; $P< 0.01$). As a result the mahogany glider also made significantly longer glides than the sugar glider (t_{62} = 6.55; $P <0.01$) with an average glide distances of 29.71 ± 2.38m compared to 20.42 ± 1.33m (Fig. 7.1). The mahogany glider also landed on trees with a larger average DBH than the sugar glider (44.12 ± 3.10cm and 23.22 ± 1.11cm respectively)(t_{47} = 4.85; $P<0.01$). There appears to be a lower limit in the DBH of landing trees, as the narrowest tree the mahogany glider landed on was 19.10cm with the narrowest for the sugar glider being 11.5cm.

Apart from a lower limit in DBH there does not appear to be a need for wider target trees for longer glides, as there was found to be no relationship between glide distance and DBH of target trees for either the mahogany glider or sugar glider ($F_{1,25} = 1.878$, $P > 0.05$ and $F_{1,16} = 0.0001$, $P > 0.05$ respectively).

The distance travelled by individual mahogany gliders and sugar gliders against height loss can be seen in Fig. 7.2. Although not significantly better ($t_{42} = 0.711$; $P>0.05$), the mahogany glider was found to have a slightly greater glide ratio than the sugar glider (1.91 and 1.82 respectively). This in turn resulted in the mahogany glider having a slightly flatter angle of descent than the sugar glider (28.26 ± 0.84 degrees and 29.69 ± 1.10 degrees respectively).

Although both gliders do make short glides, direct observations, and the significantly greater height of launch and landing points, show the much larger mahogany glider preferred more open habitat and to glide from the top of tall trees, where longer glides could be made. In contrast the sugar glider clearly preferred the mid storey with a higher density of trees, where shorter glides would be preferred.

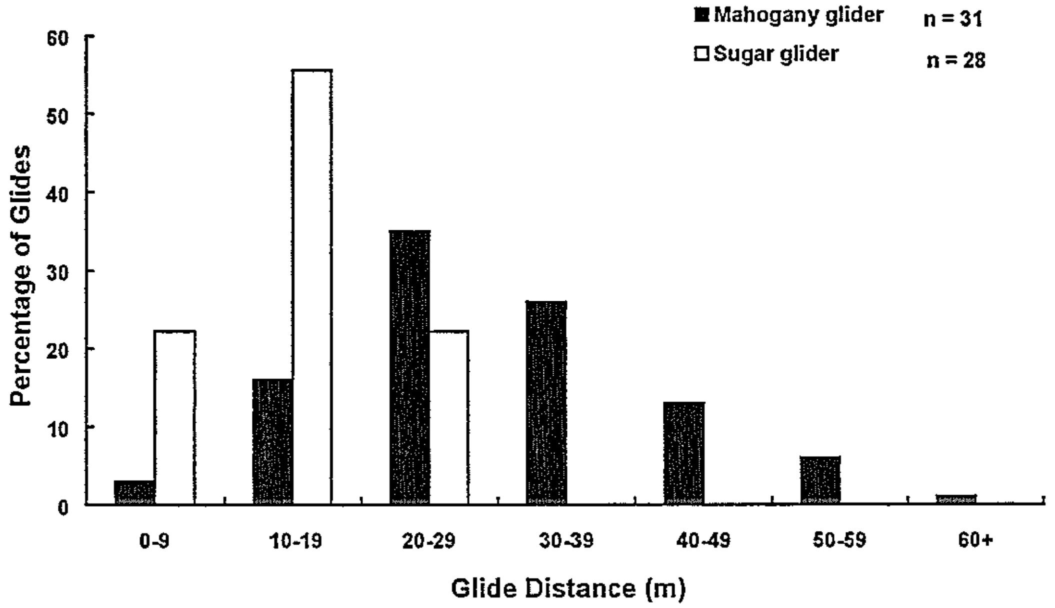


Figure 7.1. Frequency distribution of measured glides for the mahogany glider and the sugar glider at Mullers creek.

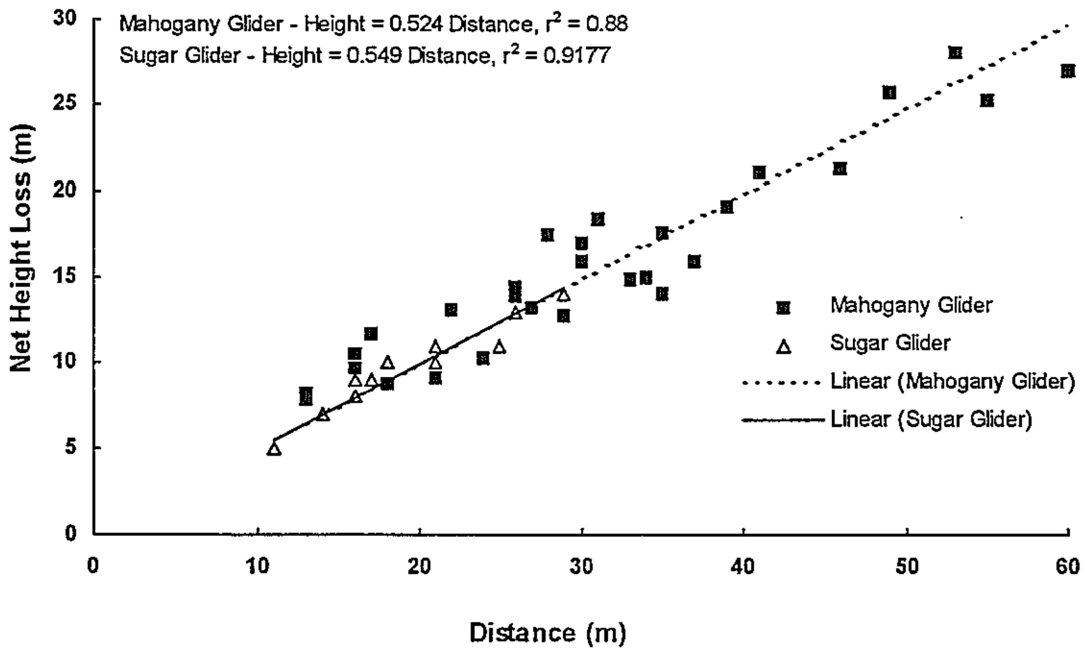


Figure 7.2. Gliding distance and height loss for the mahogany glider and the sugar glider.

As would be expected the average lift in the mahogany glider is significantly greater than the sugar glider because of its larger size (Table 7.1). However with this lift comes a significantly greater drag for the heavier mahogany glider compared to the lighter sugar glider. Therefore the lift:drag ratios of the mahogany glider and the sugar glider are not significantly different, resulting in very similar glide ratios and glide angles. A summary of all results, including those using these equations can be found in Table 7.1.

Table 7.1. Summary of glides recorded for the mahogany glider and the sugar glider. Differences were tested between the mahogany glider and the sugar glider using t-tests with a significance level of 0.01.

	Mahogany glider		Sugar glider		t	Sig.
Number of glides	31		13		value	
Parameter	Mean ± SE	Range	Mean ± SE	Range		* or NS
Height of launch (m)	19.75 ± 1.01	8.80 - 30.50	11.96 ± 0.48	8.00 - 16.10	4.66	*
Height landing (m)	4.48 ± 0.31	1.50 - 9.28	1.95 ± 0.17	0.50 - 3.75	4.87	*
DBH of Landing tree (cm)[a]	44.12 ± 3.10	19.10 - 97.08	23.22 ± 1.11	11.46 - 34.95	4.86	*
Net height loss (m) (H)	15.20 ± 1.04	7.30 - 28.00	10.01 ± 0.51	4.45 - 13.70	3.02	*
Glide distance - on ground (m)[b] (D)	29.71 ± 2.38	8.00 - 60.00	20.42 ± 1.33	8.00 - 42.00	6.55	*
Glide distance - in air (m)	33.44 ± 2.57	10.83 - 65.80	20.62 ± 1.10	10.96 - 32.01	3.05	*
Lift (L) (Newtons)	3.18 ± 0.08	2.03 - 4.41	0.74 ± 0.02	0.60 - 0.91	20.18	*
Drag (DR) (Newtons)	1.72 ± 0.06	0.88 - 2.54	0.42 ± 0.02	0.30 - 0.64	12.53	*
Glide ratio - D/H = Ratio L/DR	1.91 ± 0.06	1.10 - 2.50	1.82 ± 0.07	1.07 - 2.47	0.71	NS
Glide angle (θ)	28.26 ± 0.84	21.80 - 42.39	29.69 ± 1.10	22.03 - 43.12	0.83	NS

[a] - included 18 *P. breviceps* records. [b] - included 33 *P. breviceps* glides.

7.3.2 Body Proportions and Adaptations of Gliding Marsupials

7.3.2.1 Ratio of Interorbital Width to Maximum Skull Width

With the exception of the greater glider, gliding mammals were found to have a wider interorbital width than the majority of non gliding possums (Table 7.2). Members of the genus *Petaurus* were found to have an average interorbital ratio of approximately 0.3, with the feathertail glider having a very wide interorbital ratio of 0.33. In contrast to the other gliding possums, the greater glider has a ratio of only 0.19 which is similar to the other members of the Pseudocheiridae. Amongst the non gliding possums, the majority of genera have an interorbital width of approximately 0.2 except for the honey possum (*Tarsipes rostratus*) which has an intermediate interorbital width, and the pygmy possums (*Cercartetus* spp.) which have an average interorbital ratio similar to the gliding possums at 0.29. Other exceptions were the New Guinea feathertail possum (*Distoechurus pennatus*) with a ratio the same as its relative *A. pygmaeus*, Leadbeater's possum (*Gymnobelideus leadbeateri*) which has a ratio intermediate in width, and the Phalangeridae genus *Spilocuscus* which has an average ratio of 0.29. Therefore there appears to be a number of factors that are acting on the interorbital ratio, including phylogeny, potentially gliding requirements and possibly behavioural factors.

Table 7.2. Ratio of Interorbital Width to Maximum Skull Width in gliding and Non Gliding possums.

Species	Family	Number	Ratio Interorbital Distance/ Maximum Skull Width
Gliding Possums			
Acrobates pygmaeus	Acrobatidae	15	0.33
Petaurus abidi	Petauridae	1	0.30
Petaurus australis	Petauridae	6	0.27
Petaurus biacensis	Petauridae	1	0.29
Petaurus breviceps	Petauridae	15	0.30
Petaurus gracilis	Petauridae	6	0.29
Petaurus norfolcensis	Petauridae	12	0.31
Petauroides volans	Pseudocheiridae	14	0.19
Non Gliding Possums			
Distoechurus pennatus	Acrobatidae	10	0.33
Burramys parvus	Burramyidae	1	0.30
Cercartetus caudatus	Burramyidae	13	0.30
Cercartetus concinnus	Burramyidae	3	0.26
Cercartetus lepidus	Burramyidae	2	0.35
Cercartetus nanus	Burramyidae	5	0.26
Dactylopsila palpator	Petauridae	7	0.20
Dactylopsila tatei	Petauridae	1	0.21
Dactylopsila trivirgata	Petauridae	21	0.21
Gymnobelideus leadbeateri	Petauridae	3	0.27
Hemibelideus lemuroides	Pseudocheiridae	4	0.21
Pseudocheirus peregrinus	Pseudocheiridae	26	0.19
Pseudochirops albertisii	Pseudocheiridae	2	0.19
Pseudochirops archeri	Pseudocheiridae	5	0.17
Pseudochirops corinnae	Pseudocheiridae	11	0.17
Pseudochirops cupreus	Pseudocheiridae	15	0.16
Pseudochirulus forbesi	Pseudocheiridae	12	0.19
Pseudochirulus herbertensis	Pseudocheiridae	4	0.19
Pseudochirulus mayeri	Pseudocheiridae	6	0.19
Phalanger carmelitae	Phalangeridae	15	0.21
Phalanger gymnotis	Phalangeridae	17	0.19
Phalanger intercastellanus	Phalangeridae	19	0.20
Phalanger lullulae	Phalangeridae	4	0.19
Phalanger orientalis	Phalangeridae	16	0.20
Phalanger ornatus	Phalangeridae	11	0.20
Phalanger rothschildi	Phalangeridae	7	0.20
Phalanger sericeus	Phalangeridae	18	0.19
Phalanger vestitus	Phalangeridae	14	0.20
Spilocuscus kraemeri	Phalangeridae	9	0.25
Spilocuscus maculatus	Phalangeridae	15	0.28
Spilocuscus rufoniger	Phalangeridae	6	0.33
Strigocuscus pelengensis	Phalangeridae	12	0.22
Trichosurus arnhemensis	Phalangeridae	5	0.21
Trichosurus caninus	Phalangeridae	17	0.19
Trichosurus vulpecula	Phalangeridae	19	0.20
Tarsipes rostratus	Tarsipedidae	2	0.25

7.3.2.2 Relationship Between Body Length and Patagium Surface Area

Amongst the gliding mammals there was found to be a general trend in the relationship between body weight and the ratio of tail length to body length, with tail length becoming relatively larger with increasing body size (Fig. 7.3). In particular the mahogany glider was found to have a longer than expected tail to head-body ratio (1.5), while the greater glider had a much shorter than expected tail length to head and body ratio (1.25).

The surface of the patagium and the log of body weight were highly correlated amongst all species of gliding possum despite the membrane in *P. volans* extending from the elbow as opposed to the wrist in other marsupial gliders (Fig. 7.4). This suggests the greater glider has developed elongated limbs to overcome this shortcoming, and the gliding efficiencies of all species of gliding possums should be very similar, although the smaller species will still be effected by turbulence more than larger species.

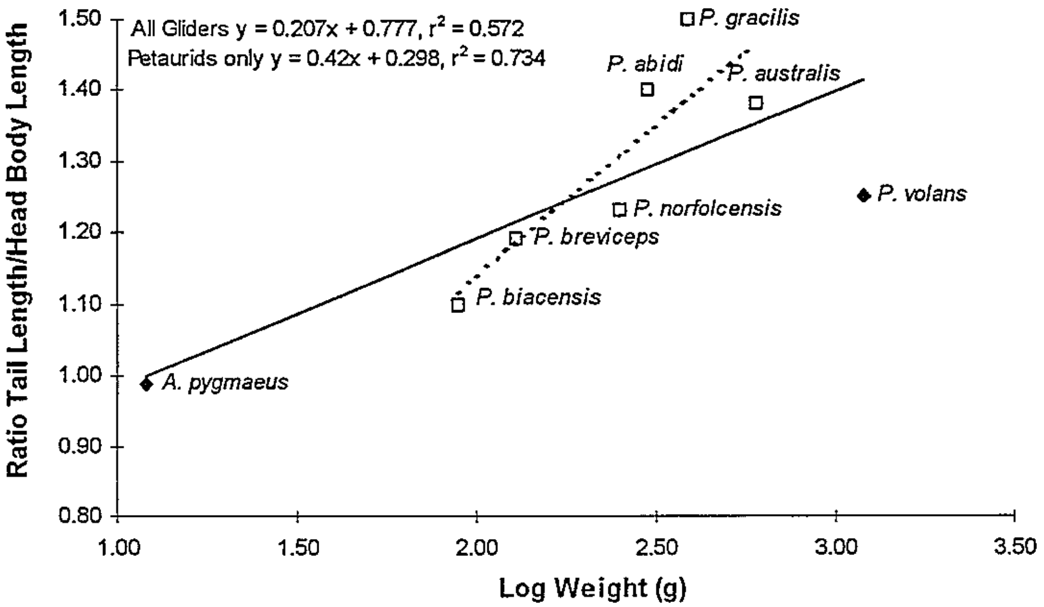


Figure 7.3. Ratio of tail length/head body length with log weight for all species of gliding marsupials (full line), and for the genus *Petaurus* (dotted line).

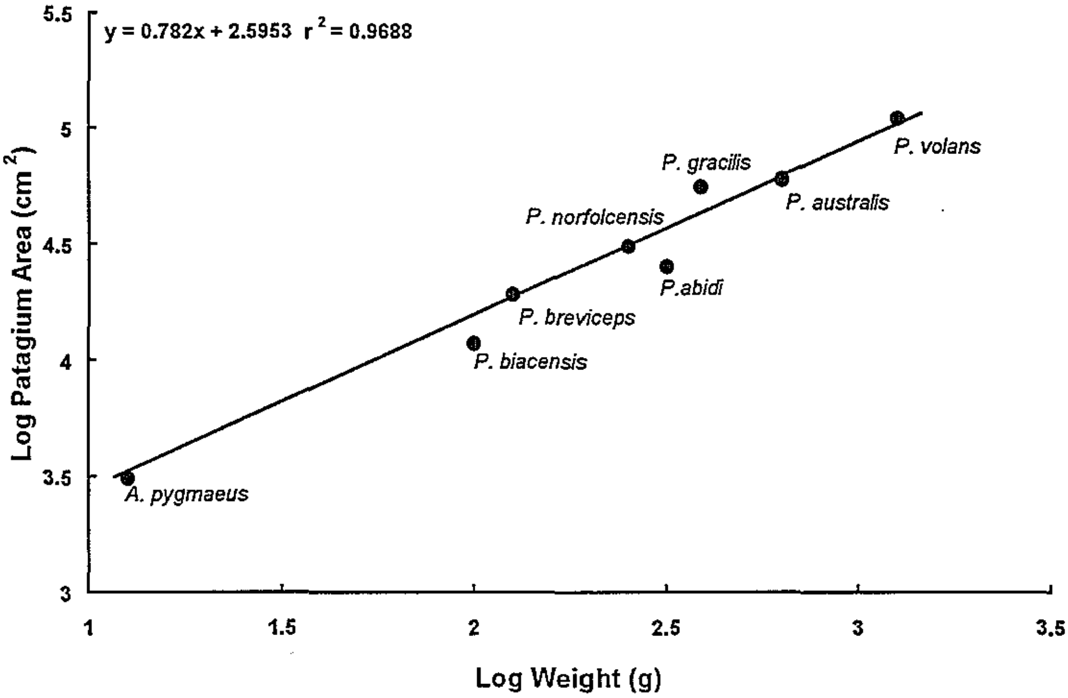


Figure 7.4. Relationship between log body weight and log patagium surface area for all species of gliding marsupials.

7.3.3 Gliding Behaviour of *Petaurus* Compared to Other Gliding Mammals

7.3.3.1 Preparation

For distances of 1-1.5m the mahogany glider generally jumps without extending its patagium, while for distances of greater than 1.5m within and between trees, the patagium is generally spread. The mahogany glider was often observed to jump vertically from the branch of one tree to an overhanging branch of a neighbouring tree rather than glide.

When gliding longer distances, the mahogany glider appears to carefully assess the direction and potential landing point of each glide. The mahogany glider often looked very hesitant prior to launch as they would often appear to want to head in a particular direction, then back down the branch again, often retrying on the same side of the tree or even the same branch. They frequently found alternative routes other than gliding, even going the long way around with the use of interconnecting branches. On some occasions the mahogany glider was observed to leap with little or no pause. The yellow-bellied glider (*Petaurus australis*) has also been observed to run along a slender branch, and without pause leap to an adjacent tree (Wakefield 1970).

Prior to gliding, individuals climb to the top of the tree and generally sway or weave from side to side, and bob their head up and down appearing to assess if they should glide or not. Swaying from side to side prior to gliding has also been observed in flying squirrels (*Glaucomys* spp.) in which they were observed to lean far to one side, then far the other side (Nowak 1991), which has been suggested to be a method of triangulation to measure distance. This hypothesis is supported by observation in the possums and by Scheibe *et al.* (1990) who found arboreal and gliding rodents to have wider interorbital widths than ground dwelling forms. In contrast Wells-Gosling (1985) suggested the eyes of flying squirrels are placed far to the sides of the head to provide a wide field of vision to detect predators. Wells-Gosling (1985) suggested that this eye placement restricts the field of visual overlap to the front and therefore limits depth perception.

When preparing to launch from a tree, the weight of the head and body is somewhat counterbalanced by the long tail which hangs down on the opposite side of the branch, allowing a steady launch. The patagium is under a high degree of muscular control, as it is important the body is not tangled in any foliage when climbing or prior to launch. Gliders still appear to have problems launching in twiggy trees such as some acacias, as the patagium can become tangled, making it difficult to make a clean launch. Gliders generally take off from a roughly horizontal surface although they do also take off from a vertical position such as from a tree trunk.

Because of difficulties in getting a clear launch from the canopy of several species of trees such as *Melaleuca viridiflora* and sometimes acacias, the mahogany gliders often did not jump from the canopy, but instead climbed down the trunk within 1.5-2m from the ground and either jump or make a short glide to the trunk of the next tree (ie. trunk to trunk).

Despite the larger size of mahogany gliders, in windy conditions they clearly find it more difficult to glide and are much more hesitant. Therefore in windy conditions the sugar glider would appear to have an advantage as it generally keeps to the more closed mid strata and makes shorter glides so it may be less affected by wind.

Alternatively they may have to use these closed areas because, as they are small, they are more likely to be affected by turbulence caused by wind.

7.3.3.2 Gliding Manoeuvrability

On launching, the head is held low as the body somewhat crouches, allowing a more powerful spring. The tail is raised as they kick into the air with their hind limbs to provide momentum that decreases the time until the terminal speed is reached.

After launch the mahogany glider and the sugar glider move their forearms forward and spread out, and their hind limbs backward and out, to stretch the patagium almost immediately. In comparison Kingdon (1974) found scaly-tailed squirrels not to stretch out their limbs at once but only after gaining momentum by dropping a metre or more.

Immediately after launch, the angle of descent in both the mahogany and sugar glider is quite steep, decreasing as they built up speed to their terminal or equilibrium speed when the glide path flattens to maximise the horizontal distance covered (pers. obs.). Similar observations have been made on the greater glider, Petauristinae and the Anomaluridae (Fleay 1947; Nowak 1991). Although not measured, it is suggested that as the mahogany glider is much heavier than the sugar glider (400g compared to 100g respectively), it takes longer to reach terminal velocity than the sugar glider. The heavier weight of the mahogany glider is partly compensated for by the larger surface area of the patagium over short distances, however it appears to provide greater benefit over longer glides.

Both the mahogany glider and the sugar glider have a remarkable ability to steer during gliding, giving them a highly accurate landing position. They are able to steer by changing the position of the limbs and the tension of the muscular gliding membrane (Pers. obs.; Nachtigall *et al.* 1974). Although it has been suggested by several authors (Nachtigall *et al.* 1974; Nachtigall 1979a) that the tail of gliding mammals helps steering by acting as a rudder. However, in agreement with Wells-Gosling (1985), it is proposed that except in species with a well developed uropatagium, the tail trails behind and acts more as a means of creating drag and to act as a counterbalance during flight, similar to the tail on a kite.

A left turn is accomplished by lowering the left arm below the right. This creates aerodynamic drag against the right membrane and the glider is spun into a turn (Muul & Alley 1963). As the mahogany glider is significantly heavier and larger than the sugar glider, it is less agile and cannot turn as tightly an the sugar glider. During long glides, several turns are sometimes made in succession when travelling around obstacles such as non target trees and branches. Banking (turns less than 90°) was observed on several individual animals during this study. One individual launched from the canopy of a tree, completed a full u-turn and land on the trunk of the same tree. Banking has been observed in the greater glider (McKay 1983) and yellow-bellied glider (Wakefield 1970). Wakefield (1970) observed an individual yellow-bellied glider to bank steeply, execute a tight half circle, and then land in a tree back in the direction from which it had come. Amongst the gliding rodents Diller (1977) and Kingdon (1974) noted seeing banking in the scaly-tailed squirrels and Nowak (1991) reports banking in the *Petaurista* (Petauristinae). While Dolan and Carter (1977) report *Glaucomys volans* to make 90° and 180° turns in avoiding obstacles.

7.3.3.3 Landing

In preparation for landing, both the mahogany glider and the sugar glider raise the angle of their tail, several metres before landing. At the same time the forelimbs and hind limbs are moved down and forward helping to trap air creating maximum air resistance so the patagium billows like a parachute. As a result of these movements they increase the angle of attack from a horizontal to a more vertical plane (Johnson-Murray 1977). They generally swoop upwards over the last few metres before landing until the speed is reduced by gravity providing them with a softer landing. During landing all four feet are used, increasing traction, with the front feet landing on the tree slightly before the hind feet. Except for the sound of the strong claws gripping the bark, the landing is almost silent, like the rest of the glide so they gain little attention from predators. Similar landings have been observed for other species of gliding mammals such the squirrel glider (*Petaurus norfolcensis*)(Archer & Clayton 1984), sugar glider (Suckling 1983), greater glider (Fleay 1947; McKay 1983), scaly-tailed squirrels (Kingdon 1974) and in a number of flying squirrels (Johnson-Murray 1977; Nowak 1991; Wells-Gosling 1985). In contrast to these species, the feathertail glider brings its tail well forward prior to landing making its body into somewhat of a parachute (Hare & Lambert 1995).

The petaurids may have developed the partial vertical septum in the pouch (when young are present) potentially to separate the pouch into two halves to assist in landing. Therefore as they have 1-2 young, when they land the young are positioned on either side of the centre of the body and are not subjected to the full force of impact upon landing. The yellow bellied glider has evolved this to the highest degree, having developed two pockets, one on each side of the body, that are separated by a well developed furred septum and containing only one teat each, instead of having a total of four teats as in other possums, including the mahogany glider and sugar glider (Craig & Belcher 1980).

7.4 Discussion

7.4.1 Gliding Efficiency

The average angle of descent for both the mahogany glider and the sugar glider are very similar to that recorded for the yellow-bellied glider of approximately 31° (Goldingay pers. comm.). Wakefield (1970) suggested a glide angle of 40° for the greater glider, and proposed the decrease in efficiency was caused by the attachment of the patagium to the elbow and its larger weight. Although as shown in Fig. 7.4, the patagium area is that expected for a species of its size. Similar to the mahogany glider and the sugar glider, Parker (1990) proposed a glide ratio for the flying squirrels and the scaly-tailed squirrels of between 1 and 3. In contrast to all other mammals the colugos (Dermoptera) has been observed to glide 136m with a loss in altitude of only 12m, giving a glide ratio of better than 11:1 as a result of its very large patagium surface area (Lekagul & McNeely 1977).

Although authors such as Saville (1962) suggest that small increments of lift (eg. by increasing the patagium surface area) will increase the length of the glide path (efficiency), Caple *et al.* (1983) proposed that small increments of lift add only minute distance to the length of the glide path. Caple *et al.* (1983) state that other factors such as wind, terrain, launch speed and height of launch would all have a greater effect on the length of glide path than small additions of lift.

It is difficult to compare the efficiency of gliding in the petaurids with other groups, as only approximate glide distances, angles and ratios have been recorded, with the height of launch being almost never recorded. As distance is directly related to launch height, measurements of distance alone cannot be used to determine the efficiency of gliding.

The lower height of launch and the occurrence in closed canopy observed for the sugar glider compared to the mahogany glider is supported by Thorington and Heaney (1981), who suggested that lighter gliding mammals (such as the sugar glider) have lower patagium loadings and are therefore vulnerable to gusts of wind and air turbulence, as they do not "penetrate" the air well. In contrast, heavier animals (such as the mahogany glider) have higher wing loadings and are less affected by air turbulence. Thorington and Heaney (1981) proposed that heavier flying mammals must glide faster to maximise the glide ratio, thereby leaving less time to steer. From these observations Thorington and Heaney (1981) proposed the most lightly loaded flying mammals are best adapted to gliding in the mid canopy with a thicker understorey, and where slow flight speed and high manoeuvrability are important, while heavier species with a more loaded patagium are better adapted to more open areas, where air turbulence is more of a problem and manoeuvrability is less of one. The preference of the smaller sugar glider for closed canopy and the larger mahogany glider for more open canopy has been shown in Chapter 4. Similar observations of habitat utilisation were found by Davey (1984) in southern Australia who found the smaller sugar glider to spend most of the time in the lower stratum containing *Acacia* trees while the larger squirrel glider spends more time in the upper canopy.

7.4.2 Comparison of the Patagium of *Petaurus* with Other Gliding Mammals

The patagium or gliding membrane generally consists of three parts. The neck membrane or propatagium which attaches at both sides of the neck and along the anterior edge of the arms; the flank membrane or plagiopatagium which extends between the arms and the legs; and the tail membrane or uropatagium which extends between the posterior surface of the hind legs and the tail (Parker 1990). The patagium consists of a fold of skin with the two layers bound together tightly by connective tissue. Through this connective tissue run numbers of muscles or individual muscle fibres which retract the patagium when not in use and control its attitude while gliding (McKay 1989). The musculature of the patagium has been described by Johnson-Murray (1987). She found the patagium of the members in the genus *Petaurus, Petauroides volans* and *Acrobates pygmaeus* differ greatly, suggesting an independent evolution of the structure in these three groups.

In *Petaurus*, the plagiopatagium is well developed, extending from the joint of the second and third phalange in the fifth digit (with a fringe of fur extending to the base of the claw) to the metatarsal region in the ankle. A similar arrangement is found in the plagiopatagium of the Petauristinae (Sciuridae), although they possess a thin cartilaginous spur leading from the wrist that stiffens, supports, and helps unfold the lateral leading edge of the plagiopatagium (Macdonald 1985; Parker 1990). Both the propatagium and uropatagium are poorly developed in *Petaurus, Petauroides* and *Acrobates* (Johnson-Murray 1987). In these species, the propatagium is represented by only a flap of skin and the uropatagium is represented by a slight expansion of the caudal skin (Johnson-Murray 1987). All species of flying squirrels and scaly-tailed squirrels, except the flightless *Z. insignis*, possess a propatagium. All scaly-tailed gliders, except the non gliding *Z. insignis*, have a uropatagium (Kingdon 1974; Parker 1990; Roberts 1977). The uropatagium in flying squirrels varies greatly generally increasing proportionally in size with the increasing size of the species. Ranging from a slight expansion of the caudal skin between the hind limbs and the tail in *Glaucomys* and *Petinomys* (Johnson-Murray 1977), being slightly more extensive in *Pteromys*, with *Petaurista* having a very large membrane extending between the ankle and the proximal one-third of the tail (Johnson-Murray 1977).

In the greater glider the patagium extends from the elbow to the lower portion of the tibia near the ankle. Similar to the greater glider, although somewhat more developed, the Anomaluridae have a plagiopatagium extending from between the forelimbs (between the wrist and the elbow) and the ankle (Nowak 1991). An accessory styliform cartilaginous strut projects from the elbow joint of the Anomaluridae, not the wrist as found in the Petauristinae, and helps support the leading edge of the plagiopatagium, effectively increasing the size of the patagium (Nowak 1991; Pennycuick 1972; Johnson-Murray 1987; Parker 1990). Similar to the Anomaluridae and Petauristinae, and unique amongst Australian gliders *Petauroides* has a styliform cartilage, which like the Anomaluridae extends from the elbow, although is only poorly developed (Johnson-Murray 1987).

The lemuroid ringtail possum (*Hemibelideus lemuroides*), a true rainforest species of possum (which is closely related to *Petauroides volans*) has a vestigial flaps of skin, less then 25mm wide in the axilliary and inguinal regions. It does not glide, instead it leaps from branch to branch appearing to somewhat flatten its body (Cairn & Grant 1890; Johnson-Murray 1987; McKay 1989). Winter (1983) noted that leaps of two to three metres are frequently made, with legs outstretched like those of a glider, landing heavily on a cushion of foliage. Nowak (1991) went further suggesting that some of these long jumps have the appearance of true glides. This is supported by Johnson-Murray (1987) who proposed the lemuroid ringtail possum should be capable of limited gliding. Potentially the lemuroid ringtail possum is in a state of progressive, rather than regressive, evolution. This idea is supported by Johnson-Murray (1987) who proposed the lemuroid ringtail possum is both morphologically and functionally intermediate between the gliding and non-gliding phalangers, and Fleay (1947) who suggested the lemuroid ringtail possum was some distance along the road to development as a volplaning type.

The feathertail glider possesses a narrow gliding membrane, compared to the gliding petaurids, along the sides of its body between the elbow and the knee, although its effective size is increased by long hairs that form a fringe along its margin (Jones 1924; Russell 1983).

In comparison with *Petaurus* and all other mammals that glide, gliding reaches its greatest development in the Dermoptera. The two species of *Cynocephalus* have become the ultimate gliders with every adaptation possible being utilised to assist gliding, allowing them to make glides of over 100m with little loss of altitude. The patagium surrounds almost the entire body. It includes a well developed propatagium, and plagiopatagium. The plagiopatagium even extends to the base of the claws on both the hands and feet, so the thumbs cannot be opposed to the other four fingers. This makes it difficult for the animal to grasp branches and twigs, resulting in their movement in trees being awkward (Parker 1990; Pennycuick 1972). The uropatagium is also far more extensive than in any other gliding mammal, enclosing the entire tail (Parker 1990). As a result of the distinctive cranial and cervical wing muscles, Thewissen and Babcock (1991) proposed the Dermoptera and bats share a common ancestor. They also suggested that Dermoptera are an appropriate structural intermediate between quadrupedal mammals and flying bats.

When examining the influence of fur cover on air flow and generation of aerodynamic force components Nachtigall (1979b) found the fur of sugar gliders acts as a lift generator during gliding flight. Similarly the flying membrane of the Petauristinae was described as heavily coated on top and sparsely covered on the underside (Parker 1990). The fur on the undersurface of the patagium of colugos was also described by Taylor (1934) to be less and shorter.

7.4.3 Development of Limbs

In association with the development of the patagium there have been other adaptations in *Petaurus* and *Petauroides* that assist in their gliding ability. As the patagium in *Petaurus* extends from the manus, compared to the elbow in *Petauroides*, the need for longer bones to increase the surface area to weight ratio is reduced (McKay 1989). McKay (1989) found the skeletons of *Petaurus* and *Gymnobelideus* to show only a slight elongation of the bones of the limbs, and virtually no elongation of the tail compared to similar sized non-gliding possums. In contrast Runestad and Ruff (1995) found the relative humeral and femoral lengths between gliding and non gliding mammals (including possums) to increase progressively at larger body masses. Similar results were observed by Thorington and Heaney (1981), who found that large gliding squirrels to have longer forelimbs than do large nongliding arboreal squirrels. A marked difference has been observed in *Petauroides* which has developed longer bones in both the arms and the legs compared to the limbs of the similarly weighted non gliding *Pseudochèirus* (McKay 1989). This is reflected in the patagium surface of *Petauroides* being of the area predicted for an animal of its size (Fig. 7.4).

Similar to *Petauroides* the arms and legs of the Petauristinae are relatively longer than those of the equally sized tree squirrels (Parker 1990; Thorington & Heaney 1981).

Unlike *Petaurus* and *Petauroides*, *Acrobates* shows no marked elongation of vertebrae or limb bones associated with the evolution of volplaning (McKay 1989). McKay (1989) suggested that in such a small animal the presence of the patagium alone presumably is sufficient to provide the necessary increase in surface area.

7.4.4 Tail Morphology and Weight

Gliding mammals weighing 70g or less, regardless of taxonomic group, have dorsoventrally flattened featherlike tails, with the exception of *Petinomys vordermanni* and *Petinomys setosus* and which have tails that are flattened on the bottom and bushy on top (Table 7.3). The presence of a flattened tail was suggested by Norberg (1985) to help in the longitudinal (or pitch) control during gliding. Between 70g and approximately 350-450g there is a transitionary group of tail types that includes genera that have flattened, featherlike tails such as within the genus *Hylopetes*, tails that are flattened on the bottom and bushy on top such as in *Petinomys* and *Belomys* and a number of species within the genera *Petaurus* and *Anomalurus* that have a rounded and bushy tail. Species weighing more than approximately 450g, with the exception of *Petinomys crinitus* and the two species of *Cynocephalus* (whose tail is totally enclosed as part of a uropatagium) all have rounded bushy tails and include the genera *Petaurista*, *Aeromys*, *Eupetaurus*, *Petaurus* and *Petauroides*. Within the genus *Petaurus* there is some variation in tail type with the lighter sugar glider having a less bushy tail than the other heavier members of the genus. Potentially the same occurs with other genera such as *Hylopetes* and *Petinomys* which have several species of different weights.

Scaly-tailed squirrels have a relatively long thin, bushy tail which has an underside that contains an area of rough, overlapping scales near the base of the tail extending from one fourth to one third the length of the tail (Parker 1990). Although authors such as (Parker 1990) have referred to these scales as an "anti-skid" device during landing or climbing, Kingdon (1974) suggests they do not put the whole weight of their body onto the scaly tail while climbing. He suggested that the tail plays an incidental role in climbing, and is often used in the normal passive resting posture.

There is a tradeoff between the weight of an animal, the maximum available patagium surface area, and the distance an animal can glide. Therefore when considering all of the gliding mammals there should be a most efficient weight and size range. As the weight of a species increases further from the optimum weight range it should theoretically result in an increasingly less efficient glide, with decreasing glide ratio and increasing glide angle until a point where gliding is no longer feasible. Every species of gliding mammal has been assigned to a different weight class in Fig. 7.5. This clearly shows the most common weight range is approximately 500g or less. Above approximately 500g the efficiency is predicted to decrease until the upper weight limit is reached which is approximately 4200g (Fig. 7.5 & Table 7.3).

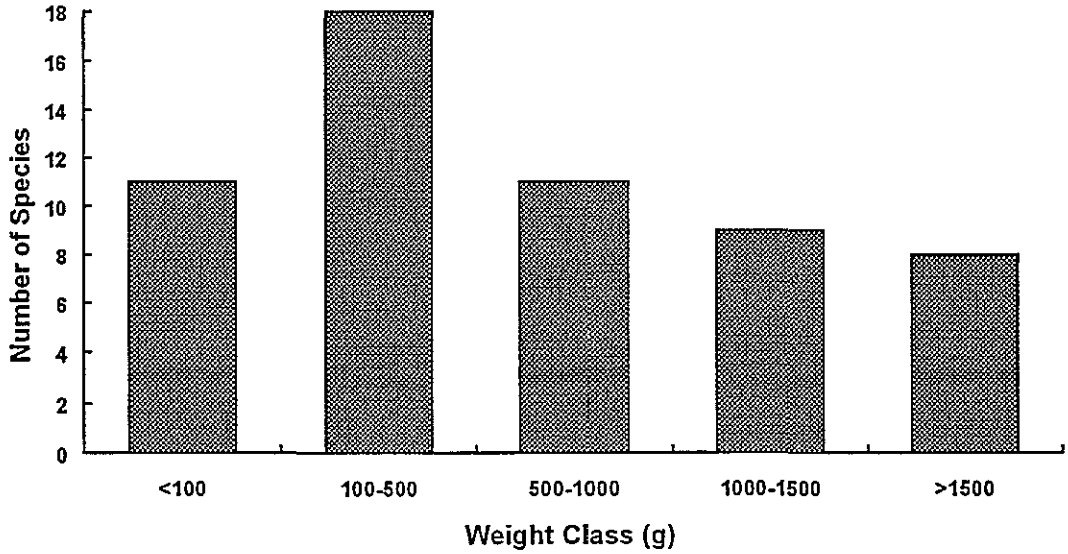


Figure 7.5. Weight classes of all species of gliding mammals. Weights classes derived from Table 7.3.

Table 7.3. List of all species of gliding mammals according to known or derived weight. Also includes known tail types, head lengths and body lengths. Marsupial gliding mammals are in bold. Taxonomy follows Wilson & Reeder (1993) and Flannery (1994).

Species	Taxonomic Group	Description of Tail	Weight (g)	HB (mm)	TL (mm)	Ref.
Acrobates pygmaeus	Acrobatidae	flattened, featherlike	10-14	65-80	70-80	1
Petaurillus emiliae	Petauristinae	flattened, featherlike	c. 13.5	68-72	62-67	2,3,4
Idirurus zenkeri	Anomaluridae	flattened, featherlike	14-17.5	65-90	70 -130'	5,6.
Petaurillus hosei	Petauristinae	flattened, featherlike	c. 21.1	75-90	80-98	2,3,4
Petaurillus kinlochii	Petauristinae	fattened, featherlike		c. 87	c. 83	7
Hylopetes lepidus	Petauristinae	flattened, featherlike	21-51.5	117-150	85-130	2,3,7,8
Petinomys vordermanni	Petauristinae	flattened/bottom-bushy/top	23-52	92-120	90-120	2,3,9
Idiurus macrotis	Anomaluridae	flattened, featherlike	25-35	87-93	121-127	10
Petinomys setosus	Petauristinae	flattened/bottom-bushy/top	31-58	105-128	93-118	2,7,8,9
Hylopetes spadiceus	Petauristinae	flattened, featherlike	37-157	135-184	102-166	2,7,9
Glaucomys volans	Petauristinae	flattened, almost parallel sided.	46.5-85	198-255	81-120	10, 11
Petinomys genibarbis	Petauristinae	flattened, broad.	52-110	142-180	160-185	2,7,8,9,12
Petaurus breviceps	Petauridae	rounded, bushy - short haired.	69-150	160-210	165-210	1,13,14
Petaurus biacensis	Petauridae	rounded, bushy	87-90	140-150	145-175	15
Hylopetes bartelsi	Petauristinae	flattened, featherlike	c. 87.5	133-145		3,4
Hylopetes sipora	Petauristinae	flattened, featherlike	c. 89.2	c. 140		3,4
Hylopetes winstoni	Petauristinae	flattened, featherlike		c. 142		3
Glaucomys sabrinus	Petauristinae	flattened, featherlike	110-185	135-190	115-160	10, 16
Iomys horsefieldi	Petauristinae	flattened	120-231	146-231	159-210	2,12
Iomys sipora	Petauristinae	flattened		c.173-205	c.185-192	17
Pteromys momonga	Petauristinae	flattened	120-220	140-200	100-140	18,19,20
Pteromyscus pulverulentus	Petauristinae	flattened, bushy.	134-315	204-290	177-236	2,7,9,12
Pteromys volans	Petauristinae	flattened.	140-200	120-228	100-140	10,12,20
Petinomys sagitta	Petauristinae	flattened, broad		c. 190	c. 170	21
Hylopetes phayrei	Petauristinae	flattened, featherlike	153-189	144-197	135-174	3,4,8
Petaurus norfolcensis	Petauridae	rounded, bushy	190-300	180-230	220-300	1
Belomys pearsoni	Petauristinae	flattened, fairly bushy on top.	c.217	194-250	125-158	4,8
Petaurus abidi	Petauridae	rounded, bushy	228-332	245-276	345-385	14
Hylopetes alboniger	Petauristinae	flattened, featherlike	c.244-236	175-225	181-200	3,4,8
Petinomys hageni	Petauristinae	flattened/bottom-bushy/top	c. 388	230-250	235-250	3,4.
Petinomys fuscocapillus	Petauristinae	flattened/bottom-bushy/top	300-712	c. 250		3,4
Anomalurus pusillus	Anomaluridae	rounded, bushy	300-600	210-246	138-157	6,10
Hylopetes fimbrianus	Petauristinae	flattened, featherlike	300-510	235-297	252-330	4,10,22
Petaurus gracilis	Petauridae	rounded, bushy	350-450	c. 250	c. 350	13
Trogopterus xanthipes	Petauristinae	rounded, bushy		267-305	267-280	12
Petinomys lugens	Petauristinae	flattened/bottom-bushy/top	c. 433	230-270	210-235	3,4.
Petaurus australis	Petauridae	rounded, bushy	450-700	270-300	420-480	1
Anomalurus derbianus	Anomaluridae	rounded, bushy	450-1100	270-380	220-320	5,6,10
Hylopetes nigripes	Petauristinae	flattened, featherlike	c. 534	250-330	250-310	3,4,23,
Anomalurus beecrofti	Anomaluridae	rounded, bushy?	600-700	253-310	186-238	5,6,10
Aeretes melanopterus	Petauristinae	rounded, bushy		c. 305	330-356	12
Petauroides volans	Pseudocheiridae	rounded, bushy	650-1700	350-450	450-600	1
Hylopetes baberi	Petauristinae	flattened, featherlike	c. 712	c. 300		3
Petinomys fuscocapillus	Petauristinae	flattened/bottom-bushy/top	c. 794	c. 320	244-290	24
Petaurista leucogenys	Petauristinae	rounded bushy	700-1500	270-490	280-410	18,19,20
Petaurista elegans	Petauristinae	rounded, bushy	840-1560	338-365	340-370	2,3,4,8
Cynocephalus variegatus	Dermoptera	totally enclosed in uropatagium	925-1750	340-420	175-270	2,8
Cynocephalus volans	Dermoptera	totally enclosed in uropatagium	1000-1500	330-380	220-270	10
Petaurista petaurista	Petauristinae	rounded, bushy	1070-3190	285-464	375-610	2,3,4,7,8,10
Aeromys tephromelas	Petauristinae	rounded, bushy	1128-1250	355-426	410-527	2,7,8
Petinomys crinitus	Petauristinae	flattened/bottom-bushy/top	c.1130	310-400	300-400	3,4

Table 7.3 cont.

Aeromys thomasi	Petauristinae	rounded, bushy	1380-1490	350-403	340-430	2
Anomalurus peli	Anomaluridae	rounded, bushy	1035-1800	400-460	320-450	5
Biswamoyopterus biswasi	Petauristinae	rounded, bushy		c. 405	c. 605	12
Petaurista magnificus	Petauristinae	rounded, bushy	c. 1780	420(max)	480 (max)	3,4
Petaurista xanthotis	Petauristinae	rounded, bushy	c. 1900	430 (max)	345 (max)	3,4
Petaurista nobilis	Petauristinae	rounded, bushy	c. 2710	490 (max)	460 (max)	3,4
Petaurista philippensis	Petauristinae	rounded, bushy		490 (max)	550 (max)	3
Petaurista alborufus	Petauristinae	rounded, bushy	c. 4290	440-580	430-615	3,4,8,
Eupetaurus cinereus	Petauristinae			515-610	380-480	22

References: 1 Strahan 1995; 2 Payne *et al.* 1985; 3 Corbet & Hill 1992; 4 Silva & Downing 1995; 5 Diller 1977; 6 Kingdon 1974; 7 Medway 1978; 8 Lekagul & McNeely 1977; 9 Muul & Liat 1971; 10 Parker 1990; 11 Dolan & Carter 1977; 12 Nowak 1991; 13 Chapter 3; 14 Flannery 1995b; 15 Flannery 1995a; 16 Jameson & Peters 1988; 17 Chasen & Kloss 1928; 18 Ando & Shiraishi 1984; 19 Ando & Shiraishi 1991; 20 Abe *et al*, 1994; 21 Harrison 1973; 22 Roberts 1977; 23 Taylor 1934; 24 Phillips 1980.

7.4.5 Gliding Techniques

Petaurus glides with fore- and hind limbs fully extended at right angles to the rest of the body and the forefeet flexed slightly upward (Fig. 7.6). A similar technique is used by the Petauristinae (Nowak 1991). The aerodynamics of gliding in the sugar glider has been studied in detail by Nachtigall *et al.* (1974) and Nachtigall (1979a & 1979b). In *Petaurus* and *Petauroides* the limbs and musculature attached to the patagium are used to control the attitude of the airfoil (Nachtigall *et al.* 1974; McKay 1989). Remarkably, Adams (1958) reported seeing an individual of the flying squirrel (*Hylopetes lepidus*) gain 1m of elevation over a distance of 6m by using vigorous flapping movements of the skin between the fore and hind feet. This has been suggested by Parker (1990) to add support to the idea that active flight developed from gliding flight. Norberg (1985) also proposed that even slight flapping in a gliding animal can produce a horizontal net thrust force while the necessary vertical lift is still maintained. Although Padian (1982) suggested that gliders are structurally and aerodynamically different from active fliers, and that gliding and active flight are used for two different things. Caple *et al.* (1983) went further suggesting that flapping motions would modify the shape of the patagium causing major shifts in the location of the centre of lift relative to the animals centre of mass creating serious problems with stability and lift. Indeed Caple *et al.* (1983) suggest that flapping a proximal, flexible membrane will result in a loss of lift.

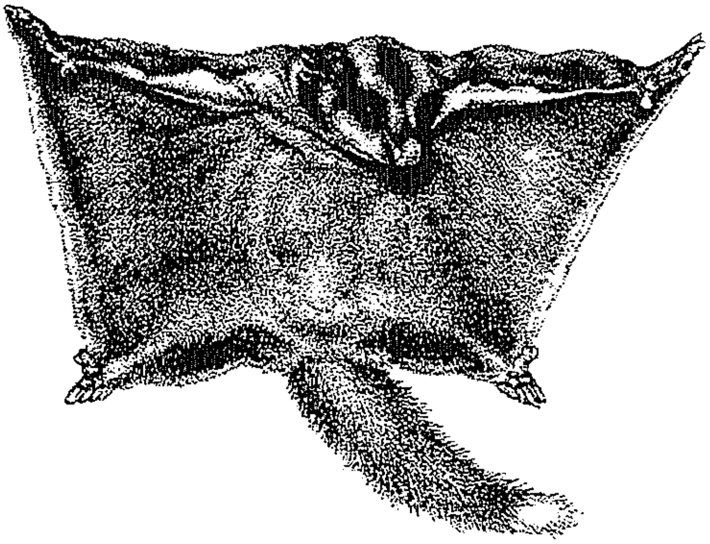


Figure 7.6. Gliding behaviour of the sugar glider. Figure from McKay 1989.

Petauroides glides with the hind limbs fully extended, but with the forefeet tucked under the chin and the elbows extended (Fig. 7.7). Wakefield (1970) suggested the yellow-bellied glider, and hence *Petaurus* in general, are more manoeuvrable in the air than *Petauroides.* This may indeed be the case as they can change the angle of the arms, and therefore the shape of the patagium more easily than *Petauroides.*

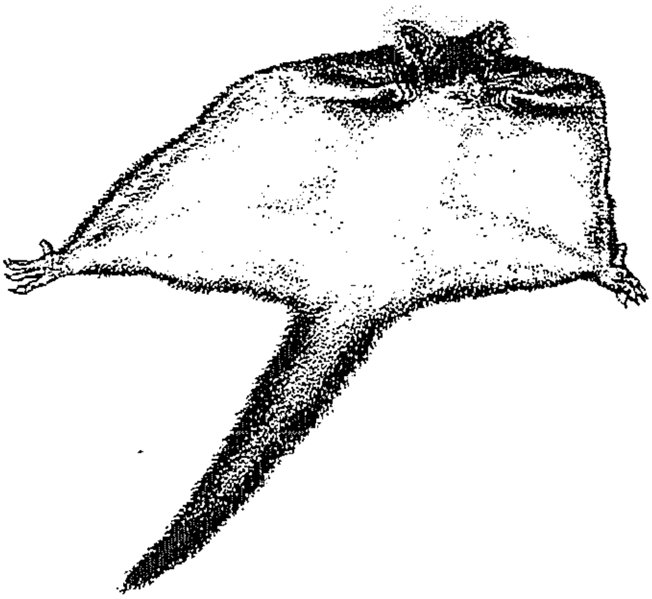


Figure 7.7. Gliding behaviour of the greater glider. Figure from McKay 1989.

The feathertail glider uses its flattened tail for steering as it jumps from branch to branch (Fig. 7.8). When gliding larger distances such as from the top of a tree they are able to glide quickly from tree to tree, or can spiral somewhat like a falling leaf (Pers. obs).

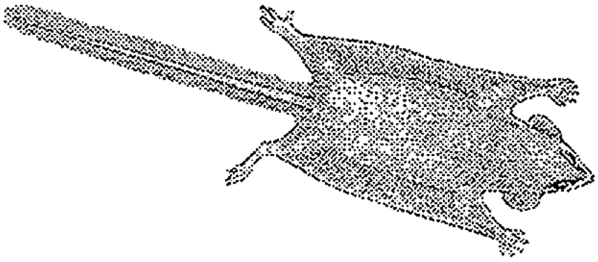


Figure 7.8. Gliding behaviour of the feathertail glider. Figure from Turner & McKay 1989.

7.4.6 The Evolution of Gliding in Australian Marsupials

Petaurids have been poorly represented in the fossil record until with the oldest reported material found being from the early Pliocene Hamilton Local Fauna (5.2 - 2 million years ago, MYA) (Turnbull & Lundelius 1970; Turnbull *et al.* 1987). Definite petaurids have been collected in material collected of middle Miocene age (15.5 - 11 MYA) from the Riversleigh deposits of north-western Queensland (Aplin & Archer 1987). A rich pile of petaurid-like animals has been found, yet to be examined in detail, that contains taxa in many of the Oligo-Miocene local faunas some 23 million years ago (Archer *et al.* 1991). Archer *et al.* (1991) suggest that none of them appear particularly close to any living petaurid genus, with one genus being temporarily labelled '*Pre-petaurus*' which has *Petaurus*/ *Gymnobelideus*-type morphology.

The fossil record of *Petauroides* also appear at least as early as the early Pliocene in the Hamilton Local Fauna deposits, with the presence of *Petauroides stirtoni* (Archer & Clayton 1984). No fossils of the genus *Petauroides* have been found in the Riversleigh deposits so far and suggest the evolution of this lineage could have started in rainforest, where the lemuroid ring-tail still persists (Archer *et al.* 1991). Archer and Clayton (1984) however suggest the greater glider's original habitat is likely to have been more like the open forests it occupies today.

Archer *et al.* (1991) have found the fossil record of *Acrobates* to be quite poor with the first fossils of the genus not being found until 1985. They found since found a number of teeth and a whole jaw have since been found from the Oligo-Miocene period, although it has been suggested that it has yet to be established whether this taxon is a species of *Acrobates*, *Distoechurus* or a new taxon structurally between the two living forms (Archer *et al.* 1991).

The most reasonable explanation for developing the ability to glide may be an adaptation to the opening up of Australia's forests as the climate dried. As the trees moved further apart the possums had to jump further and further, ultimately ending up with a membrane to facilitate gliding so they could travel between the now well spread out trees. This idea was proposed by Archer and Clayton (1984) who suggested that, at least as far as the species of the genus *Petaurus* is concerned, their apparent lack of appearance prior to the Pliocene may reflect the fact that open forests (the habitat of gliders) were not as widespread as they are today until the very end of the Tertiary. Archer and Clayton (1984) go on to suggest that in closed forests, there would be little point in evolving the capacity to glide. Perhaps it was not until the late Miocene, when the central Australian closed forests were beginning to open out there was a selective pressure on arboreal possums to develop the ability to glide (Archer & Clayton 1984). Flannery (1994) also suggests that gliding membranes are an adaptation to life in forests with an incomplete canopy, such as eucalypt forest, but not rainforest.

More recently, Archer *et al.* (1991) revisited several fossil finds from Hamilton, which were similar to, but different from, living squirrel gliders (*Petaurus norfolcensis* and sugar gliders. They questioned whether these could have been inhabitants of Victorian rainforests, although they suggested that it was difficult to conceive of a need to glide in a rainforest where all the crowns are touching, and noted the presence of a pre-greater glider in the same fossil deposits would indicate the idea of rainforest gliders should not be too quickly abandoned.

Although it appears most likely that gliding in the Australian possums evolved because of the opening up of the native vegetation, the evolution of gliding within Australia's rainforests should not necessarily be ruled out. Strong evidence for the evolution of gliding in rainforest is provided by the northern glider (*Petaurus abidi*) which is found at an elevation of approximately 1000m in thick undisturbed rainforest on Mount Somoro in the Torricelli mountains in New Guinea (Zeigler 1981; Flannery 1995b). The colugos, which are by far the most well developed gliding mammals, live in evergreen rainforests of southeast Asia (Parker 1990). Parker (1990) also noted that scaly-tailed squirrels are found only in tropical Africa, where they inhabit rainforests. Similarly Harrison (1973) and Lekagul and McNeely (1977) found that flying squirrels are mostly confined to rainforest. Hopefully as more fossil petaurid marsupials are found a clearer picture will emerge on the origin and reasons for the development of gliding within the marsupials.

7.4.7 Advantages of Gliding

However gliding evolved, there are several advantages that this increased ability in movement has allowed. The primary energetic cost of life in the trees is the mechanical work of lifting the body (Dawson *et al.* 1989). This work is the product of the body size times the gravitational acceleration times the height to be climbed (Calder 1984). Gliding between trees is much cheaper energetically and much quicker than running (Norberg 1985). When gliding, the animal makes use of potential energy gained during the previous climb up the tree, with little energy required for steering, making gliding a very cheap way of moving from one place to another (Norberg 1985).

Gliding allows animals to forage more quickly and over a wider area than would otherwise be possible (Hildebrand 1988). In some habitats where food is limited and widely spread, adaptations such as gliding increase mobility and therefore food harvesting rates (Smith 1982). Gliding also allows an animal to have a large enough home range to fulfil the energy requirements for their mass and optimise foraging efficiency, particularly when there is a patchy food resource (Suckling 1983). Gliding mammals also have an advantage over flying animals in that as their forelimbs are not greatly specialised, they remain useful for climbing and the manipulation of food (Hildebrand 1988).

Gliding may have developed not so much caused by an opening of the forest but more as a result of diet. Possums such as those within the families Pseudocheiridae and Phalangeridae are folivores and have a ubiquitous diet which is easily obtained within a fairly small area. The greater glider which is the most folivorous of the Pseudocheiridae may have had to develop gliding in order to conserve energy because of the poor quality of its diet and the inefficient digestion of its food caused by their small body size. Possums such those within the genera *Petaurus* and *Acrobates* which feed on exudates from plants such as sap, manna, honeydew and nectar and supplement their diet with insects, have a much more widespread and patchy food source. Therefore the development of gliding allows them to cover the larger distances to obtain their dietary requirements more efficiently.

Although the trend of smaller mammals with a spatially patchy diet may hold for most marsupials, amongst the flying squirrels, scaly tailed rodents and the colugos there are many species that have a herbivorous diet (Muul & Liat 1978). These groups nonetheless follow the same trend as the marsupials with the smaller species feeding on more digestible food items and becoming more folivorous with an increase in weight (Muul & Liat 1978). Therefore gliding does not appear to have been selected in these groups because of food being scattered or patchy.

Gliding has major advantages over climbing for arboreal mammals, as it potentially provides better predator avoidance by assisting in escaping from predators while in trees. Gliding also decreases the opportunity of being taken by predators from the ground, as gliding mammals are able to jump from tree to tree instead of going to ground to travel from one tree to the next, although Stapp (1994) suggested that a nocturnal gliding lifestyle may not afford flying squirrels such as *Glaucomys volans* and *Glaucomys sabrinus* with any greater immunity to predators than that already achieved by being arboreal and a cavity nester as they have numerous avian and mammalian predators. Indeed Scheibe *et al.* (1990) suggested that although gliding may provide flying squirrels with an escape from mammalian and reptilian predators, they may actually suffer increased levels of predation from owls.

The patagium itself can also be useful as a trapped mahogany glider was observed to pull its patagium over its head somewhat like an umbrella when it was raining (pers. obs.). Although not mentioning which species, Parker (1990) noted an observation of gliding squirrels using their patagium apparently as a blanket by wrapping it around their bodies, therefore protecting themselves from heat loss, although it was suggested that when the weather was hot, the gliding membrane has no heat-dissipating effect. Another advantage of gliding is that, at least in the case of the mahogany glider and sugar glider in north Queensland, the ground underneath is often very muddy during the wet season, therefore this allows them to keep clean and dry as they move around. Gliding also means they do not leave a continuous scent trail.

7.4.8 Disadvantages of Gliding

Although the members of Petauristinae, Anomaluridae and the marsupial gliders are generally considered to be excellent climbers (Parker 1990), the presence of the patagium in gliding mammals has been suggested to make them less agile than non gliders (Harrison 1973; Macdonald 1985). The extreme case of this is the Dermoptera which have evolved by far the most sophisticated patagia, however as a result their movements on the ground and in the branches are awkward and sloth like (Lekagul & McNeely 1977; Parker 1990). In particular the membranes between their fingers and toes appears to greatly decrease their climbing ability (Parker 1990).

Macdonald (1985) proposed that it is probably significant that mammals that have adopted a gliding habit are active only at night when they are less conspicuous to keen-sighted birds of prey. This suggestion is well supported by all of the gliding mammals, as the colugos are strictly nocturnal (Lekagul & McNeely, 1977; Parker, 1990), while Parker (1990) also noted that unlike tree squirrels, the flying squirrels are active only at night. Similar observations have been made by Hall & Kelson (1959), Roberts (1977) and Medway (1978) for the Petauristinae and Diller (1977) who noted the Anomaluridae to be nocturnal.

The gliding members of the Phalangeroidea (possums) may be different to the Dermoptera, Petauristinae and Anomaluridae as they were almost certainly already nocturnal, then developed a gliding membrane. Whereas at least some of the eutherian gliding mammals may well have been diurnal, then developed a gliding membrane and secondarily become nocturnal.

7.4.9 Management Considerations for Gliding Possums

Arboreal mammals such as the gliding possums are limited in their movement by the maximum gliding distance between successive trees. Therefore they are highly sensitive to habitat fragmentation and are easily isolated by gaps in their habitat, as they do not readily cross open ground (pers. obs.). If they do come to the ground they are prone to predation from cats, dogs and snakes.

Barbed wire fences are often located parallel along the edge of gaps such as roads, tracks and powerlines. Barbed wire is a significant problem for all species of gliding possums with numerous gliding possums being known to have fallen victim to barbed wire fences (pers. obs.; Lyon 1993; Smith, K. pers.comm.; Van Dyck 1993). The incidence of gliding possums being caught on barbed wire fences is certainly likely to have increased recently as their habitat has become more fragmented, and the need to travel to isolated patches to feed has increased. In order to reduce the incidence of mortality from barbed wire fences, they should only be used when absolutely necessary, with plain wire being used instead. When a track or fenceline is made through glider habitat, the gap between points should not exceed 20m, assuming an average height of trees on each side of 15-20m. This will hopefully allow the animals to land somewhat up the target tree and above any fences.

Chapter 8

Climatic Modelling of the Distribution of the Mahogany Glider and Squirrel Glider, with Implications for their Evolutionary History.

8.1 Introduction

Extensive surveys have revealed that the mahogany glider *Petaurus gracilis* is very restricted in its distribution (Eyre 1993; Lyon 1993; Van Dyck 1993; Goldingay & Carthew 1996; Smith 1996; McKay 1997; per. obs.). The mahogany glider has only been recorded in a narrow band of woodland on the coastal lowlands between the Hull River near Tully and approximately 30km south of Ingham in north Queensland, a distance of 108km north to south and 2 to 12km east to west (Fig. 1.1). Throughout its distribution, the species has been found at elevations up to approximately 500m, with most records below 120m. Considering these geographic and altitudinal limits, a maximum available area approximately 87,200 hectares is potentially habitat (Qld. Dept. of Env. & Heritage, pers. comm.).

As climate sets broad limits to the distribution of most species (Lindenmayer *et al.* 1990b), techniques that utilise information of the climate where species occur in known locations can be valuable in predicting where they may occur outside their known range. A useful method for predicting the potential distribution of species is the advanced bioclimatic program BIOCLIM. This program uses locational and climatic information to reflect the key processes that restrict the distribution of species (Switzer 1991), and has been used on several species of Australian mammals including the squirrel glider *Petaurus norfolcensis* (Menkhorst *et al.* 1988), Leadbeaters's possum *Gymnobelideus leadbeateri* (Lindenmayer *et al.* 1990b, 1991a), golden-tipped bat *Phoniscus papuensis* (Walton *et al.* 1992), common blossom bat *Syconycteris australis* (Law 1994), long-footed potoroo *Potorous longipes* (Busby 1988) and a number of rainforest mammals (Winter 1991).

A preliminary BIOCLIM analysis was conducted on the mahogany glider by Van Dyck (1993) using 28 records collected from December 1989 until October 1992, with one record from 1974. Since 1992, more than 116 additional locations have been determined, which have significantly extended the distribution of the species by approximately 33km (44% increase since Van Dyck (1993)) further south, and significantly increased the maximum known elevation from 90m to approximately 500m. With the inclusion of these recent locations, significant insights can be gained into the climatic limitations that have restricted the mahogany glider to such a small area, and potentially help to predict areas outside the known distribution where it could occur.

The mahogany glider is closely related to the more widespread squirrel glider (*Petaurus norfolcensis*: Van Dyck 1990 & 1993; Colgan & Flannery 1992) which is found along the east coast of Australia from Victoria to north Queensland. In north Queensland the species is found to the south, west and north-west of the mahogany glider's range, therefore all but surrounding it. Considering the close taxonomic relationship of these two species and their geographic closeness to each other, an examination of the present climate within the distribution of these species (and the development of these differences) within Queensland might help explain the evolutionary history of the mahogany glider and why it has such a limited distribution.

8.2 Methods

8.2.1 Species Localities

Mahogany glider locations were determined through extensive spotlighting surveys since 1989 (Eyre 1993; Lyon 1993; Van Dyck 1993; Goldingay & Carthew 1996; Smith 1996; McKay 1997; per. obs.) and from chance localities of individuals caught on fences, road victims and deaths from domestic animals. During these surveys there has been a large amount of effort to extend the known range north, south and west and to higher elevations. A total of 144 mahogany glider locations were used in the subsequent BIOCLIM analysis.

Squirrel glider locations were obtained for localities only within Queensland from Adrian Boorsboom (Qld DPI, pers. comm.), Scott Burnett (pers. comm.), Alex Kutt (pers. comm.), David McFarland (pers. comm.), Queensland Museum, Qld. Dept. of Environment (Nature Search), Daryn Storch (QDE, pers. comm.), Williams *et al.* (1993) and Winter (pers. comm). A total of 237 squirrel glider localities were used in the analysis. For both the mahogany glider and squirrel glider records, the locations were recorded as latitude and longitude which were determined from either a GPS or 1:50,000 topographic maps. Altitudes for each of these records were derived from either an altimeter or from 1:50,000 topographic maps. Any records that appeared to have incorrect latitudinal and longitudinal points were not included.

8.2.2 Distribution Models

The computer program BIOCLIM (Hutchinson *et al.* 1984; Nix 1986; Busby 1991) was used to predict the climatic distributional limits of the mahogany glider and the squirrel glider. BIOCLIM uses accurately determined geocoded points (which have been assigned by their latitude, longitude and elevation) to estimate long-term mean climatic data. This process incorporates mathematical surfaces to a network of existing meteorological station data using Laplacian smoothing splines (Hutchinson & Bischof 1983; Hutchinson *et al.* 1984; Hutchinson 1984). An outline of the procedure followed in bioclimatic analyses can be found in Nix (1986) and Lindenmayer *et al.* (1990b, 1991a). BIOCLIM was used to derive 35 climatic indices at each geocoded site. The 0-100% envelopes were used for the predicted range as there are presently arguments over what is 'core' (optimal climate) and 'marginal' climate (minimum and maximum values) and at what level does habitat and climate become 'marginal' (A. Claridge, ANU pers. comm.). Nix and Switzer (1991) suggest that species may be equally abundant in the 'core' and 'marginal' bioclimatic distributions, but populations in marginal distributions, by definition, are more at risk in the event of habitat disturbance or climate change. The BIOCLIM analysis was run by Dr Andrew Claridge at the Australian National University, Canberra.

8.3 Results

8.3.1 Bioclimatic Profiles of the Mahogany Glider and Squirrel Glider in Queensland

The bioclimatic profiles for the 35 climatic indices derived for the mahogany glider and squirrel glider (Tables 8.1 & 8.2) show the former species to be confined to areas with higher annual mean temperatures (Fig. 8.1a), a smaller temperature range (Fig. 8.1b) and higher temperatures throughout the year (Figs. 8.1c-d). The mahogany glider was also predicted to occur in areas with a much higher annual precipitation (Fig. 8.2a), higher precipitation seasonality (Fig. 8.2b), higher moisture index seasonality and higher precipitation in the wettest quarter (Fig. 8.2c) and warmest quarter (figure similar to 8.2c). The predicted envelope for the squirrel glider had a slightly larger mean precipitation in the driest quarter (Fig. 8.2d), and as result of its much larger geographic range, had a larger variation in most of the bioclimatic variables (Table 8.2). The cumulative frequency curves of a selected subset of climatic variables for both the mahogany glider and squirrel glider are shown in Figures 8.1-8.2. These plots allow a comparison of the bioclimatic domains of the mahogany glider and squirrel glider and show quite clearly the differences between the predicted distribution of these species along these gradients.

Although mahogany gliders have been found up to 500m elevation, 80% of known localities are below 100m with 97% being below 200m, despite considerable effort having been spent searching for mahogany gliders at higher altitudes (Fig. 8.3). Similarly the squirrel glider in Queensland has been found mostly at lower elevations, although there are records over 800m in elevation.

Table 8.1. The bioclimatic envelope of the mahogany glider using BIOCLIM. The associated predicted potential distribution of the species is presented in Figure 8.2. All values for temperatures are in °C and those for precipitation in mm.

Index No.	Description of Bioclimatic Index	Mean	Min.	5%	95%	Max.
1	Annual mean temperature	23.90	22.30	23.70	24.00	24.10
2	Mean diurnal range	10.90	9.60	9.90	12.40	13.40
3	Isothermality (2/7)	0.55	0.53	0.54	0.56	0.57
4	Temperature seasonality	1.00	1.00	1.00	1.00	1.00
5	Max. temperature of the warmest period	32.70	31.80	31.90	33.90	34.30
6	Min. temperature of the coldest period	12.90	9.80	11.90	13.90	14.00
7	Annual temperature range (5-6)	19.80	17.80	18.10	21.80	23.50
8	Mean temperature of the wettest quarter	26.90	25.30	26.60	27.10	27.10
9	Mean temperature of the driest quarter	20.50	18.80	19.60	21.00	22.50
10	Mean temperature of the warmest quarter	27.30	25.80	26.90	27.50	27.50
11	Mean temperature of the coldest quarter	19.80	17.80	19.60	20.00	20.00
12	Annual precipitation	1856.00	1151.00	1380.00	2908.00	3275.00
13	Precipitation of the wettest period	417.00	260.00	314.00	589.00	619.00
14	Precipitation of the driest period	26.00	15.00	16.00	64.00	76.00
15	Precipitation seasonality (C of V)	100.00	80.00	88.00	107.00	108.00
16	Precipitation of the wettest quarter	1192.00	712.00	933.00	1734.00	1825.00
17	Precipitation of the driest quarter	89.00	53.00	55.00	205.00	237.00
18	Precipitation of the warmest quarter	965.00	398.00	721.00	1383.00	1457.00
19	Precipitation of the coldest quarter	100.00	61.00	63.00	231.00	302.00
20	Annual mean radiation	19.60	18.80	19.10	19.80	19.90
21	Highest period radiation	25.40	24.90	25.10	25.50	25.50
22	Lowest period radiation	14.50	13.40	14.10	14.90	14.90
23	Radiation seasonality	19.00	18.00	18.00	19.00	21.00
24	Radiation of the wettest quarter	20.10	19.80	19.80	20.50	20.80
25	Radiation of the driest quarter	18.10	16.10	16.30	18.80	20.70
26	Radiation of the warmest quarter	22.10	21.50	21.60	22.50	24.20
27	Radiation of the coldest quarter	16.30	15.20	15.90	16.60	16.60
28	Annual mean moisture index	0.70	0.60	0.62	0.86	0.92
29	Highest period of moisture index	1.00	1.00	1.00	1.00	1.00
30	Lowest period of moisture index	0.21	0.10	0.11	0.45	0.60
31	Moisture index seasonality	48.00	15.00	24.00	60.00	61.00
32	Mean moisture index of the highest qtr.	1.00	1.00	1.00	1.00	1.00
33	Mean moisture index of the lowest qtr.	0.26	0.14	0.15	0.60	0.72
34	Mean moisture index of the warmest qtr.	0.84	0.54	0.76	0.94	0.96
35	Mean moisture index of the coldest qtr.	0.64	0.38	0.45	0.95	1.00

Table 8.2. The bioclimatic envelope of the squirrel glider in Queensland using BIOCLIM. The associated predicted potential distribution of the species is presented in Figure 8.3. All values for temperatures are in °C and those for precipitation in mm.

Index No.	Description of Bioclimatic Index	Mean	Min.	5%	95%	Max.
1	Annual mean temperature	20.20	16.50	18.50	23.40	26.10
2	Mean diurnal range	11.60	7.90	9.40	14.10	15.20
3	Isothermality	0.52	0.47	0.49	0.56	0.62
4	Temperature seasonality	1.00	1.00	1.00	2.00	2.00
5	Max. temperature of the warmest period	30.00	25.70	28.30	33.20	36.80
6	Min. temperature of the coldest period	7.70	1.40	4.10	12.20	17.40
7	Annual temperature range	22.30	16.40	18.50	26.50	29.60
8	Mean temperature of the wettest quarter	24.30	20.70	23.10	26.80	27.90
9	Mean temperature of the driest quarter	16.00	12.00	13.80	19.90	24.00
10	Mean temperature of the warmest quarter	24.50	20.70	23.30	27.30	28.80
11	Mean temperature of the coldest quarter	15.10	10.70	12.40	19.00	23.50
12	Annual precipitation	1078.00	536.00	705.00	1633.00	2173.00
13	Precipitation of the wettest period	176.00	79.00	110.00	298.00	474.00
14	Precipitation of the driest period	32.00	0.00	5.00	51.00	63.00
15	Precipitation seasonality	58.00	35.00	42.00	114.00	122.00
16	Precipitation of the wettest quarter	492.00	225.00	297.00	817.00	1323.00
17	Precipitation of the driest quarter	117.00	0.00	28.00	191.00	226.00
18	Precipitation of the warmest quarter	458.00	225.00	295.00	682.00	1285.00
19	Precipitation of the coldest quarter	141.00	8.00	36.00	241.00	313.00
20	Annual mean radiation	18.90	17.90	18.00	20.40	20.80
21	Highest period radiation	24.90	23.80	24.00	25.60	26.40
22	Lowest period radiation	12.40	11.10	11.20	15.10	15.90
23	Radiation seasonality	23.00	14.00	17.00	26.00	28.00
24	Radiation of the wettest quarter	21.60	19.00	19.60	24.10	25.60
25	Radiation of the driest quarter	16.40	14.10	15.50	19.10	21.00
26	Radiation of the warmest quarter	23.00	21.10	21.70	24.10	25.20
27	Radiation of the coldest quarter	14.00	12.90	12.90	17.00	17.50
28	Annual mean moisture index	0.65	0.26	0.40	0.91	0.94
29	Highest period of moisture index	0.88	0.46	0.58	0.99	1.00
30	Lowest period of moisture index	0.36	0.01	0.06	0.67	0.78
31	Moisture index seasonality	31.00	9.00	13.00	81.00	101.00
32	Mean moisture index of the highest qtr.	0.85	0.41	0.54	0.99	1.00
33	Mean moisture index of the lowest qtr.	0.41	0.01	0.09	0.69	0.80
34	Mean moisture index of the warmest qtr.	0.71	0.34	0.48	0.90	0.98
35	Mean moisture index of the coldest qtr.	0.66	0.03	0.16	1.00	1.00

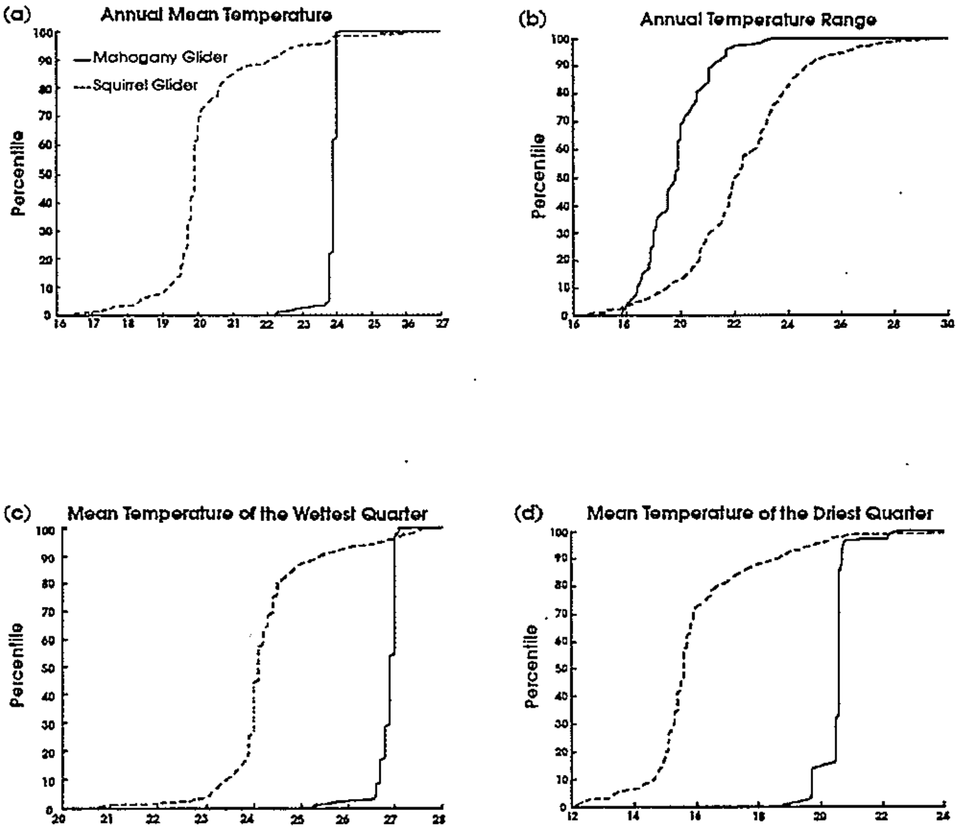


Figure 8.1. Cumulative frequency curves showing the relationship between different percentile values of the BIOCLIM-modelled temperature (°C) of sites occupied by the mahogany glider and squirrel glider (See Tables 8.1-2). Curves are: (a) annual mean temperature, (b) annual temperature range, (c) mean temperature of the wettest quarter, and (d) mean temperature of the driest quarter.

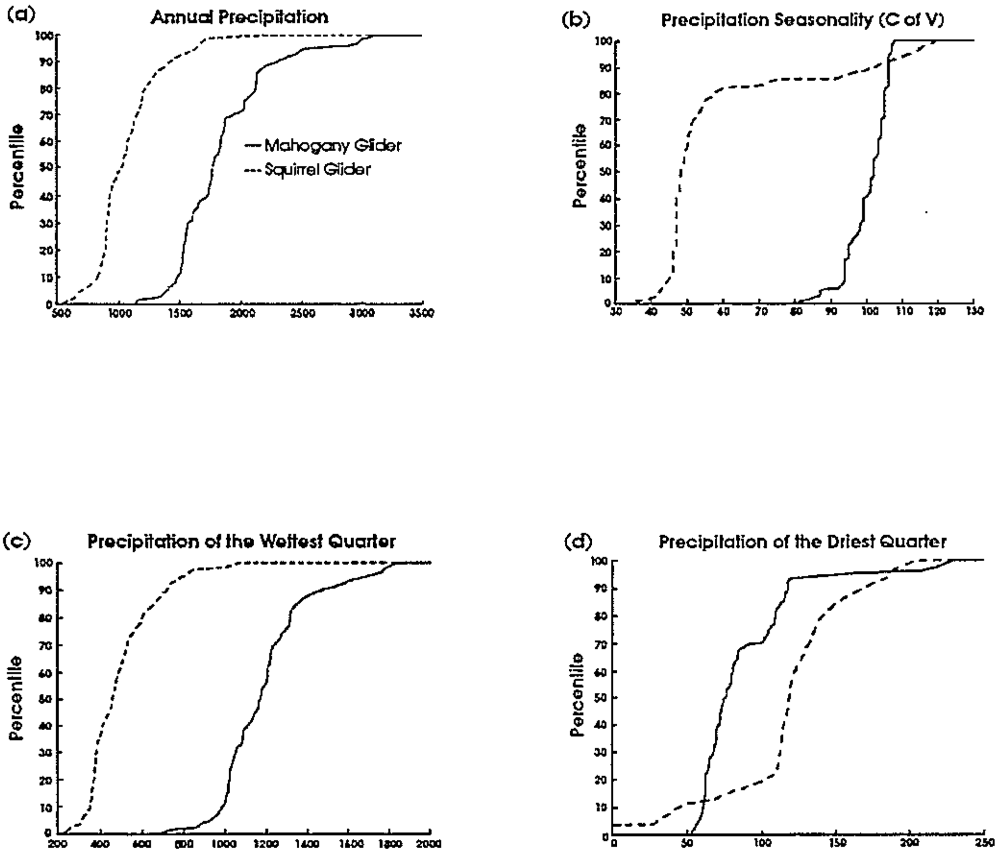


Figure 8.2. Cumulative frequency curves showing the relationship between different percentile values of the BIOCLIM-modelled precipitation (mm) of sites occupied by the mahogany glider and squirrel glider (See Tables 8.1-2). Curves are: (a) annual precipitation, (b) precipitation seasonality, (c) precipitation of the wettest quarter, and (d) precipitation of the driest quarter.

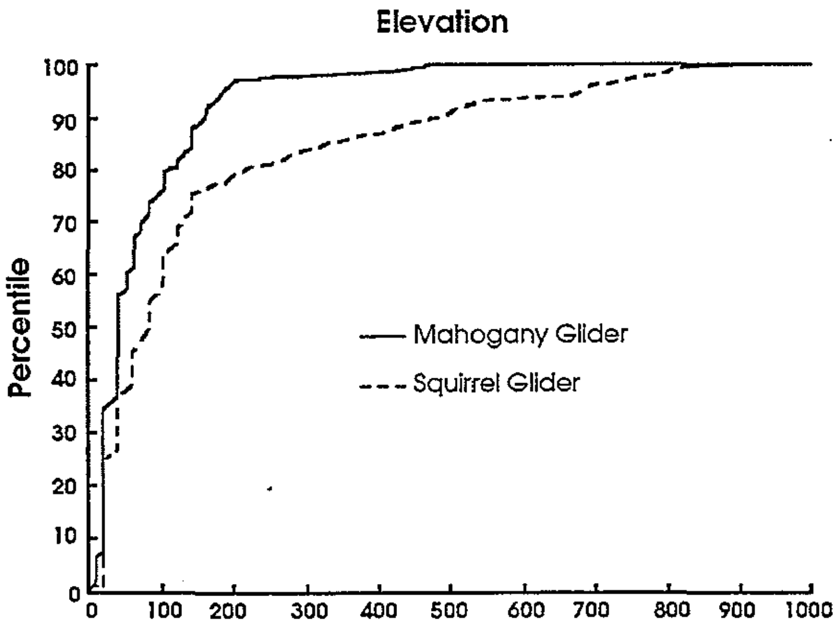


Figure 8.3. Altitudes of mahogany glider (black column) and squirrel glider (white column) records in Queensland used in the BIOCLIM analysis.

8.3.2 Potential Bioclimatic Domains of the Mahogany Glider and Squirrel Glider in Queensland

The predicted distribution of the mahogany glider does not extend outside the known range on the mainland, but the species is predicted to occur on Hinchinbrook Island and the Palm Islands where it has not been historically recorded (Fig. 8.4). The predicted distribution of the mahogany glider suggests that it is likely to occur up to 500m elevations in many areas, with several locations being above 500m. Despite this, field surveys and an examination of the vegetation suggest the occurrence of mahogany gliders up to 500m is more the exception than the rule (pers. obs). Caution also needs to be used when examining the predicted distribution and elevations as there is likely to be some error in the position of the elevation contours when transferred from topographic maps.

In contrast to the mahogany glider, the predicted distribution of the squirrel glider extends greatly beyond geocoded points used, particularly to the west (Fig. 8.5). The species is also predicted to occur throughout almost the entire mahogany glider distribution when using 100% of geocoded points (Fig. 8.6). However as mentioned above there are clear differences in the overall predicted distribution of these species along most climatic gradients within the study area. At present there are no known records of the squirrel glider within the distribution of the mahogany glider, although they are known to occur within approximately 25km (between Taravale near Paluma and Crystal Creek, south of Ingham for the squirrel glider and mahogany glider respectively) and 40km (between Princess Hills and the west of Ingham for the squirrel glider and mahogany glider respectively).

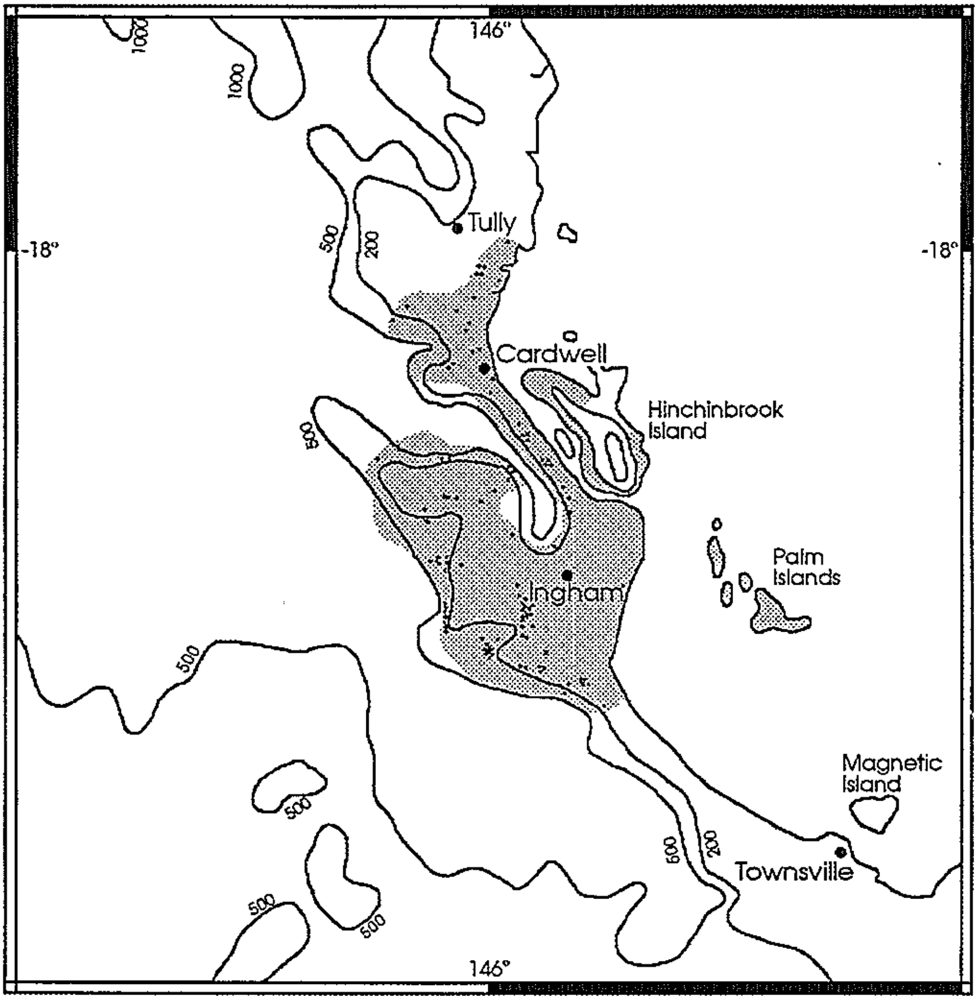


Figure 8.4. The predicted bioclimatic domain of the mahogany glider. Glider locations are presented as dots.

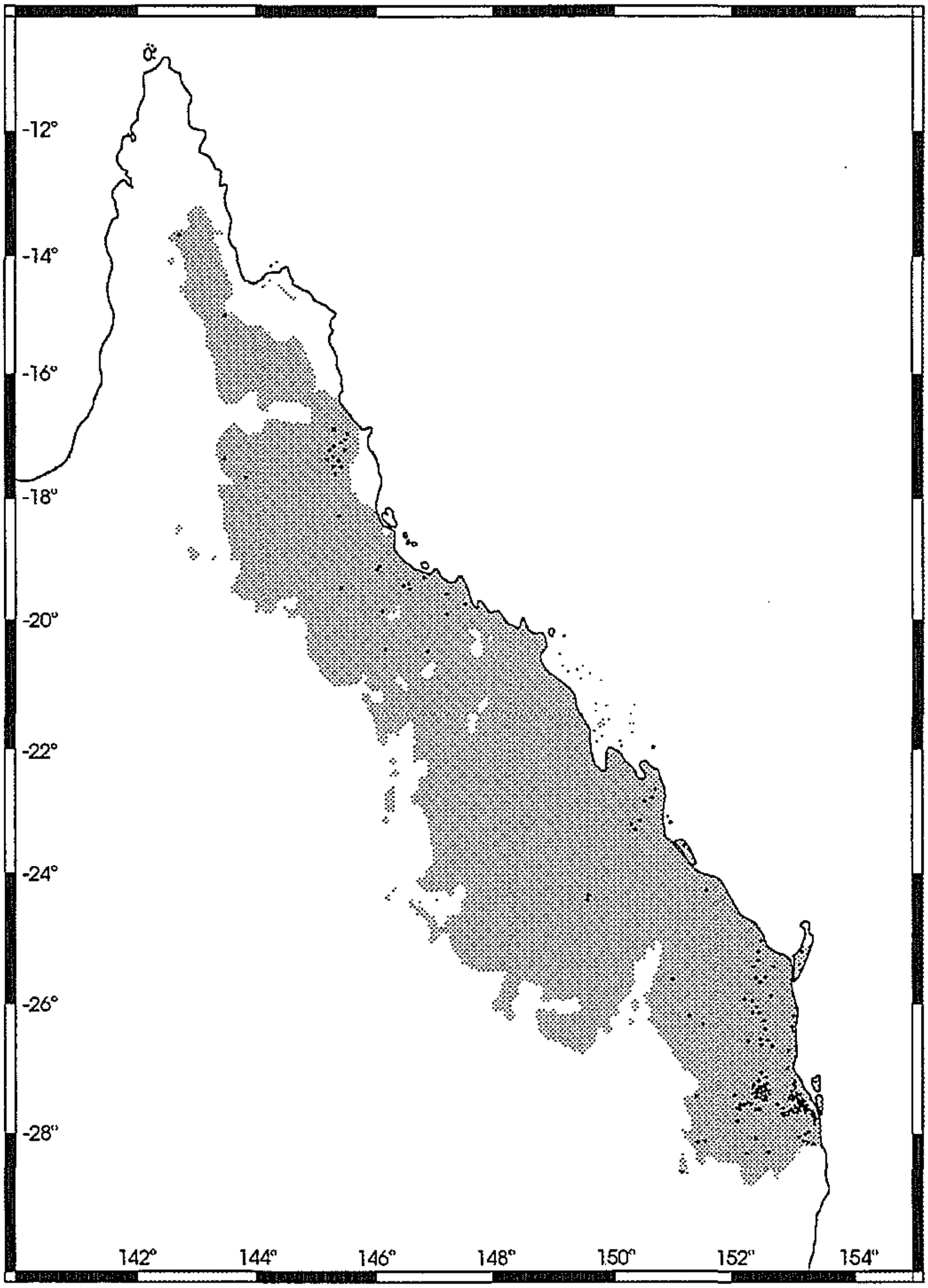


Figure 8.5. The predicted bioclimatic domain of the squirrel glider in Queensland. Glider locations are presented as dots.

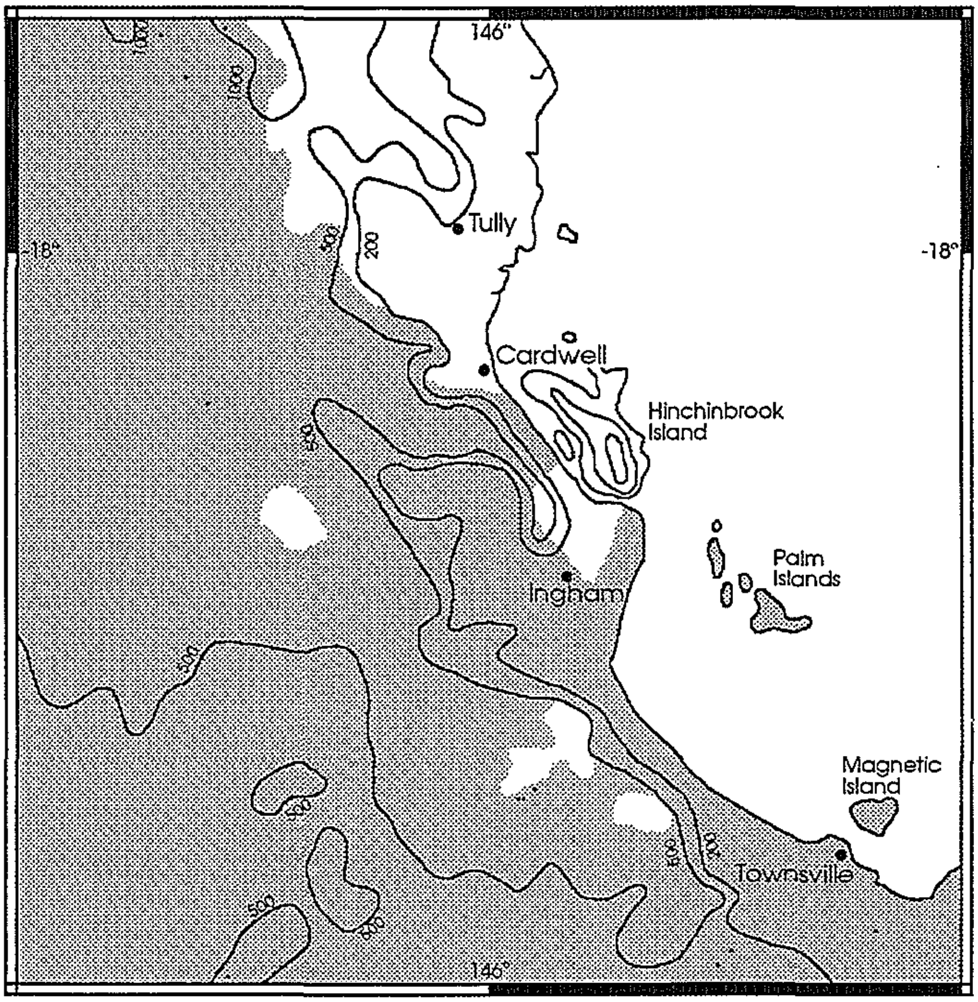


Figure 8.6. The predicted bioclimatic domain of the squirrel glider in Queensland within that known to be occupied by the mahogany glider. Glider locations are presented as dots.

8.4 Discussion

8.4.1 Predicted Distribution and Climatic Limitations of the Mahogany Glider and Squirrel Glider in Queensland.

The predicted distribution of the mahogany glider falls within a unique climatic regime. To the north of this distribution the climate is significantly wetter, whereas to the immediate west and south the climate is drier. This differing climate appears to provide the mahogany glider with habitat that has a high diversity of myrtaceous food plants, while not being dominated by rainforest species. Areas supporting the mahogany glider are characterised by very high and very seasonal rainfall, and a diverse woodland vegetation that is shaped and maintained by fire (Van Dyck 1993). Van Dyck (1993) suggested the ultimate climatic parameter limiting the distribution of the mahogany glider is a moisture threshold of approximately 100mm of rainfall for the driest quarter, below which moisture demands of the habitat cannot be satisfied. The predicted mean rainfall of the driest quarter in this study (89mm) was similar to that suggested by Van Dyck (1993), with weather station records also showing the average driest quarter to be 96.4mm for Cardwell and 100.3mm for Ingham. Van Dyck (1993) proposed that the surrounding areas with rainfall below this threshold appear to have poorer plant species diversity and abundance than elsewhere, and are unable to adequately satisfy the dietary requirements of the mahogany glider. This hypothesis, however, is complicated by the higher mean precipitation in the driest quarter observed for the smaller squirrel glider (117mm), which suggests that total annual rainfall is also very important to the mahogany glider, as the average rainfall where the mahogany glider is predicted to occur is 1856mm compared with 1078mm for the squirrel glider. Although the predicted envelope for the mahogany glider has rainfall in the driest quarter less than that of the predicted envelope for the squirrel glider, the heavy winter flowering of food species such as *Melaleuca viridiflora*, *Melaleuca leucadendra*, *Corymbia torelliana*, *Eucalyptus tereticornis*, *Eucalyptus platyphylla*, *Xanthorrhoea johnsonii* and several species of mistletoe provide ample food for the former species (Chapter 5), so there is effectively little food shortage during this time.

The vegetation communities utilised by the mahogany glider are characterised by high species diversity and productivity, which are likely to be a result of the high rainfall of the area (4188mm for Tully per year, data from Van Dyck 1993). In contrast to the mahogany glider, previous bioclimatic modelling of the squirrel glider throughout its entire range indicated they occurred in low and high extremes of seasonality, and low to moderate productivity (Quin 1993). Heavy winter flowering of eucalypts and banksias was suggested by Menkhorst *et al.* (1988) and Quin (1993) to be an important component of squirrel glider habitat in Australia.

The overlap of the potential squirrel glider distribution with that of the mahogany glider suggests they could potentially occupy the same areas. As 100% of records were used, it is not known if the area of potential squirrel glider distribution within that of the mahogany glider would be marginal for the squirrel glider. Nonetheless the bioclimatic envelopes and cumulative frequency curves generated in this study show clear differences between the two species in a number of climatic attributes, implying that the predicted overlap zone of the two species is marginal. As both species occupy similar niches, they are likely to face severe competition particularly during periods of food shortage (Chapter 4). Therefore the mahogany glider could be potentially excluding the squirrel glider from its high productivity habitat.

The BIOCLIM prediction of the mahogany glider by Van Dyck (1993) did not predict the subsequent findings further south. As BIOCLIM generates the most accurate predictions when the climatic gradient is comprehensively sampled for a species, the low number of records used in the initial BIOCLIM analysis may explain this result (Nix & Switzer 1991). The results from this more extensive BIOCLIM analysis, using many more records of the species, nonetheless suggest that the mahogany glider is not likely to occur much beyond the present known distribution.

In contrast to the altitudes and high rainfall of localities at which squirrel gliders are found in Queensland, all localities of the squirrel glider in Victoria have been found below 250m above sea level, with rainfall averaging only 500-600mm per year (range 345 to 921mm) (Menkhorst *et al.* 1988). Similar observations were made by Bennett *et al.* (1991) who found the squirrel glider to be limited to drier forests below 300m elevation. In both of these cases the occurrence of animals only at low elevations could potentially be a result of: (1) a latitudinal effect in that it is too cold at higher elevations at higher latitudes, (2) a low search effort at higher elevations, or (3) a lack of suitable habitat.

The high rainfall and resulting productivity which determines the mahogany gliders' presence, potentially undermines the long term viability of this species, particularly in the isolated fragments of habitat that remain (Van Dyck 1993). Many of the dryland communities suitable for the mahogany glider are changing from sclerophyll to vine forest as a result of the greatly reduced frequency of fire (Van Dyck 1993; Harrington & Sanderson 1994; pers. obs). Van Dyck (1993) observed rapidly developing rainforest communities in woodlands at the Hull River, Edmund Kennedy National Park, Murray Upper, Hinchinbrook Island and Barrett's Lagoon. Many other creeklines have also been observed to show a large amount of rainforest expansion leaving only emergent eucalypts (pers. obs.).

The results of this BIOCLIM analysis suggest potential for the mahogany glider to occur on Hinchinbrook Island. Van Dyck (1993) spent two nights in September 1992 spotlighting for mahogany gliders on Hinchinbrook Island without success, although he suggested the area should be resurveyed. Winter (Thorsborne & Thorsborne 1988) has seen *Petaurus* sp. on the island, so it is highly likely that sugar gliders *Petaurus breviceps* are there, because of their broader habitat tolerance, but mahogany gliders may also be present. Van Dyck (1993) suggested that many potential sites for mahogany gliders appear to be contracting as a result of the encroachment of rainforest species. Therefore if mahogany gliders are confirmed on the island there may be urgent need for fires in the northern end of Hinchinbrook Island to assist in pushing back the rainforest.

8.4.2 Hypotheses for the Evolutionary History of the Mahogany Glider and its Limited Distribution.

Until recently, petaurids were found to be only poorly represented in the fossil record (Aplin & Archer 1987). The oldest reported material found was from the early Pliocene Hamilton Local Fauna (5.2 to 2 MYA) (Turnbull & Lundelius 1970;

Turnbull *et al.* 1987). Material collected of middle Miocene age (15.5-11MYA) from the Riversleigh deposits of north-western Queensland appears to include definite petaurids (Aplin & Archer 1987). Archer *et al.* (1991) suggested there was a rich pile of remains of petaurid-like animals which had yet to be examined in detail, with some of the taxa occurring in many of the Oligo-Miocene local faunas some 23MYA. They go on to suggest that none of them appear particularly close to any living petaurid genus, with one genus being temporarily labelled *'Pre-petaurus'* which has *Petaurus/Gymnobelideus*-type morphology.

Speciation is ultimately an adaptive process that involves the establishment of barriers to gene flow between closely related populations and the development of reproductive isolating mechanisms (Bush 1975). Of the several modes of speciation that include allopatric, parapatric and sympatric, the mahogany glider appears to have undergone allopatric or potentially parapatric speciation from the squirrel glider. Allopatric speciation involves the total isolation of one or more demes (a deme is local group of randomly interbreeding individuals) of a species from their sister demes by a barrier which prevents the interchange of individuals between the two groups (Bush 1975; White 1978; Cogger 1987). In contrast, parapatric speciation involves the development of fixed genetic differences from one or more peripheral demes from the remainder of the population. This results in two species that have continuous but non-overlapping distributions.

When considering allopatric speciation, the mountain ranges to the west of the present mahogany glider distribution were initiated approximately 90MYA with the present gross morphology extending back at least 65MYA (Veevers 1984), long before any of the possum groups were present. Because of the generally low altitude that both the mahogany glider and squirrel glider occupy, the presence of mountains has the potential to act as a barrier. Although this scenario is complicated by the presence of squirrel gliders at high elevations (approximately 700-800m) in areas surrounding the mahogany glider, there is generally a thin strip of rainforest and/or *Casuarina* forest on the eastern edge of the mountains to the west of the mahogany glider that may have contributed to the separation between these now separate species. To the north of the present mahogany glider distribution, the lowland and higher elevation vegetation is dominated by rainforest species that do not appear able to support the mahogany glider (Chapters 5 & 6). It is proposed that there was once a continuous population of squirrel gliders (or a common ancestor) to the south and potentially to the west of the present mahogany glider distribution before the climate became as dry as it is today. When the area to the south and west of the mahogany glider's present distribution dried out (predicted to be approximately 2-5MYA; Bowler 1982), the lower rainfall is predicted to have resulted in a decreased productivity in this area, and a subsequent decline in tree species diversity and adequate food. Potentially this resulted in the isolation of a small separate group of squirrel gliders (or a common ancestor) which eventually evolved into the present mahogany glider.

Alternatively, when considering parapatric speciation, the area of high productivity where the mahogany glider occurs could have resulted in a population that developed into a larger size, compared to those populations to the south, west and north. Eventually the mahogany glider population may have developed and maintained fixed genetic differences from the squirrel glider, despite the interchange of individuals, and eventually established a separate species. As mentioned previously, the mahogany glider and squirrel glider are known to occur within 25km from each other and could potentially be a lot closer, being almost contiguous populations. With this in mind, caution should be exercised as the present distributions do not necessarily reflect those of the past. For example, there could have been a well established boundary to the south and west of the present mahogany glider and squirrel glider distributions which could have resulted in the speciation event, however because of more recent climate changes, the squirrel glider has been allowed to come much closer in distribution than previously. Potentially the decrease in sea level during ice ages may result in the distribution of the mahogany glider going further out into the continental shelf and to oscillate up and down the coast. This is because the increased aridity may result in the present distribution being too dry and areas to the north (which are presently too wet) having adequate habitat. A phylogeny of the genus *Petaurus*, with particularly emphasis on the mahogany glider and squirrel glider, is required to provide further information on the potential timing of genetic separation of these species. Such information will assist in understanding the timing of climatic changes that may have contributed to the speciation of these two closely related species.

Productivity and seasonality have been proposed to be the two ultimate determinants of the range limits of exudivorous mammals (Quin 1993). Contrary to Boyce (1978 & 1979) and Owen (1989) who found that selection favours smaller body size in areas of low food availability, Quin *et al.* (1996b) suggested the larger body size of the squirrel glider may be an advantage in aseasonal environments where climate and food are less predictable. However, it appears that species larger than the squirrel glider, such as the mahogany glider and the yellow-bellied glider *Petaurus australis* (with higher associated energy needs) follow Boyce's hypothesis as they appear to be restricted to more productive areas with seasonal environments.

The area known to be inhabited by the mahogany glider has high rainfall which in turn results in high evapotranspiration. Evapotranspiration has been shown to be a highly significant predictor of productivity in terrestrial ecosystems (Rozenzweig 1968). Similarly the yellow-bellied glider seems to be restricted to high productivity areas in wet sclerophyll forest in north Queensland (Winter 1997). In Victoria and south-eastern Australia they have been found in open woodland (Craig 1985), while in northern New South Wales they have been found in dry sclerophyll forest (Mackowski 1986). The yellow-bellied glider occurs in a range of habitats which have high productivity and populations that are characterised by low density and a patchy disjunct distribution (Smith & Russell 1982; Braithwaite 1983, Henry & Craig 1984; Kavanagh 1984; Craig 1985; Goldingay 1989; Davey & Norton 1990; Goldingay & Kavanagh 1993).

The limited distribution of the mahogany glider and the large distribution of the squirrel glider appear to support Rapoport's rule (Stevens 1989). Rapoports's rule suggests the greater annual range of climatic conditions to which individuals in high-latitude environments are exposed (such as the squirrel glider) relative to those experienced by wholly low latitude species (such as the mahogany glider), has favoured the evolution of broad climatic tolerances of high-latitude species and narrow climatic tolerance low-latitude species. The broad climatic tolerance of the squirrel glider may have led to a wider latitudinal distribution than the mahogany glider which has become restricted within its limited distribution as a result of the climate affecting the vegetation within this region which in turn limits its distribution.

In light of the close taxonomic relationship of the mahogany glider and squirrel glider, and the predicted large overlap of the distribution of both species as identified by BIOCLIM, it would be interesting to know if the mahogany glider and the squirrel glider would interbreed successfully if their distributions were to overlap in part of their range. Interbreeding has been observed between other species of petaurids in captivity as Fleay (1947) reported that a female Victorian sugar glider and a male Queensland squirrel glider produced a fertile hybrid. Similar observations were made by Zuckerman (1953), although more recently Smith (1979) failed to successfully mate sugar gliders and squirrel gliders in captivity.

Chapter 9

Preliminary Predictions of the Impacts of Habitat Area and Catastrophes on the Viability of Mahogany Glider Populations.

9.1 Introduction

Throughout its distribution the mahogany glider *Petaurus gracilis* has lost almost 80% of its habitat as a result of clearing for agriculture, grazing and urban development, and only 16% of the remaining habitat is protected within national parks (Van Dyck 1993; Chapter 1). The remaining habitat is highly fragmented and is comprised of patches of habitat of different sizes (and therefore containing different population sizes), which are differentially prone to extinction (See Fig. 1.1).

In order to understand the susceptibility of small populations to extinction, population viability analysis (PVA) has been developed and has been widely used (see Lindenmayer & Possingham 1994 for a review). PVA was defined by Burgman *et al.* (1993) as the analysis of all those factors and their interactions that act on populations and contribute to the risks of both short-term and long-term decline or extinction. PVA is a modelling tool that assists in predicting the probability that a species will become extinct in a particular area over a specific time period using the available scientific knowledge and analytical procedures (Clark *et al* 1991; Possingham 1991; Lindenmayer *et al.* 1993a).

Uncertainty is central to the study of population viability (Possingham 1991). In both real and simulated populations there are five interacting factors that should be understood to make predictions about the extinction of a species (Clark *et al.* 1991). These include: (1) demographic uncertainty, (2) inbreeding, (3) loss of genetic diversity, (4) environmental uncertainty, and (5) catastrophes (Shaffer 1981; Possingham 1991). Each of these factors may contribute and interact with others to result in the extinction of species, and need to be understood in order to make informed decisions when managing threatened species.

Population viability analysis incorporates life history information and identifiable threats to population survival into models of the extinction process under a range of management options (Possingham 1991; Lacy 1993). Management options that can be simulated include reducing mortality, translocation, and increasing reserve size (Clark *et al.* 1991). Population viability analysis has been used in numerous cases and a number of these have been reviewed by Lindenmayer *et al.* (1993a) and Lindenmayer and Possingham (1994).

Of the many simulation models available (See Lindenmayer *et al.* 1993a), the VORTEX computer program has been most extensively used to simulate demographic and genetic events in the history of populations (Clark *et al.* 1991; Lacy 1993; Lindenmayer *et al.* 1993b). VORTEX models population processes as discrete, sequential events, with probabilistic outcomes determined by a pseudo-random number generator (Lacy 1993). VORTEX has the capacity to simulate the different stochastic processes and is able to represent the range of pressures to which small populations are vulnerable (Lacy 1993). It has been used on a number of species within Australia, including Leadbeater's possum *Gymnobelideus leadbeateri*, mountain brushtail possum *Trichosurus caninus*, greater glider *Petauroides volans*, mountain-pygmy possum *Burramys parvus*, eastern-barred bandicoot *Perameles gunnii*, long-footed bandicoot *Potorous longipes*, orange-bellied parrot *Neophema chrysogaster* and the helmeted honeyeater *Lichenostomus melanops cassidix* (Clark *et al.* 1991; Lindenmayer 1993b; Lindenmayer & Lacy 1995a & b).

Lindenmayer *et al.* (1993a) suggested that although not a panacea, PVA can significantly improve management and can be highly useful in many instances to organise data and as a forecasting tool. Lindenmayer *et al.* (1993a) also suggested that PVA can be crucial in the process of policy formulation, implementation, and appraisal for the restoration of endangered species. Population viability analysis provides managers with a powerful tool to aid in assessing the viability of small populations, and for setting target numbers for species recovery as a basis for planning and carrying out recovery programs (Clark *et al.* 1991). In addition, having performance-based management programs enables quantifiable assessment of progress towards achieving the programs' aims (Clark *et al.* 1991).

Even though there is uncertainty about the value of some of the demographic and environmental parameters for the mahogany glider, Possingham *et al.* (1993) suggested that PVA is a worthwhile process as it can place a quantitative value on the impact of proposed resource development and exploitation activities. In addition, the assembling of data for analysis will focus future research by highlighting gaps in existing knowledge (Possingham *et al.* 1993).

The aims of this chapter are to: (1) examine the probability of extinction of different sized populations of the mahogany glider (representing different reserve sizes); (2) examine the impact of a one in a hundred year catastrophe, of different severities, on the viability of different sized populations of mahogany gliders; and 3) identify areas of knowledge that are presently lacking and which need further research to assess the risks of extinction for mahogany glider populations.

9.2 Methods

9.2.1 PVA Computer Program

VORTEX (Version 7.3) was used for the analysis of the viability of different population sizes and the effects of catastrophes. The structure, algorithms and assumptions of the VORTEX program are outlined by Lacy (1993). Simulations were repeated 100 times over a 100 year period, with extinction reports every 10 years. Following Goldingay & Possingham (1995) a population was considered as viable if it had a greater than 95% probability of persistence for 100 years.

9.2.2 Data Input

Values used are based on the information obtained from two years of intensive trapping of the mahogany glider (Chapter 3), and information from studies on other petaurids (Lindenmayer *et al.* 1993b; Quin 1995; Goldingay & Possingham 1995)(Table 9.1). The density of mahogany gliders averaged approximately 0.2 animals per hectare (Chapter 3), therefore using this density an approximate population size can be estimated for a particular area of habitat. As age-specific mortalities are presently not known, estimates were derived from studies of Leadbeater's possum (Lindenmayer *et al.* 1993b), and the yellow-bellied glider *Petaurus australis* (Goldingay & Possingham 1995). Sensitivity analysis was used on the mortalities to assess the effect of different mortalities on different population sizes of mahogany gliders.

Table 9.1. The range of values of life-history parameters of the mahogany glider input to the computer program VORTEX for Population Viability Analysis.

Parameter	Value
Populations modelled	1
Inbreeding Depression	Recessive Lethals
EV (reproduction) to be correlated with EV (survival)	Yes
Number of catastrophes - fire and disease.	1
Breeding System	Monogamous
Age at First Breeding - females	2
Age at First Breeding - males	2
Maximum Longevity	6
Sex ratio at birth	1:1
Maximum number of young per year	2
Adult males in breeding pool	100%
Percentage of females breeding each year	95%
Adult females producing	
0 young	5%
1 young	54%
2 young	41%
Standard deviation in producing litters	5%
Reproduction density dependent	No
Mortality of females	
0-1 (SD)	25% (5)
1-2 (SD)	35% (5)
>2 (SD)	20% (5)
Mortalities of males	
0-1 (SD)	25% (5)
1-2 (SD)	35% (5)
>2 (SD)	20% (5)
Probability of catastrophe type 1 (fire/cyclone)	0.01
Effect on reproduction	0.1-0.7
Effect on survival	0.1-0.7
Start at Stable age distribution	Yes
Initial population size (N)	50-1000
Population carrying capacity (K) (SD)	K = N * 1.10 (SD = 0)
Is there a trend in K	No
No. of years over which K changed	N.A.
No. of computer simulations	100
No. of years modelled	100
Harvest or Supplement	Not applicable

9.2.3 Scenarios Modelled

9.2.3.1 Scenario 1 - Different Areas of Habitat

Areas of habitat were modelled from 250ha to 5000ha, representing populations of 50 to 1000 based on a density of 0.2 animals per hectare, and assuming that 100% of the habitat is utilised. This allowed the viability of different sized patches of habitat to be examined.

9.2.3.2. Scenario 2 - Effect of a Catastrophe

The inclusion of catastrophes in examining population viability was considered by Mangel and Tier (1994) as important because it forces us to think differently about the evaluation of conservation measures. Within the distribution of the mahogany glider, the habitat is prone to catastrophes such as severe fires and cyclones, which in turn can greatly reduce survival and reproductive success. Therefore, a one in 100 year catastrophe was included with different effects on mortality and reproduction to assess the impact on different population sizes of the mahogany glider.

9.3 Results

9.3.1 Viability of Different Areas of Habitat

The results of the population viability simulations showed that areas of habitat up to 1500ha with an estimated population 300 individuals have a negative population growth rate, high losses of genetic diversity and a greater than 5% chance of extinction within 100 years (Fig. 9.1a & 9.1b). With a habitat area of 2000ha (400 individuals), the population growth rate is positive and there is only a 1% probability of extinction within 100 years and a 6.46% loss in heterozygosity. Populations of 400-700 however still showed a decreasing trend in population size as a result of the very large standard deviations in growth rate (r), suggesting they are still likely to go extinct in greater than 100 years. It is not until a population of approximately 800 individuals (an area of 4000ha) that the population size appeared to stabilise.

9.3.2 Sensitivity Analysis

The sensitivity analysis suggested that juvenile annual mortality of 30% and greater is important in increasing the probability of extinction. With a population of approximately 700 individuals, only a mortality of 35% had a greater than 5% chance of extinction (Fig. 9.2a). Variation in sub adult mortality (Fig. 9.2b) was less important in population viability, as only an annual mortality of 40% resulted in a greater than 5% chance of extinction for populations up to 900 individuals. Variation in adult mortality (Fig. 9.2c) had a pronounced affect on the probability of extinction if annual mortalities were 25% or greater. Even with a population size of 1000 individuals, the population still had an 82% chance of extinction within 100 years if the adult mortality was 30%, while it was 3% if the mortality was 25%.

9.3.3 Effect of a Catastrophe

Populations of 400 individuals were quite resilient to a 1 in 100 year catastrophe which had up to 20% mortality and 20% decrease in reproduction (Fig. 9.3 & Table 9.2). With a catastrophe resulting in 30% mortality and 30% decrease in reproduction, a population of 500 was required to maintain a viable population over 100 years (Table 9.2). When the mortality was 70%, with a 70% decrease in reproduction, a population of 1000 still had a 12% chance of extinction ($r = -0.003$). The results therefore suggest, that populations of individuals above 500 individuals are quite likely to be able to tolerate mild catastrophes.

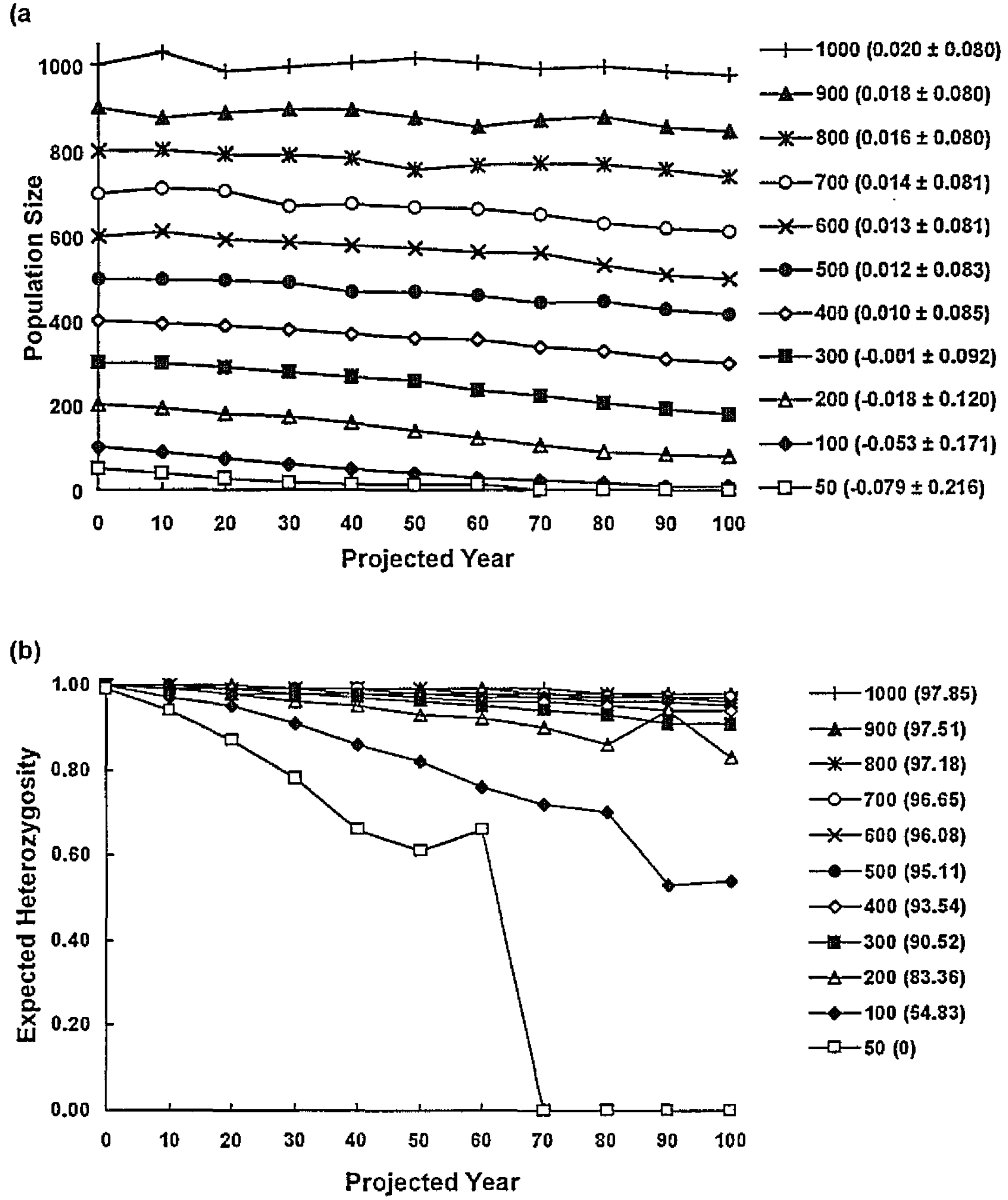


Figure 9.1. Changes in mean (a) Population size. The population growth rate (r ± SD) is in brackets after the population size, and (b) Heterozygosity in various population sizes over 100 years using 100 simulations and with no catastrophes. The final heterozygosity is in brackets after the population size.

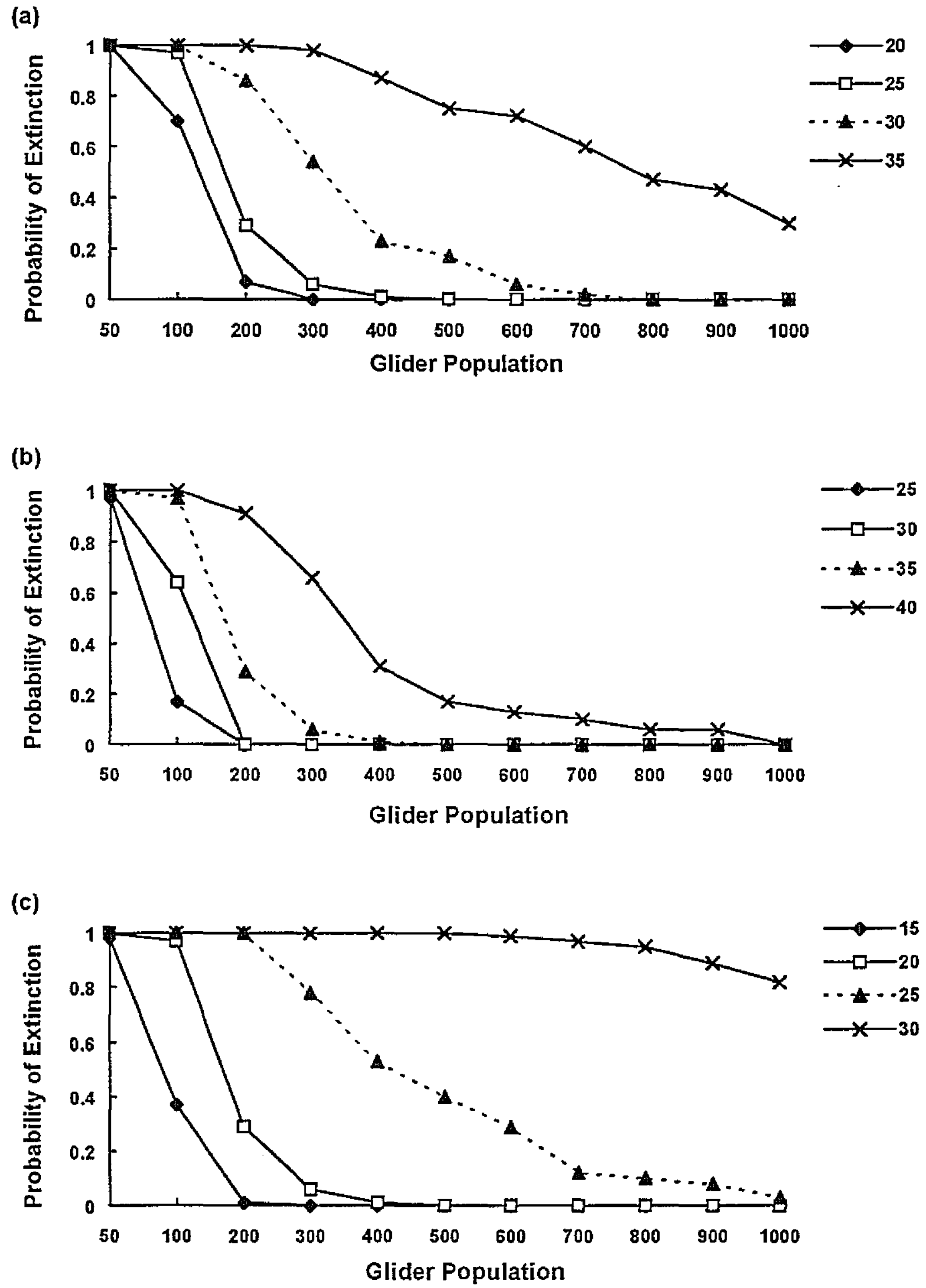


Figure 9.2. Probability of extinction when the annual mortality of mahogany glider (a) Juveniles, (b) Sub adults, and (c) Adults is varied for populations from 50 to 1000 individuals.

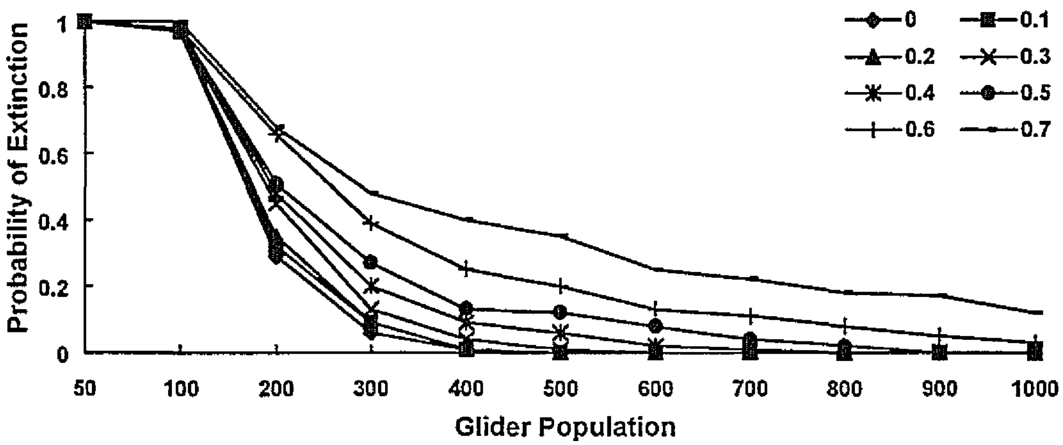


Figure 9.3. Probability of extinction as a result of a one in a hundred year catastrophe with different mortalities and decreases in reproduction for populations of 500 to 1000 individuals.

Table 9.2. Population size at which there is a less than 5% chance of extinction in 100 years and positive population growth rate (r) as a result of a 1 in 100 year catastrophe. With different mortalities and decreases in reproduction.

Mortality / Decrease in Reproduction	Viable Population Size over 100 years	Population Growth Rate (r)
0	400	0.010
0.1	400	0.008
0.2	400	0.004
0.3	500	0.005
0.4	600	0.004
0.5	700	0.002
0.6	900	0.001
0.7	-	-

9.4 Discussion

9.4.1 Viable Habitat Areas and Population Sizes Required

The results of the viability analysis suggest that a population of approximately 400 individuals will have less than 5% chance of extinction within 100 years. Populations of 400-700 however did show a decreasing trend, and were therefore likely to become extinct eventually. The gradual decline in size of populations of 400-700 individuals which have positive growth rates is probably a result of the much larger standard deviations in growth rate which fluctuate and as a result slowly decrease the population size (R. Lacy pers. comm.). Therefore populations of 800 or more appear to be the best target population to aim for in order to provide long term viability.

An area of 2000-4000ha is suggested to be adequate to maintain a viable population of 400-800 individuals, if 100% of the area is utilised. However, throughout the distribution of the mahogany glider, there are large areas in which the forest does not appear to be of sufficiently high diversity to provide adequate food throughout the year, being dominated by only one or two species such as *Eucalyptus platyphylla*, or *Melaleuca viridiflora* (pers. obs.).

A number of surveys have been conducted since the rediscovery of the mahogany glider to determine the limits of its distribution, and the areas within its distribution in which it occurs. Van Dyck (1993) found the Mahogany Glider at 16 of 27 sites within the known distribution, Eyre (1993) found the Mahogany Glider at 4 of 6 sites, while Lyon (1993) found Mahogany Gliders at approximately 8 of 27 sites within the known distribution. Lyon (1993) and Van Dyck (1993) generally found that where Mahogany Gliders were absent Brushtail Possums *Trichosurus vulpecula* dominated. Similarly Smith (1996) found mahogany gliders at 5 out of 10 (50%) localities surveyed, and although there was some overlap with brushtail possums, the brushtail possum was clearly more common, and dominated where no mahogany gliders were found. It should be noted that these surveys are likely to overestimate as they targeted diverse habitat (as opposed to monotypic habitat) where mahogany gliders were likely to be found. Therefore the mahogany glider could potentially be utilising only 50% of the available habitat remaining. With this in mind the estimated area of habitat required to maintain a viable population of mahogany gliders could be at least 4000ha (for 400 individuals) and as high as 8000ha (for 800 individuals) for long-term viability. Therefore it is very important to examine the size of the remaining fragments of habitat to assess their viability and examine the potential for corridors to increase their population size if required.

Observations of low utilisation of available habitat have been recorded for other petaurids such as the yellow-bellied glider which have been found to occupy only 28-54% of total forested area available (Braithwaite 1983; Milledge *et al.* 1991; Kavanagh & Bamkin 1995). Similarly Lindenmayer *et al.* (1991b) found that 40% of sites suitable for Leadbeater's possum were apparently vacant.

If the occurrence of a catastrophe is to be considered, then the minimum viable population increases further than already predicted. Although populations of 400 or more are able to absorb mild catastrophes, larger populations are needed to allow persistence through more severe catastrophes which require an increasingly larger population size in order to recover from the resulting mortality and decrease in reproduction. The importance of incorporating catastrophes should not be dismissed as they are generally considered very important in determining the persistence times of populations (Menges 1990; Mangel & Tier 1994).

9.4.2 Sensitivity Analysis

The sensitivity analysis showed that population viability can vary greatly in response to change in mortality rates, particularly with juvenile mortalities above 35%, and adult mortalities above 25%. With this in mind steps should be taken to reduce adult mortality, from causes such as entanglement in barbed wire fences, road deaths and (potentially) predation by feral animals such as cats.

Goldingay and Possingham (1995) also found a pronounced effect of adult mortality in yellow-bellied glider population viability using the PVA program ALEX, however they did not find juvenile mortality to be as critical to extinction risk. In agreement with Goldingay and Possingham (1995) the sensitivity analysis shows that caution should be exercised in deciding which parameter values are used in PVA. It should be noted that the mortalities used in this analysis were more conservative than have been used with PVA analysis on other petaurids. Goldingay and Possingham (1995) used mortalities for newborn, subadult and adults of 30%, 40% and 20% respectively, while Lindenmayer *et al.* (1993b) used mortalities of 40-50%, 30% and 20% respectively.

9.4.3 Strengths and Limitations of PVA

Population viability analysis programs have a number of strengths and limitations, which have been reviewed by Lindenmayer *et al.* (1993a).

Strengths of PVA identified include:- (1) it can identify gaps in data; (2) it can identify trends in population behaviour; (3) it can identify processes threatening to the species; (4) it can define the minimum critical area and therefore assist in designing reserves;

(5) it can clarify management needs; (6) it can enhance management and decision-making; and (7) it has applications in species recovery, reintroduction, and captive breeding programs.

Limitations of PVA identified include: (1) it is a data-intensive technique, and data sets on endangered species are usually incomplete; (2) it does not examine the functional role of taxa; (3) it simplifies all the interactions between parameters; d) it is a simplification of population dynamics; (4) there is no generic model appropriate for all species; and (5) it is very difficult to model the interaction between populations and resources which is likely to be very important for species such as the mahogany glider which do not have a predictable food supply (as it is for herbivores). Other limitations PVA programs such as VORTEX have include: (1) the effect of density dependence of juvenile or adult survival cannot be simulated, as only reproduction can be simulated with density dependence; (2) cannot model ecological stochasticity; and (3) there has been little or no attempt to validate the results that are produced by VORTEX and other programs. When asking this same question Lindenmayer *et al.* (1993b) found that trends in population behaviour predicted from VORTEX have been quite accurate, including those on the Puerto Rican parrot *Amazona vittata* (Lacy *et al.* 1989), the eastern barred bandicoot *Perameles gunnii* (Lacy & Clark 1990), and the whooping crane *Grus americana* (Mirande *et al.* 1991). A recent retrospective PVA on the Lord Howe Island woodhen *Tricholimnas sylvestris*, using several different programs found VORTEX to provide the most conservative estimates (Brook *et al.* 1997). Brooke *et al.* (1997) also found that density dependence has an important influence on the predictions of a PVA. However they showed that if an appropriate density dependence was used (by setting a suitable carrying capacity), all PVA simulations produced projections that were realistic and highly similar.

All population viability analysis programs contain a large number of assumptions and simplistically model the behaviour of organisms (Lindenmayer *et al.* 1995). As a result Lindenmayer *et al.* (1995) suggest the results of viability analyses provide only an estimation of the actual dynamics of wild populations. Indeed, the extinction probability estimated using PVA may be too low as not all the feedback between parameters can be included in a computer simulation program (Lacy & Clark 1990; Lindenmayer *et al.* 1993b). Caution should be used when interpreting and applying the results of any such analyses (Lindenmayer *et al.* 1995).

9.5 Conclusion

The results of the PVA suggest that a minimum population of 400 individuals (an area of 2000-4000ha) is required to maintain a population of mahogany gliders over a 100 year period. However for longer term viability a minimum population of approximately 800 individuals (an area of 4000-8000ha) is required.

Although it has at present not been accurately determined, it appears that there are very few areas of habitat that are of adequate size to maintain populations of the mahogany glider over the long term. In order to increase the effective size of some of the remaining populations of mahogany gliders, it is important that effective corridors are established (and maintained) between key subpopulations to allow individual gliders to move between subpopulations.

The analyses conducted in this PVA study are preliminary, even though they are based on the best available information, and should be repeated as more information becomes available. Lindenmayer *et al.* (1993b) proposed that the integrated use of PVA, data collection and monitoring and evaluation of management actions should be interlinked in an adaptive management approach. Despite the limitations of PVA such as the limited availability of some life history and mortality parameters, its use does have an important role in managing species, and the benefits of PVA far outweigh its limitations (Lindenmayer *et al.* 1993a and 1993b).

There are several important areas of research that are considered important to provide further information of the mahogany glider so that it can be managed more effectively in the future. These include: (1) a broad scale study of the movement of gliders within corridors; (2) examination of the most appropriate fire regimes to control rainforest expansion in key corridors and remnant habitat; (3) a baseline study to examine the present genetic diversity in each of the major remaining populations so that it can be referred to in the future to examine if inbreeding is occurring; and (4) detailed examination of the remaining habitat in regard to vegetation types, size of habitat fragment remaining, and the potential use of corridors between fragments.

Chapter 10

General Discussion and Recommendations for the Conservation and Management of the Mahogany Glider.

10.1 Introduction

The mahogany glider *Petaurus gracilis* is a large species of gliding possum that is unusual amongst the members of the genus *Petaurus* in that it has a very limited distribution (Chapters 1 and 8). As a consequence of the naturally restricted geographic range, previous loss of habitat, potential for further loss of habitat, and the poor representation of habitat in conservation reserves, the mahogany glider has been listed as an endangered species under both the Federal Endangered Species Protection Act (1992) and the Queensland Nature Conservation (Wildlife) Regulation 1994. The legal requirements of this listing are an obligation to remove the threatening processes that have resulted in the endangered status. As part of these requirements the Commonwealth must prepare a recovery plan in which management actions are proposed and implemented.

In determining the appropriate management actions required for the mahogany glider, it is important to understand the resources required to sustain mahogany gliders such as food, nest sites, area of habitat required to maintain a sustainable population, and the factors affecting their availability. The aim of this review is to tie together the ecological information and use this to assist in the management of this species.

10.2 Dietary Requirements and Habitat Diversity

The mahogany glider was found to have a diverse, largely opportunistic, diet consisting of nectar and pollen from primarily Myrtaceae species, arthropods, *Acacia* arils, with sap from *Albizia procera* (Mimosaceae) being important at all times of the year, particularly when nectar was scarce (Chapter 5). The high reliance on nectar is the result of a high species diversity of myrtaceous plants which provide food throughout the year. This high species diversity in turn is a result of the unique geographical position the mahogany glider occupies. This region appears to be an intermediate zone between wet rainforest to the north, and seasonally dry woodlands to the south, which in turn limits its distribution (Chapter 8). In obtaining their diverse diet, mahogany gliders utilise a variety of tree species at different times of the year to provide food. The area required to provide adequate food is very large, averaging 19.25ha for males and 20.34ha females, and 23.18ha for a males and females as a group in continuous habitat (Chapter 6). The socially monogamous mating system and largely exclusive home ranges (Chapter 6), low population density (Chapter 3) and the high number of individuals required to maintain a viable population means that large areas of habitat are needed to maintain populations (Chapter 9).

10.3 Size and Location of Reserves

It is estimated that the total habitat remaining for the mahogany glider has a total area of only 720km^2, and this is highly fragmented into many patches of unknown size (Blackman *et al.* 1994). Therefore it is critical that as much of the remaining habitat as possible be retained, regardless of tenure, and that a system of reserves dedicated to the mahogany glider be established. Other threatened species that will also benefit from this include the southern cassowary *Casuarius casuarius johnsonii*; ant plant *Myrmecodia beccarii* and its associated obligate mutualistic ant *Iridomyrmex cordatus* and the apollo jewel butterfly *Hypochrysops apollo apollo,* ullyses butterfly *Papilio ulysses* and the Cooktown azure butterfly *Ogyris aenone* (Braby 1992). Several other species of butterflies in the region are considered seriously at risk if their habitats continue to decline include the senta skipper butterfly *Neohesperilla senta,* orange white-spot skipper butterfly *Trapezites heteromacula,* cedar bushbrown butterfly *Mycalesis sirius sirius* and the narcissus jewel butterfly *Hypochrysops narcissus narcissus* (Braby 1992). A number of orchids that are either endemic and/or endangered also occur within this region including *Calochilus psednus*, *Genoplesium tectum*, *Arthrochilus stenophyllus* and *Phaius tancarvilliae* (Australian Nature Conservation Agency 1996); with a further 5 species of orchid considered rare (*Dipodium ensifolium*, *Eulophia bicallosa*, *Habenaria rumphii*, *Habenaria xanthantha* and *Pachystoma pubescens*)(Australian Nature Conservation Agency 1996).

The results of a preliminary population viability analysis (PVA; Chapter 9) suggested that a minimum population size of 400 individuals is required for a less than 5% chance of extinction within 100 years. However for populations of 400 to 700 the rate on increase tended to be negative suggesting that populations of this size were likely to eventually become extinct (>100 years). Only populations greater than 800 individuals appeared stable after 100 years. Based on these results, the minimum area of habitat should be at least 2000ha (400 animals) to over 4000ha (800 individuals). Because a large area is likely to include some unsuitable habitat, the total area required may be greater than this. Therefore a minimum continuous area of habitat of approximately 8000ha may be required for population viability. Nonetheless, the size of reserves should not be the minimal size but should be as large as possible to allow the maximum opportunity for populations to be self sustaining.

Despite a number of extensive surveys, the present distribution of the mahogany glider appears to be mostly limited to altitudes below 200m elevation, as 80% of locations have been recorded below 100 metres of elevation, and only 3% of records are above 200m elevation. A number of observations suggest that the elevations at which mahogany gliders occur within their distribution are not uniform. In some areas there does not appear to be any evidence of mahogany gliders above 80m, while in other areas they may occur at well above 200m elevation. Therefore it is clear that the retention of as much lowland habitat as is feasible will be critical for the long-term conservation of the mahogany glider.

It is also critical that reserves are chosen that not only contain adequate glider populations, but also comprise a wide diversity of woodland vegetation. In particular, a diversity of species of Myrtaceae and Mimosaceae such as those from the genera *Melaleuca*, *Eucalyptus*, *Corymbia* and *Acacia* is required (See Table 10.1) as these provide the mahogany glider with adequate food and shelter.

10.4 Habitat Requirements

Considering their diverse dietary requirements, optimal habitat for the mahogany glider appears to consist of a combination of (Chapters 4 and 5):

(1) at least one species of bloodwood (eg. *C. intermedia* or *Corymbia clarksoniana*);
(2) generally *E. tereticornis*;
(3) one or two species of *Melaleuca* such as *M. dealbata*, *M. leucadendra* or *M. viridiflora*;

(4) two or more species of *Acacia* such as *A. crassicarpa*, *A. flavescens* and *A. mangium*, which are utilised for arils and sap;

(5) *Albizia procera* for sap, which is an important food source during times when there is nothing flowering; and

(6) *E. pellita* and *Xanthorrhoea johnsonii*. Sub-optimal habitat includes areas that are dominated by only one or two species including *C. clarksoniana*, *C. intermedia*, *Eucalyptus platyphylla* and *M. viridiflora* (pers. obs; Van Dyck 1993).

10.5 Corridors

10.5.1 Role of Habitat Corridors

The remaining habitat of the mahogany glider is highly fragmented, with most of the remaining fragments probably not large enough to sustain viable populations. Therefore the remaining fragments of habitat should be connected wherever possible to allow the movement of gliders between fragments, and increase effective population size. The reduction of gaps between patches of habitat and the maintenance of corridors is particularly important for arboreal mammals such as the mahogany glider, as they are limited in their movement to areas where trees are closer together than their maximum glide distance (and hence tree height) (Chapter 7). Therefore they are highly sensitive to habitat fragmentation and are easily isolated by gaps in their habitat, as they do not readily travel along the ground (pers. obs.). If they do come to the ground they are prone to predation from cats, dogs and snakes. Therefore the presence of wildlife corridors (linear remnants of habitat) that link the remaining fragments of habitat will be critical in allowing the transfer of animals between patches of habitat.

The function of corridors is to provide continuity between populations by maintaining or restoring natural linkages between isolated habitats (Bennett 1990). Corridors assist in the movement of animals throughout their range, therefore promoting gene flow between otherwise isolated populations. As a result of their facilitation of movement, corridors help to increase the effective size of populations, and reduce the vulnerability to local extinction because of inbreeding, disease, catastrophes, and environmental and demographic stochasticity (Simberloff & Cox 1987; Bennett 1990; Simberloff *et al.* 1992; Lindenmayer & Possingham 1994).

A number of both trapping and spotlighting observations (pers. obs.) show that the mahogany glider is highly mobile, travelling 590-3430m (av. 1506m) per night, and will readily utilise corridors if they are of adequate width and plant species composition (Chapters 5 and 6). Observations of the mahogany glider show that both adult and juvenile mahogany gliders will use corridors as part of their home range over the short and longer term (Chapter 6). Harrison (1992) suggested that mammals are most likely to utilise corridors during juvenile dispersal, because once dispersal is completed most mammals remain faithful to a home range. Observations also show the mahogany glider will cross gaps in habitat (such as roads, tracks and powerline easements) of up to 40m, if trees of appropriate height occur on either side of the break to provide an adequate glide distance.

10.5.2 Location and Design of Corridors

The different ways that species use corridors and the different elements of corridor quality have implications for corridor use, management and restoration (Bennett *et al.* 1994). Critical variables in determining the effectiveness of corridors include habitat type, width, length, human activities and location (Harrison 1992). There is an urgent need to identify key areas which require the establishment or maintenance of a wildlife corridor in order to connect isolated patches of habitat within the distribution of the mahogany glider. Where possible, several corridors should be established between large isolated populations to increase the effective population size.

Corridors should be established along creek lines and around paddocks as these are areas that often have existing vegetation. Wherever possible, corridors should be located away from human disturbances such as roads (Bennett 1990). Where a source of disturbance is unavoidable, it should be located to one side, not within the corridor. For example, it is preferable to locate a wide strip of roadside vegetation to one side of the road rather than having narrow strips on either side (Bennett 1990). The width required for the corridor to be effective often depends on its length (Harrison 1992). Corridors for the movement of the mahogany glider should be at least 30m wide from the top of the creek bank on each side to minimise edge effects. In addition to providing adequate room for wildlife such as the mahogany glider, a buffer strip of

30m is also the most commonly recommended width to minimise stream erosion (Clinnick 1985). The edge of the buffer strip could be extended: (1) to maintain a reasonably straight plantation boundary; (2) where a marked change in slope would hamper site preparation or runoff control; and (3) where a bank is actively collapsing and further protection is warranted (DPI Forestry).

10.5.3 Plant Species Composition of Corridors

Riparian vegetation offers some advantages such as an increased species diversity of plants, with species such as *Corymbia intermedia*, *Corymbia tessellaris*, *Eucalyptus pellita*, *Eucalyptus tereticornis*, *Melaleuca dealbata* and *Melaleuca leucadendra* often being more common along creeks than in adjacent open areas. If tree species are to be planted in order to establish or restore a corridor, they should consist of species from within the families Mimosaceae (acacias and *Albizia*) and Myrtaceae (bloodwoods, eucalypts and melaleucas) (Table 10.1). Rainforest species (with the exception of *Corymbia torrelliana*) are not recommended, as mahogany gliders do not appear to utilise these species for either food or shelter (Chapters 5 and 6). In planting trees, it will be important to combine a number of species that provide food throughout the year (See Chapter 5 for a full list of potential plant food species). In addition it is important to include a number of individuals of each species because of the potentially high failure rate of flowering with species.

Table 10.1. List of plant species recommended for planting along corridors. * known food tree species (derived from Chapter 5).

Scientific Name	Common Name	Flowering Time	Ref.
*Acacia crassicarpa**	Brown Salwood	October-December (arils)	1,2,3
*Acacia flavescens**	Wattle	October-November (arils)	1
*Acacia mangium**	Wattle	October-January (arils)	1
*Albizia procera**	Albizia	All year -sap	1
*Corymbia clarksoniana**	Clarkson's Bloodwood	March-May	1,2,3,4
Corymbia dallachiana	Bloodwood	November-April	2,4
*Corymbia intermedia**	Pink Bloodwood	November-April	1,2,3,5,6
*Corymbia tessellaris**	Moreton Bay Ash	November-January	1,2,3,4,6
*Corymbia torelliana**	Cadargi	July-November	1,4,6
Eucalyptus acmenoides	Yellow Stringybark	October-February	1,2
Eucalyptus drepanophylla	Narrow-leaved Ironbark	November-July	1
*Eucalyptus pellita**	Red Mahogany	January-March	1,3
*Eucalyptus platyphylla**	Poplar Gum	September-October	1
*Eucalyptus tereticornis**	Blue Gum	June-September	1,3
*Melaleuca dealbata**	Cloudy Tea-tree	September-November	1,2,3
*Melaleuca leucadendra**	Long-leafed Paper Bark	June-July	1,2
Melaleuca nervosa	Paper bark / Tea-tree	May-September	2,7,8
Melaleuca quinquenervia	Coastal Tea-tree	May-July	2
*Melaleuca viridiflora**	Broad-leafed Tea-tree	Jan.-Feb and May-Jul.	1

1 Pers. Obs.; 2 James Cook University, Townsville plant records; 3 Van Dyck 1993; 4 Hill & Johnson 1995; 5 Williams 1979; 6 Brooker & Kleinig 1994; 7 Tweddel 1982; 8 Williams 1984.

10.5.4 Problems with Corridors

10.5.4.1 Use of Corridors by the Mahogany Glider

Although mahogany gliders have been found within corridors (Chapters 3 and 6), the number of dispersing animals that find and use a specific corridor within a reasonable time period is likely to be very small (Harrison 1992). It is also very difficult to determine the rate of migration of individuals through corridors, although this is particularly important in maintaining isolated populations (Simberloff & Cox 1987). Simberloff and Cox (1987) noted that studies cited to support the contention that corridors actually increase migration and/or decrease extinction are, upon close examination, often insufficiently controlled to demonstrate this point. It has also been suggested that low-quality corridors could act as sinks (ie. have very high mortality rate), decreasing the size of the metapopulation (a population made up of several subpopulations - often linked by corridors)(Henein & Merriam 1990; Soule & Gilpin 1991).

10.5.4.2 Edge Effects on Corridors

A number of edge effects can contribute to the decreased effectiveness of wildlife corridors for threatened species such as the mahogany glider. Corridors present throughout the range of the mahogany glider often have high levels of weed invasion from introduced vines, grasses and herbs which can decrease the effective width of the corridor as they can suppress regeneration of trees (Table 10.2; See Panetta & Hopkins 1991, for a review of weeds in corridors). In addition some native species, in particular *Acacia flavescens* can grow in very high densities along creek lines and the edges of corridors. The high density of understorey plants, particularly *Acacia flavescens*, appears to result in a decreased utilisation by the mahogany glider, and to favour the sugar glider *Petaurus breviceps* (See Chapter 4). As a result of increased shading and competition from these plants, recruitment of required Myrtaceae species may be reduced.

Increased predation may also be a problem with predators such as owls and pythons having a greater opportunity to prey upon the mahogany glider in corridors. Scrub pythons for example appear to favour the wetter creekline vegetation and are significant predators of the mahogany glider (pers obs). Therefore if this is the only habitat available, as is the case with corridors, the opportunity for predation is increased (pers. obs). The edges of corridors are also more exposed to weather events such as strong winds, which can result in an increased number of trees being blown over, reducing the value of the corridor (Chen *et al.* 1992; Esseen 1994; Lindenmayer 1996).

Table 10.2. Exotic plants of potential concern as weeds in corridors within the distribution of the mahogany glider.

Scientific Name	Common Name	Family	Plant Type	Ref.
Exotic Species				
Thunbergia alata	Orange Thunbergia	Acanthaceae	Vine	1
Thunbergia grandiflora	Blue Thunbergia	Acanthaceae	Vine	2
Ageratum houstonianum	Billygoat weeds	Asteraceae	Herb	1
Tridax procumbens	Tridax Daisy	Asteraceae	Herb	1
Allamanda carthartica.	Yellow Allamanda	Apocynaceae	Vine	2
Senna obtusifolia	Sicklepod	Caesalpiniaceae	Shrub	1
Ipomoea indica	Blue Morning Glory	Convolvulaceae	Vine	2
Ipomoea triloba	Pink Convolvulus	Convolvulaceae	Vine	2
Centrosema pubescens	Centro	Fabaceae	Vine	1,2
Clitoria laurifolia	Butterfly Pea	Fabaceae	Vine	2
Crotalaria goreensis	Pea Rattlepod	Fabaceae	Herb	1
Crotalaria pallida	Pea Rattlepod	Fabaceae	Herb	1
Macroptilium atropurpureum	Siratro	Fabaceae	Vine	1,2
Neonotonia wightii	Pea Flower	Fabaceae	Vine	2
Mimosa pudica	Sensitive Weed	Mimosaceae	Herb	1
Passiflora subpeltata	White Passion Fruit	Passifloraceae	Vine	2
Passiflora foetida	Stinking Passion Flower	Passifloraceae	Vine	1,2
Passiflora suberosa	Corky Passion Vine	Passifloraceae	Vine	1,2
Rivina humilis	Rivina	Phytolaccaceae	Shrub	1
Brachiaria mutica	Paragrass	Poaceae	Grass	1
Panicum maximum	Guinea Grass	Poaceae	Grass	1
Pennisetum purpureum	Elepant Grass	Poaceae	Grass	1
Urochloa mosambicensis	Grass	Poaceae	Grass	1
Lantana camara	Lantana	Verbenaceae	Shrub	1,3
Stachytarpheta jamaicensis	Snakeweed	Verbenaceae	Herb	1
Stachytarpheta urticifolia	Snakeweed	Verbenaceae	Herb	1

1) Kemp and Cumming (Qld. Dept. of Env. and Herit.); 2) Calvert 1996; 3) pers. obs.

10.5.4.3 Riparian Rainforest Expansion Within Corridors

Observations to date suggest the mahogany glider does not utilise any species of rainforest trees for shelter, with only a few species (such as *C. torelliana* and *Melicope elleryana*) being utilised for food (Chapters 5 and 6). Throughout most of the distribution of the mahogany glider, rainforest expansion occurs along creek lines from the centre of the corridor toward the edge of the corridor taking over the woodland species. This reduces the effective corridor width and eventually rainforest can occupy the entire width of the corridor, leaving only emergent food trees such as

C. intermedia, *E. pellita*, *E. tereticornis* and *M. leucadendra* so that use of the corridor by mahogany gliders is likely to be greatly reduced.

As sclerophyllous trees are unable to regenerate in shade, a long term transition to rainforest may ensue (Harrington & Sanderson 1994). As grass is excluded because of shading by the rainforest canopy, the hot fires required to reduce rainforest are difficult to start (Harrington & Sanderson 1994). The limited space within corridors and the loss of available habitat through the expansion of rainforest is of real concern, as the presence of rainforest can render corridors effectively useless for the movement of the mahogany glider. Care needs to be taken that fires do not occur too frequently as these can predispose natural communities to weed invasion (Panetta & Hopkins 1991).

10.5.5 Maintenance of Corridors

Key corridors will need to be maintained throughout the distribution of the mahogany glider so that weeds do not take over and prevent the establishment of trees that are utilised by the mahogany glider. Corridors which are under threat from the expansion of riparian rainforest or which have a thick *Acacia* understorey will need to be routinely burnt. Burning could potentially be conducted every 2-3 years, immediately after harvesting of sugar cane so that produce is not burnt. In addition burning will assist in allowing the establishment of seedlings and remove the grass understorey (over a short period) that provides harbourage for problem rodents including the canefield rat *Rattus sordidus* and the grassland melomys *Melomys burtoni*, which cause significant losses to sugar cane.

10.5.6 Incentives for Land Owners to Establish and Maintain Corridors

The presence of corridors around paddocks and particularly along water courses results in better water quality as a result of a decreased runoff of pesticides, herbicides and siltation. They also help to decrease soil erosion by increasing bank stability.

Each year significant losses of sugarcane are attributed to the canefield rat and the grassland melomys as a result of their chewing stalks and secondary losses occur because of damaged stalks becoming infected with bacterial and fungal rot, lowering sugar content (Rampaud 1993; Robertson *et al.* 1995). Damage from native rodents results in losses of more than $6 million per year to the sugar industry in north Queensland (Robertson *et al.* 1995). In central and north Queensland approximately 50% of the cane growing area is affected by rodents, resulting in losses of 5-10% of cane (Rampaud 1993; Wilson & Whisson 1993).

The most efficient to manage rodents is to prevent the build up of numbers, rather than trying to reduce numbers once they are high. Rodents use creeklines, irrigation canals and drainage ditches as refuges, feeding on grasses there and re-entering sugarcane from these permanent refuges as the crop matures (Rampaud 1993; Robertson 1995). As a result, damage to sugarcane is greater in areas adjacent to drainage channels, fencelines and drains as the adjacent grassy areas are used as harbourage by native rodents (Redhead 1973). Therefore the control of weeds which attract rodents, particularly grasses, in areas adjoining the cane fields will help to reduce the invasion of rodents, resulting in higher sugar yields (Rampaud 1993; Robertson *et al.* 1995).

One strategy to reduce weeds which attract rodents near canefields is to establish closed-canopy forest along creeks and around paddocks which shade out weeds (Robertson *et al.* 1995). Although mahogany gliders appear to favour an open understorey and canopy, a compromise in plant species used could potentially be made to minimise grass cover and also allow the mahogany glider to utilise these areas. Once established, spraying with herbicides is no longer necessary, resulting in long-term low maintenance and a greatly reduced need for rodenticides (Anonymous 1995). This will also stop secondary poisoning of birds of prey caused by rat baiting which in turn will allow more rodents to be eaten by birds of prey, further reducing rodent numbers. Preliminary results of a trial that revegetated grassy drains with trees (mostly rainforest species) to exclude rodents, resulted in up to 75% fewer rodents after one year's growth of trees (Robertson *et al.* 1995). Therefore rodent control and maintenance of corridors for mahogany gliders could be integrated.

10.6 Rainforest Expansion and the Use of Fire as a Management Tool

Apart from riparian rainforest along creeks, large scale expansion of rainforest occurs throughout parts of the mahogany gliders distribution, further threatening the value of the remaining habitat. Van Dyck (1993) noted rapidly invading rainforest communities in several locations including the Hull River area, parts of Barrett's Lagoon, Edmund Kennedy National Park, Murray Upper and Hinchinbrook Island.

To maintain the woodland species, fire management is clearly indicated. Fire has been shown to be important in maintaining the dominance of sclerophyllous trees in forest and woodland communities elsewhere in Australia (Ashton 1981; Ash 1988; Unwin 1989). Catling (1991) proposed that rather than using annual low intensity burns, a range of fire frequencies and intensities should be used, including the occasional planned intense fire. This was suggested to allow a more heterogeneous habitat to develop with increased variation in forest structure, particularly as some species of animals become more prone to predation with increased exposure resulting from decreased cover. Catling (1991) suggested that a number of native mammal species including members of the Phalangeridae, Burramyidae, Acrobatidae and the Petauridae including the sugar glider and squirrel glider *Petaurus norfolcensis* would be disadvantaged by a simplification of forest structure from frequent, low-intensity prescribed burns.

10.7 External Causes of Mortality

10.7.1 Effects of Mortality on Population Viability

Adult mortality has been shown to have a great influence on population viability of the mahogany glider (Chapter 9) and other petaurids such as the yellow-bellied glider *Petaurus australis* (Goldingay & Possingham 1995). Therefore adult mortality resulting from non natural events can have a large affect on the viability of sub-populations of the mahogany glider.

10.7.2 Fences

As a result of the increased fragmentation within the distribution of the mahogany glider, there has been an increased need for the mahogany glider to cross gaps in habitat which often have barbed wire along their edges. Mahogany gliders use the open areas along the edges of habitat to make longer glides (pers. obs.). As a result of having to glide over barbed wire fences, death by entanglement on barbed wire appears to have become a significant cause of mortality for the mahogany glider (pers obs.; Lyon 1993; K. Smith DoE pers. comm.; Smith 1996). Therefore it is important that gliders have adequate clearance to glide over fences. To achieve this, a maximum clearing distance of 20m is suggested along fencelines.

10.7.3 Predation

Significant natural mortality occurs as a result of owls, such as the rufous owl *Ninox rufa*, barking owl *Ninox connivens*, masked owl *Tyto novaehollandiae*, and potentially the lesser sooty owl *Tyto multipunctata* (John Young pers. comm.), and snakes, such as the scrub python *Morelia amethistina* (pers. obs). The significance of predation by feral cats and dogs is at present unknown, although the greater climbing and hunting ability of cats is likely to make them a greater threat than dogs. Predation of both sugar and squirrel gliders by cats has been observed previously (Storch pers. comm.; Potter 1991). Because of the increased isolation of populations and the resulting increased need to cross open space in order to find food, the opportunity for predation by dogs and particularly cats can only increase. To date there have been several records of predation of mahogany gliders by feral and domestic cats and dogs (Lyon 1993; K. Smith Qld DE pers. comm.).

10.7.4 Roads

As a result of the increased fragmentation and need to disperse more widely to access food, the need to cross over roads has also increased. Mortality has been observed on a number of occasions as a result of animals being run over while coming to the ground to cross roads (pers. obs; Smith 1996).

10.8 Recommendations

Recommendation (1): Habitat Conservation.

- Because of the shortage of habitat remaining it is critical to retain as much coastal lowland woodland as possible, regardless of tenure. Habitat should consist of both critical habitat and surrounding vegetation wherever possible, to maximise population viability.

Recommendation (2): Habitat Management.

- Examine different fire regimes to determine which ones will maximise woodland diversity of myrtaceous plants and decrease rainforest expansion and the likelihood of catastrophic fire.

Recommendation (3):Wildlife Corridors.

- Establish an active program of establishing wildlife corridors (re-planting if required), targeting key sub-populations and involving consultation with local landowners.
- Conduct research to determine the composition of plants that will provide shade to reduce weeds so that rodent harbourage is minimised, and also provide food and shelter for mahogany gliders.
- Examine the potential of spraying the edge of corridors with herbicides to remove grass that may provide harbourage for rodents.

Recommendation (4):Gaps in Habitat.

- Because of the ease with which mahogany gliders are isolated it is recommended that gaps along fencelines and roads do not exceed 20m.
- Retain trees to the edge of gaps such as roads, tracks and drainage lines to allow gliders to glide over these gaps in habitat.

Recommendation (5): External Mortality.

- Monitor predation by domestic and feral animals, particularly cats, to determine if further action needs to be taken.

- Use only plain wire (ie. without any barbs) for fencing if no cattle are present. If cattle are present then it is recommended that the top strand of wire be made of plain wire.

10.9 Future Research

- Conduct a baseline study to examine the present genetic diversity in each of the major remaining populations so that it can be referred to in the future to examine if inbreeding is occurring.
- Complete a detailed examination of the remaining habitat in regard to vegetation types, size of habitat fragments remaining, and the potential use of corridors between fragments.
- Examine the large scale habitat requirements with the aim of developing a model to predict the occurrence of mahogany gliders in particular habitat.
- Complete a broad scale study to examine the use of corridors of different lengths and widths of corridors in order to determine the limits to which they will utilise.
- Undertake further surveys that concentrate on altitudinal limits within the known range. Techniques could include spotlighting, owl pellet analysis and hair tubing, although it should be noted that owl pellets cannot be used to determine altitudinal limits, as owls can take gliders several kilometres from their nest.
- Assess the impact of rainforest expansion along corridors and in continuous habitat.
- Examine the impact of different fire regimes in controlling rainforest expansion within key corridors and remnant habitat.

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Appendices.

Appendix 1

(a) Mistletoe (Loranthaceae) likely to occur within the mahogany glider distribution and likely to occur within glider habitat (derived from George 1984). Species confirmed within the mahogany glider distribution have been marked with an asterisk.

Species	Host
Amyema bifurcatum	Range of species
Amyema conspicuum	Open forest and rainforest margins, on various hosts but common on *Alphitonia*.
Amyema miquelii	Open forest and Woodland on *Eucalyptus* and *Acacia*.
*Amyema sanguineum**	Range of species
*Dendrophthoe falcata**	Wide range of hosts
*Dendrophthoe glabrescens**	Open forest and Woodland in *Eucaltyptus*, *Melaleuca*, *Tristania*, *Barringtonia*.
*Dendrophthoe homoplastica**	Open forest and woodland on *Eucalyptus*, *Tristania* and *Melaleuca*.
*Dendrophthoe vitellina**	Open forest, mostly on Myrtaceae
Diplatia furcata	Open forest on *Melaleuca* and *Callistemon*, rarely *Eucalyptus*.
Diplatia grandibractea	Open forest and woodland on *Eucalyptus*.
Lysiana spathulata	Mostly on Acacias

(b) Mistletoe (Loranthaceae) species less likely to occur in within the mahogany glider distribution but less likely to occur in mahogany glider habitat (derived from George 1984).

Species	Host
Amyema biniflorum	Dry and mesic sclerophyll forest, exclusively on *Eucalyptus*
Amyema cambagei	Open woodland on *Casuarina*
Amyema villiflorum villiflorum	Rainforest, open forest and coastal scrub on *Terminalia*, *Acacia*, *Lysiphyllum*
Amyema glabrum	Rainforest and mangroves.
Amyema congener congener	Open forest on *Acacia* and Casuarinaceae.
Amylotheca dictylophleba	Mesic forests on rainforest trees
Amylotheca subumbellata	Casuarinaceae & *Grevillea*
Decaisnina brittenii brittenii	*Melaleuca*, *Parinari*, *Syzygium*, *Ficus*, *Alstonia*, *Tristania*
Decaisnina hollrungii	Rainforest and dense coastal scrub
Diplatia tomentosa	In swamp forests on *Melaleuca*
Lysiana maritima	Mangroves in *Ceriops* and *Rhizophora*, and adjacent Casuarinaceae and *Myoporum*.
Lysiana linearifolia	*Flindersia*, *Eremophila*, *Acacia*
Lysiana filifolia	Open Casuarinaceae

Appendix 2

Food availability of all known and predicted *primary* food trees of the mahogany glider within their entire range. * Known food species, - nectar and pollen availability, S also provides sap seasonally, = sap availability, F also provides fruit, # fruit availability, + *Acacia* arils availability.

```
                                                                             Month
Species                     J         F         M          A         M         J         J        A         S         O         N         D
A. mangium*              +++                                                                                                 ++++++++
A. sanguineun*            ###            -------- ######                                  ---------######                 ------------------####
D. falcata* (F)*         ######                          ----------########                    --------#######                  --------##
C. tessellaris *        ----------                                                                                              -------------
C. intermedia *          -----------------                                                                                     --------------
E. acmenoides            ----------------                                                                                     -------------------
C. dallachiana           -----------------------------                                                                             ----------
E. drepanophylla          ----------------------                                                                               ----------------
E. pellita*                 --------------------
M. viridiflora*               ----------------------           -------------------
C.clarksoniana*                               ------------------------------
X. johnsonii (S) *                                             ====================---------------------
M. quinquenervia                                                ----------------------
M. nervosa                                                      -------------------------------------------
M. leucadendra   *                                                         ------------------
C. torelliana*                                                                    ---------------------------------------------------
E. tereticornis*                                                                  --------------------------------
E. platyphylla*                                                                                      --------------------
L. suaveolens                                                                                        ------------------------------------
M. dealbata*                                                                                             -------------------
A. crassicarpa *                                                                                                 ++++++++
A. flavescens *                                                                                                  ++++++++
                            J       F         M          A         M         J       J        A         S        O         N         D
```

Note that *A. crassicarpa, A. flavescens* and *A. mangium* are primary food sources for arils but secondary food souces for pollen.

Appendix 3

Food availability of all known and predicted *secondary* food trees of the mahogany glider within their entire range. * Known food species, - nectar and pollen availability, = sap availability, S provides pollen only, # fruit availability, + Acacia arils availability.

```
                                                              Month
Species                  J       F        M       A        M       J       J      A       S       O        N       D
F. congesta           ################################################################################################
F. hispida            ################################################################################################
F. opposita           #################################################################################################
F. racemosa           #################################################################################################
F. variegata          ##################################################################################################
P. careya              #########                                                                -----------------#######
E. falcata            ------########                                                           --------------------------
S. tierneyanum         ##############                                                                          ----------
T. exiflora           -------------------                                           -------------------------------------
B. aquilonia*          ------------------                                           -------------------------------------
T. sericocarpa         ---------                 #################################                        ----------------
T. muelleri           -----------##############################                                              -------------
E. cloeziana          ----------------------------------
D. alata              ################                                                            ------------------#####
C. australianum        ---------------------
B. incana             ----------------------------
S. australe           #########                                                                  ------------------------
N. orientalis                  #####################                                               ---------------------
A. aulacocarpa                    -------------------------------------------------         ++++++??
A. flavescens (P)                       ------------------------
M. elleryana*                          --------------###############
R. fitzalanii                          #######################################          --------------------
A. mangium (P)                                    ----------------
X. chrysanthus                                    -------------------- ########################
A. holosericea                                       -------------------------------         +++??
E. angustifolius                                        ---------
A. crassicarpa (P)*                                        -------------------
C. brachiata                                              --------------------------                   ##############
A. leptocarpa (P)                                             --------------------------           ++++++++
G. pteridifolia                                               ----------------------------------
G. parallela                                                  --------------------------------
T. timon                                                      --------------------------------------------
D. diphyllostegia                                             ----------------------------------------------------
E.vespertilio                                                    -----------------------------------
B. plagiocarpa                                                   --------------------
C. viminalis                                                              -----------------------------------------
D. tetraphylla*                                                                 ------------
L. grandiflora                                                                                   ----------------
S. forte                                                                                           ----------------
                         J       F        M       A        M       J       J      A       S       O        N       D
```