Ecology of the squirrel glider (Petaurus norfolcenis) in subtropical Australia

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ECOLOGY OF THE SQUIRREL GLIDER (PETAURUS NORFOLCENSIS) IN SUBTROPICAL AUSTRALIA

by

David Sharpe
(BAppSci – Hons)

Submitted in fulfilment of the requirements for the degree of Doctor of Philosophy
School of Environmental Science and Management, Southern Cross University
September 2009
CANDIDATE DECLARATION

I certify that the work presented in this thesis is, to the best of my knowledge and belief, original, except as acknowledged in the text, and that the material has not been submitted, either in whole or in part, for a degree at this or any other university.

I acknowledge that I have read and understood the University’s rules, requirements, procedures and policy relating to my higher degree research award and to my thesis. I certify that I have complied with the rules, requirements, procedures and policy of the University (as they may be from time to time).

David Sharpe

23 September 2009
ABSTRACT

Human activities have resulted in increasing levels of habitat loss and fragmentation, threatening many species with extinction. Contemporary wildlife management seeks to provide an understanding of the ecology and behaviour of animal species that can assist their management and conservation. Describing the population ecology of wildlife species can assist conservation planning, for example, by providing input data for population viability assessments. Similarly, understanding animal behaviour provides insights into additional aspects of a species’ biology that ultimately affect population processes.

The squirrel glider (*Petaurus norfolcensis*), which is the subject of this thesis, provides a good example of a species where conservation planning is required. It has an extensive distribution in eastern Australia, covering a geographic distance of approximately 3000 km. However, its habitat continues to be threatened by habitat loss and fragmentation throughout its range. The squirrel glider is listed as threatened in the southern half of its range, while its status needs to be reviewed in the northern part. Prior to the late 1990s, when research for this thesis commenced, few detailed studies had been conducted on the squirrel glider. This hindered the ability of land managers to provide better management of the squirrel glider or its habitat to prevent a further decline in its conservation status. This thesis aimed to target gaps in knowledge of the squirrel glider and to provide information that will assist its conservation and management.

The influence of flowering patterns on the population ecology of the squirrel glider was described at a site in north-east NSW over a 5-year period (1997 – 2001). The population on a 38 ha trapping grid was relatively stable over the first four years of study and contained at least 12 adult gliders. Following reproduction, their associated offspring created population peaks that rarely exceeded 20 individuals. During the winter of 2000, there were more than 30 gliders present, including juveniles, which was a 5-year high. *Eucalyptus robusta* and *Banksia integrifolia* flowered heavily during that winter and were important food resources. *Eucalyptus robusta* had not flowered in the previous four years, while *B. integrifolia* was a reliable winter nectar resource. Despite the availability of nectar, reproductive success appeared to be low due to the loss of pouch young. Gliders rapidly lost weight between July and September 2000, which coincided with extremely dry conditions and a lack of flowering in *Eucalyptus siderophloia*, an important nectar source. The number of gliders on the grid fell by almost 80% between September and November 2000. However, the total population
declined by 55% and the adult population by 42% when compared to their numbers averaged across the previous four years. Between September 2000 and March 2001, only seven squirrel gliders were known to be resident. Glider numbers remained low during 2001, indicating that recovery was slow. The observed decline appeared to be widespread throughout the region. Therefore, there was little opportunity for migration to assist population recovery. These observations suggest the squirrel glider may be sensitive to flower failure in key winter/spring flowering species.

The population ecology of the squirrel glider was also examined in a forest remnant in Brisbane, where nectar was a dominant food item. A total of 201 gliders (adults and juveniles) were captured 705 times in 3,729 trap-nights (19% trap success) over a 4-year period (2002 – 2006). The population peaked in the first year at a density of ~1.6 individuals ha$^{-1}$, but then declined to ~0.5 individuals ha$^{-1}$ by the final year. Such a fluctuation has been observed in another population of this species where nectar was dominant in the diet. In both cases the fluctuation appeared to be mediated by variation in flowering intensity. Births occurred from March to November, peaking between April and July. All females >1 year bred in each year of the study, with a mean litter size of 1.7 (n=122). The overall natality rate was 1.9, indicating that females occasionally bred twice per year. The sex ratio was at parity in the pouch and in the trappable population. Gliders first entered the trappable population at four months of age, and persisted for a mean of 32 months. The maximum longevity was seven years and eight months. The demographic characteristics of this squirrel glider population within a forest remnant surrounded by urban development were similar to that reported elsewhere.

The management of threatened species requires detailed knowledge of key population parameters to be effective. The trapping of adult squirrel gliders in Brisbane was the subject of a mark-recapture analysis. A total of 187 adult gliders (96 females, 91 males) were captured 620 times, in 19 tree-trapping sessions. A Cormack-Jolly-Seber model was employed in program MARK to quantitatively estimate the population parameters of adult survival and abundance. A variety of factors (e.g. gender, year, season) that may affect survival were examined. Survival is simply defined as the disappearance of gliders from the trappable population. Density was highest early in the study and gradually declined during the following three years. The overall annual survival probability was 0.49 ± 0.08 (females 0.51 ± 0.12, males 0.48 ± 0.12). The estimated adult population density ranged between 0.6-1.9 ha$^{-1}$. 

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This value was overestimated to some degree by the dispersal of gliders early in their second year despite having attained breeding age. However, because the study was conducted in an urban remnant mostly surrounded by relatively hostile matrix habitat, the effect of dispersal may have been relatively minor. Despite this constraint, the estimated probability of adult survival in this study was considerably lower than the main value (0.65) used in a population viability analysis previously conducted in the locality of our study site. This suggests that population viability had been substantially over-estimated and now requires re-evaluation. Further studies that assess the survival of squirrel gliders are needed to assess the extent to which this parameter varies among localities.

The vocal behaviour of the squirrel glider was described from 465 h of observation across five sites in north-east New South Wales and south-east Queensland. A monosyllabic or polysyllabic nasal grunt was the most frequent call (56% of 208 calls). It ranged from single calls to sequences up to 20 min duration (mean 2.1 min ± 0.6 s.e.) and was heard on 34% of nights (n=83) at two sites. The rate of the nasal grunt showed a positive relationship with population density at one site. The nasal grunt was typically made when conspecifics were near the caller, but responses were infrequent (7% of observations). Call playback produced no discernable change in call response. The nasal grunt appears to regulate individual spacing by facilitating mutual avoidance, a function hypothesised to be an evolutionary precursor to the use of calls in territorial defence. Threatening calls were the next most common vocalisation (17% of calls) and were accompanied by scuffles and/or chases. They were also used when gliders were preyed upon and during animal handling. The calling behaviour of the squirrel glider confirms the importance of vocal communication among petaurid gliders.

Exudivorous mammals exploit food items of high quality and rates of renewal, offset by wide dispersion, low abundance and temporally variable availability. How this influences foraging effort and size-related foraging efficiency remains poorly described. The time budget of the squirrel glider was examined in an urban forest remnant in Brisbane. During each of three seasons that were stratified by moon phase, six males and six females were observed during a series of 1 h focal observations that extended from dusk until dawn. Feeding dominated the time budget, accounting for 78% of observation time, or 85% of time when combined with behaviours associated with foraging. Females appeared to maximise feeding rates prior to entering the energetically demanding phase of late lactation. Little time was spent resting and all other behaviours combined were a relatively small component of the time budget. Longer
nights and the full moon were associated with later emergence and earlier retirement times. Animals re-entered their dens in tree hollows during the night, representing 2% of activity in spring, 18% in winter and 9% in autumn. The reasons for this are unclear but may be related to predation risk and reproductive activity. The high proportion of the time budget devoted to foraging suggests that the squirrel glider is likely to be adversely affected by all forms of habitat disturbance.

Both studies of the population ecology of the squirrel glider found that the populations varied substantially in size over time. While the squirrel glider is able to maintain population processes in fragmented habitats, its survival rate was found to be lower than assumed during an earlier population viability analysis (PVA) study. Both these factors (population variability, survival) will impact on population viability and suggest that viable populations will need to be larger than previously recognised. Further studies of population viability that incorporate this new information are now needed to guide the conservation and management of the squirrel glider throughout its range.
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Lastly, I would like to thank my partner, Deborah Perry, for field assistance in Bungawalbin, enabling my absences while in the field in Brisbane, for many discussions on squirrel gliders and ecology in general, and for allowing me to “download” after the excitement of the field.
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1. **INTRODUCTION**

1.1. **Introduction**

A primary aim of contemporary ecological management and conservation is to prevent the extinction of species (Soule 1985; Burgman *et al.* 1988; Beebee and Griffiths 2005). However, habitat loss, fragmentation and alteration due to human activities, together with the natural patchiness of habitats, causes many species to exist as a number of small, relatively isolated populations that may occasionally exchange individuals (a metapopulation) (Hanski and Gilpin 1991). Consequently, small size and vulnerability to on-going decline threatens such populations. Ultimately, a species becomes extinct due to the cumulative loss of its populations (Clark *et al.* 1991; Caughley 1994; Norris 2004). This may be true even for species that have an extensive geographic range (e.g. NSW NPWS 2003; Dique *et al.* 2004). Moreover, a species with an extensive range may face different threats across its distribution, requiring independent research and different management approaches in different regions (e.g. Reed and Lunney 1990; Dique *et al.* 2003). Studies that adopted a population level focus have made an important contribution to a species’ conservation, directly enabling population declines to stabilise or reverse (Innes *et al.* 1999; Ferreira *et al.* 2005; Varley and Boyce 2006). Landscape level approaches that facilitate metapopulation population dynamics (e.g. corridor establishment) are also important (e.g. Beier and Noss 1998; Foppen *et al.* 2000; Schtickzelle *et al.* 2005; Dixon *et al.* 2006), however, such approaches still need to be informed by site-specific population studies (Baguette and Schtickzelle 2003; Armstrong 2005).

The long-term management of wildlife in the face of expanding human populations depends upon acquiring detailed knowledge about the distribution and abundance of animal populations and the factors that influence these. Thus, key areas of knowledge include habitat selection and habitat quality, population ecology, diet, spatial requirements, behaviour, predation and response to disturbance (Clark *et al.* 1991; Bolen and Robinson 2003), which, for convenience, will be simply described as a species’ ecology. For recognised threatened species, this also includes identifying the causes of decline so that they can be halted and reversed (Armstrong 2005; Beebee and Griffiths 2005; BenDor *et al.* 2009). These are all factors to be considered in recovery plans for threatened species (e.g. Coxen's Fig-Parrot Recovery Team 2001; NSW NPWS 2003; Meyer *et al.* 2006).

1
This thesis describes aspects of the population ecology and behaviour of the Australian squirrel glider (*Petaurus norfolcensis*) at two locations, one in north-east New South Wales (NSW) (Plate 1.1) and one in south-east Queensland (Qld) (Plate 1.2), approximately 180 km apart (these sites are Bungawalbin Nature Reserve (NR) and Minnippi Parklands respectively and are described in the relevant chapters). A distinction between these locations is that this marsupial is listed as threatened in NSW but not in Qld. However, the squirrel glider is threatened by urban expansion in south-east Qld (Rowston *et al.* 2002; Goldingay and Sharpe 2004a) and is regarded as a priority species for conservation by Brisbane City Council (BCC) (BCC 2000, 2005). The study sites also occur in different landscape contexts. The NSW site is situated within an expanse of relatively natural habitat, although selective logging has occurred in the past and continues in some of the surrounding forest. The site in Qld is located within an urban matrix <10 km from Brisbane’s CBD (Plate 1.3).

In additional to the need for research due to its threatened status (see below for further review), the conservation of the squirrel glider is important for several further reasons. The squirrel glider is widespread in the forest and woodland ecosystems of eastern Australia (Suckling 1995). Nectar is an important component of its diet at some sites and it is likely that the squirrel glider is an important pollinator in forest ecosystems (Sharpe and Goldingay 1998). Canopy arthropods are also a conspicuous component of its diet (Menkhorst and Collier 1987; Sharpe and Goldingay 1998), suggesting that it may have a role in regulating phytophagous insects, thus contributing to forest health. The squirrel glider is also ecologically similar to several congeneric species (Table 1.1) and information gathered on it may provide useful insights into the conservation requirements of these related species.

A focus in this thesis is to provide an understanding of the squirrel glider’s ecology so that the management of its populations can be improved, contributing to its long-term conservation. From this perspective, the thesis documents a number of different elements of its ecology to either fill in gaps in knowledge or to extend our current understanding of the species. The diet, home-range and den use of the squirrel glider were examined in my honours thesis at the northern NSW site (Sharpe 1996). The current thesis focuses on population ecology and additional aspect of the squirrel glider’s behavioural ecology (vocal behaviour, time budget). This introduction briefly reviews the importance of these aspects of animal ecology to a species’ conservation, before providing an overview of the state of knowledge of the ecology of this species at the commencement of this thesis.
Plate 1.1: Photograph of the open grassy forest habitat at Bungawalbin Nature Reserve, north-east NSW.

Plate 1.2: Photograph of the habitat at Minnippi Parklands, Brisbane. Note the open grassy area in the background.
Plate 1.3: Aerial photograph of Minnippi Parklands showing the surrounding urban land uses. The study area is indicated by the pink line. Despite the patchiness of the canopy cover, the squirrel glider used all treed areas. Note the presence of additional habitat to the east of the study site.

Table 1.1: Australian species of *Petaurus*, showing the year each species was described and inter-specific variation in body mass.
Species are arranged in order of increasing size. The size range refers to the maximum and minimum weights found throughout each species’ range, numbers in brackets are mean weights (where available). Male (M) and female (F) weights have been provided where possible. Source: Van Dyck and Strahan (2008).

<table>
<thead>
<tr>
<th>Species</th>
<th>Common Name</th>
<th>Year Described</th>
<th>Weight Range (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Petaurus breviceps</em></td>
<td>sugar glider</td>
<td>1839</td>
<td>115 - 160 (140) M</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>95 - 135 (115) F</td>
</tr>
<tr>
<td><em>Petaurus norfolcensis</em></td>
<td>squirrel glider</td>
<td>1792</td>
<td>190 - 300 (230)</td>
</tr>
<tr>
<td><em>Petaurus gracilis</em></td>
<td>mahogany glider</td>
<td>1883</td>
<td>330 - 410 (363) M</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>255 - 407 (343) F</td>
</tr>
<tr>
<td><em>Petaurus australis</em></td>
<td>yellow-bellied glider</td>
<td>1791</td>
<td>450 - 700</td>
</tr>
</tbody>
</table>

1.2. The Contribution of Population Ecology and Behaviour to Conservation

1.2.1. Causes of Population Decline
To reverse the decline of a species, it is first necessary to identify the causative factors (Caughley and Gunn 1996). Lunney *et al.* (1997) suggested that there appear to be no broad and consistent trends threatening fauna, even between closely related species, indicating the need for species-specific information (see also Recher and Lim 1989). However, habitat loss
and fragmentation, whether associated with rural or urban land use, are regarded as the primary threats to many species (Debinski and Holt 2000; Cushman 2006; Burbidge et al. 2008), primarily affecting species with limited dispersal ability through the resulting landscape (e.g. Cooper and Walters 2002; Wiegand et al. 2005). Other factors may include altered fire regimes (Sutherland and Dickman 1999; Koprowski et al. 2005), grazing (Hobbs 2005), logging (Milledge et al. 1991; Cameron 2006), introduced predators (Wayne et al. 2006), competition (Grey et al. 1998), roads (Jones 2000; Bélisle and St. Clair 2001; Riley et al. 2006) and disease (Bradley and Altizer 2007). Each of these threats would require different management approaches.

Although there may be some generalities about how species respond to threatening processes, it remains necessary to understand how different species respond to such threats to ensure appropriate amelioration strategies are implemented (e.g. Keitt et al. 1997; Körtner et al. 2003). For species that have an extensive geographic range the causes of population decline can vary in different parts of its distribution (e.g. Belcher 2004), indicating that threat assessments should occur on at least a regional basis. Once threats have been identified, measures should be put in place to ameliorate their impacts (e.g. Fernandez-Juricic et al. 2005; Maron and Lill 2005; Donald and Evans 2006). This will require strategies that are targeted at populations, rather than at a species as a whole (Garner et al. 2005).

1.2.2. Population Ecology

Determining what constitutes habitats of differing quality is fundamental to explaining the distribution, abundance and productivity of animal populations (Doak 1995; Foppen et al. 2000). However, studies that directly examine the dynamics of individual populations are important because the link between population surrogates, such as habitat quality or food availability, and population processes is often poor (Armstrong 2005; Johnson et al. 2005). Studies of population ecology examine the processes that influence the size, density and regulation of animal populations. Thus, the features of populations, such as the birth rate, survival rate, age structure, sex ratio and mating system are described (Bolen and Robinson 2003). These processes are linked to intrinsic (e.g. density dependent reproduction) and extrinsic (e.g. food availability, predation) factors that influence variation in population density (Boutin 1990; Klenner and Krebs 1991; Ekerholm et al. 2004; Ozgul et al. 2004; Getz et al. 2006). Population processes can differ between different populations of a species, suggesting a need to replicate such studies across a species’ range (Frederiksen et al. 2005).
Knowledge of the population ecology of a species can contribute to the conservation of a species in several ways. For example, the size, trajectory and amplitude of fluctuation of a population are regarded as the most important factors contributing to its extinction proneness (Reed et al. 2003; O'Grady et al. 2004). Therefore, studies that focus on understanding the behaviour of individual populations have considerable merit. Long-term population studies are important because estimates of a population’s amplitude of fluctuation are positively related to study duration (Reed et al. 2003).

Population viability assessments should be conducted to test different management scenarios (e.g. during recovery planning) or assess a development proposal (Reed et al. 2002). Population viability can be formally and quantitatively examined using population models, such as population viability analysis (PVA) (Akçakaya and Sjögren-Gulve 2000). PVA is a computer simulation of a population’s extinction probability under a specific set of assumptions (e.g. patch size and spatial arrangement) and requires detailed life history data to be effective (Lindenmayer et al. 1993; Possingham and Davies 1995; Wiegand et al. 2002; Münzbergová and Ehrlén 2005).

A further value of conducting a PVA is that it entails the collation and critique of existing information, highlighting areas for future research (Possingham et al. 1993). Moreover, it also enables sensitivity analysis to be conducted, which can highlight the population parameters (e.g. adult survival, reproductive output) that most contribute to extinction risk. This enables specific management interventions (e.g. reducing the impact of a predator, increasing dispersal rates) to be implemented that target the elastic parameters (Katzner et al. 2006).

An understanding of population ecology is also important in monitoring programs, particularly in the context of adaptive management (Stem et al. 2005; Kendall et al. 2009). Monitoring of target species is often conducted to manage populations of threatened species (e.g. Joseph et al. 2006; Jackson et al. 2008) or to assess the effects of a development or other human activities (Hellawell 1991; Nichols and Williams 2006). For these reasons, the monitoring of a species often involves the collection and interpretation of population data to determine population trends and identify causative agents (e.g. Innes et al. 1999).

Habitat loss and fragmentation can influence the population dynamics of affected species (Laurance 1997; Lindenmayer et al. 1999; Banks et al. 2005; Wiegand et al. 2005). Threatened species are often managed in disturbed environments (e.g. Cooke et al. 2002), but
it remains important to also understand the behaviour of populations in more natural habitats. This enables comparisons of population behaviour under different circumstances, providing insights into mechanisms of population regulation and the effect of disturbance (Frederiksen et al. 2005).

1.2.3. Behaviour

The behaviour of individual animals influences factors such as their social interactions, reproductive success, spatial regulation, dispersal ability and response to disturbance (Blumstein and Armitage 1997; Breckling et al. 2005; Blumstein 2006; Chambon-Dubreuil et al. 2006). Studies of animal behaviour have, to date, been poorly integrated into conservation planning due to the difficulty in establishing a link between theory and practical outcomes. However, descriptive behavioural studies have the potential to contribute to conservation outcomes (Caro 2007) and have met with some success (e.g. Wolff et al. 1997; Schtickzelle and Baguette 2003). Thus, an understanding of animal behaviour has the potential to contribute to the conservation of wildlife in several ways.

By influencing survival and fecundity, the behaviour of animals affects individual fitness, which ultimately has the potential to affect population dynamics (Chambon-Dubreuil et al. 2006). Behavioural factors that can influence population dynamics includes the mating system (Kitchen et al. 2005; de Oliveira et al. 2006), territory or resource defence (Broom and Ruxton 2001; da Cunha and Byrne 2006), time allocation to various activities (e.g. food harvesting, social interaction) (Schaik et al. 1983; Dunbar 1992; Miller et al. 2006; Fashing et al. 2007) and dispersal ability (Keitt et al. 1997; Vuilleumier and Metzger 2006).

Vocalisations are frequently used to alert conspecifics to the presence of a predator, attract mates, advertise territories, or maintain individual or group spacing (Kinzey and Robinson 1983; Mitani 1985a,b; Eiler and Banack 2004; da Cunha and Byrne 2006). Therefore, the vocal behaviour of a species can provide insights into a number of aspects of its ecology and social behaviour (Blumstein and Armitage 1997; Engh et al. 2006; Saenz et al. 2006). These factors can ultimately affect resource access and mating success (Mitani 1985b). Because calls are species-specific, they can be used to detect cryptic species during distribution surveys or studies to assess the response to management activities (e.g. Kinzey and Robinson 1983; Debus 1995; Pellet and Schmidt 2005). Therefore, the study of a species’ vocal behaviour can be a valid exercise when attempting to understand the behavioural ecology of a species.
Behavioural studies can help to elucidate the response of animals to human disturbance or land use change (Menon and Potrier 1996; Norris 2004; Maron and Lill 2005; Caro 2007). Time budget studies can demonstrate behavioural changes that accompany habitat alteration (e.g. Wong and Sicotte 2007; Chipman et al. 2008), altered food availability or competitive interactions (e.g. Cucco and Malacarne 1997; Pezzanite et al. 2005; Namgail et al. 2007) or may reveal that a species is time limited (Dunbar 1992; Cope 2003; Korstjens et al. 2006; Korstjens and Dunbar 2007) and may find it difficult to adapt to change (e.g. Riddington et al. 1996).

1.3. The Squirrel Glider

1.3.1. History of Discovery and Taxonomy

The squirrel glider is the second smallest of the four Australian members of the gliding genus *Petaurus* (Table 1.1), which is endemic to the Australasian region (Flannery 1995; Strahan 1995). First described by Kerr (1792), the squirrel glider was originally placed in the genus *Sciurus* (Rodentia) due to its superficial resemblance to squirrels of the northern hemisphere. It was subsequently recognised as a marsupial as more specimens became available (McKay 1989). The specific name *norfolcensis* arose due to confusion about the locality of the type specimen, which was originally presumed to be Norfolk Island. Although the type specimen appears to have been lost, it was apparently obtained from the vicinity of Sydney (McKay 1988, 1989).

Confusion regarding the taxonomic status and distribution of the squirrel glider continued until recent times. Until the early 1990s the squirrel glider was thought to comprise two subspecies: *P. n. gracilis* in the extreme northern part of its range and *P. n. norfolcensis* throughout the rest of its range (Suckling 1983; McKay 1988). Van Dyck (1990) first raised doubts about synonymy within *P. norfolcensis* and a biochemical systematic review of *Petaurus* by Colgan and Flannery (1992) supported this view. Subsequent sightings of living animals and detailed morphological assessment of them demonstrated that the taxon *gracilis* indeed constituted a distinct species (Van Dyck 1993). Thus, there are no currently recognised subspecies of the squirrel glider (Suckling 1995). As currently understood, the mahogany glider (*P. gracilis*) is confined to a very small area of far northern QLD and the distribution of the squirrel glider surrounds it to the north, south and west (van der Ree and Suckling 2008).

Suckling (1983) did not originally consider the squirrel glider to occur east of the Great Dividing Range in eastern Australia, despite the type specimen having been collected from a
coastal habitat and published information (e.g. Marlow 1958; Davey 1984) documenting squirrel glider populations on the coast. The squirrel glider is now widely regarded as occurring in coastal forest in NSW and Qld (Eyre 2004; Kavanagh 2004). Indeed, bioclimatic modelling by Quin et al. (1996) suggests that coastal forests in these States provide optimal habitat for the squirrel glider. Suckling’s (1983) earlier account of squirrel glider distribution appears to have been biased by its distribution in Victoria, where much early work on arboreal mammal ecology was conducted. In Victoria, the squirrel glider is only found in habitats inland of the Great Dividing Range (Menkhorst 1995; van der Ree et al. 2004).

Despite its scientific description early in Australia's colonial history the squirrel glider long remained one of the least studied arboreal mammals of eastern Australia. Misconceptions regarding the squirrel glider's distribution and its close resemblance to its smaller, more common congener the sugar glider (Plate 1.4), which may result in erroneous identifications, appear to have resulted in a lack of awareness of the occurrence of squirrel glider populations. In turn, this may have contributed to this dearth of study of this species.

In recent years the squirrel glider’s populations have become better known and it became recognised as a threatened species (see below), attracting research interest. Table 1.2 summarises studies undertaken on the squirrel glider prior to the commencement of research for the present thesis in 1997. Coinciding with the widespread awareness of coastal squirrel glider populations (see Suckling 1995), the first detailed study of its ecology was undertaken in coastal NSW (Quin 1995). Much additional research has been conducted during the course of this thesis (Table 1.3). Therefore, only a brief overview of squirrel glider ecology is provided here with a larger synthesis provided at the end of the thesis incorporating more recent research relevant to the research topics (see Chapter7: General Discussion).

1.3.2. Distribution, Habitat and Status
The current known distribution of the squirrel glider (Fig. 1.1) extends from Cape York in northern Queensland (13.5°S) (Winter et al. 2004), through eastern Queensland (Qld) and New South Wales (NSW) (Eyre 2004; Kavanagh 2004) to northern and central Victoria (van der Ree et al. 2004). An outlying population has recently been rediscovered near Bordertown just inside the South Australian border (S. Carthew and D. Harley personal communication).

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1 The squirrel glider is larger (i.e. body mass about 80% greater), its face is more pointed and its tail base is fluffier than the sugar glider (Traill 1998; van der Ree and Suckling 2008).
Plate 1.4: The sugar glider (left) and the squirrel glider are similar in appearance, which may have led to confusion in relation to the distribution of the squirrel glider. Sources: G. Suckling (left) and E. Beaton.

In Victoria the squirrel glider occurs up to about 300 m elevation (Menkhorst et al. 1988; Bennett et al. 1991), while it has been found to 240 m in south-east Qld (Rowston et al. 2002). In NSW, however, it has been reported up to 1000 m (Gilmore and Parnaby 1994). Similarly, most mahogany glider records have come from below 120 m elevation, but there have been reports to 200 m (Jackson and Claridge 1999). The effect of elevation on the distribution of the squirrel glider and the mahogany glider may be an artefact of the distribution of suitable habitat rather than the existence of a physiologically determined altitude limit per se.

The squirrel glider is typically found in dry eucalypt forest and woodland (Menkhorst et al. 1988; Suckling 1995; Rowston and Catterall 2004). It is absent from rainforest and the wet eucalypt forests of the coastal ranges (Suckling 1995). Important habitat components appear to be a sufficient density of hollow-bearing trees and a high floristic diversity, including the presence of smooth-barked and winter/spring flowering tree species (Menkhorst et al. 1988; Quin 1995; Sharpe and Goldingay 1998). The habitat requirements of the squirrel glider are discussed further in Chapter 7.
Table 1.2: Summary of published studies undertaken on the squirrel glider prior to the commencement of this thesis in 1997. This list includes studies on arboreal mammals more generally, but that refer to the squirrel glider.

<table>
<thead>
<tr>
<th>Publication</th>
<th>Focus of Study</th>
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<tbody>
<tr>
<td>Fleay (1947)</td>
<td>Natural history of gliding possums, including the squirrel glider</td>
</tr>
<tr>
<td>Fleay (1954)</td>
<td>Natural history of the squirrel glider</td>
</tr>
<tr>
<td>Winter (1966)</td>
<td>Report of opportunistic predation of a bird’s egg</td>
</tr>
<tr>
<td>Smith (1979)</td>
<td>Captive study on growth and development</td>
</tr>
<tr>
<td>Suckling (1983)</td>
<td>General account of squirrel glider biology</td>
</tr>
<tr>
<td>Davey (1984)</td>
<td>Habitat preferences of arboreal mammals in southern NSW, includes the squirrel glider</td>
</tr>
<tr>
<td>Meredith (1984)</td>
<td>Effects of silviculture on arboreal mammals in northern Victoria, including a few data on the squirrel glider</td>
</tr>
<tr>
<td>Menkhorst and Collier (1987)</td>
<td>Diet (scat analysis), Victoria</td>
</tr>
<tr>
<td>Menkhorst et al. (1988)</td>
<td>Distribution and habitat in Victoria</td>
</tr>
<tr>
<td>Davey (1990)</td>
<td>Arboreal mammals survey methods with notes on relative abundance on the NSW south coast; includes the squirrel glider</td>
</tr>
<tr>
<td>Murray et al. (1990)</td>
<td>Examines characteristics of the chromosomes of the Family Petauridae; includes the squirrel glider</td>
</tr>
<tr>
<td>Bennett et al. (1991)</td>
<td>Distribution of arboreal mammals in northern Victoria; includes squirrel glider</td>
</tr>
<tr>
<td>Colgan and Flannery (1992)</td>
<td>Biochemical/systematic study of the genus Petaurus; includes the squirrel glider</td>
</tr>
<tr>
<td>Van Dyck (1993)</td>
<td>Morphological comparison of squirrel glider and mahogany glider; separated species, confirming original description of latter species</td>
</tr>
<tr>
<td>Kavanagh et al. (1995)</td>
<td>Habitat preferences of arboreal mammals in north-east NSW; includes the squirrel glider (though few records)</td>
</tr>
<tr>
<td>Quin (1995)</td>
<td>Population ecology, home range (grid trapping), notes on diet, NSW mid north coast</td>
</tr>
<tr>
<td>Suckling (1995)</td>
<td>General account of squirrel glider biology</td>
</tr>
<tr>
<td>Quin et al. (1996)</td>
<td>Body size variation in squirrel and sugar gliders, bioclimatic modelling of distribution</td>
</tr>
</tbody>
</table>

The habitat of the squirrel glider has been subject to considerable clearing and fragmentation in Victoria and south-western NSW (Claridge and van der Ree 2004; van der Ree et al. 2004). In Qld, location records outside the south-east of the State remain relatively uncommon (Eyre 2004; Winter et al. 2004). Coastal northern NSW and south-eastern Qld appear to be the most important areas for the squirrel glider, based on a bio-climatic analysis of its distribution (Quin et al. 1996). Despite the importance of the north coast of NSW to the squirrel glider,
Table 1.3: Summary of published studies undertaken on the squirrel glider following the commencement of this thesis in 1997. This list includes studies on arboreal mammals more generally, but that refer the squirrel glider.

<table>
<thead>
<tr>
<th>Publication</th>
<th>Focus of Study</th>
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</thead>
<tbody>
<tr>
<td>Traill and Lill (1997)</td>
<td>Hollow tree use/nest box study of squirrel gliders and sugar gliders in Victoria</td>
</tr>
<tr>
<td>Rowston (1998a)</td>
<td>Den tree use; south-eastern Qld</td>
</tr>
<tr>
<td>Sharpe and Goldingay (1998)</td>
<td>Diet (observational study using radio-telemetry), north-eastern NSW</td>
</tr>
<tr>
<td>Traill (1998)</td>
<td>Identification of sugar gliders and squirrel gliders in Victoria</td>
</tr>
<tr>
<td>Jackson and Claridge (1999)</td>
<td>Bioclimatic modelling of squirrel glider and mahogany glider distribution, Qld</td>
</tr>
<tr>
<td>van der Ree (1999)</td>
<td>Reports on the hazard of barbed wire to wildlife; includes the squirrel glider</td>
</tr>
<tr>
<td>Millis and Bradley (2000)</td>
<td>Trap success in relation to environmental variables in south-east Qld</td>
</tr>
<tr>
<td>Holland (2001)</td>
<td>Report of opportunistic predation of a bird’s egg</td>
</tr>
<tr>
<td>Millis and Bradley (2001)</td>
<td>Reproduction in south-east Qld</td>
</tr>
<tr>
<td>Rowston et al. (2002)</td>
<td>Habitat preferences and response to fragmentation, Brisbane Qld</td>
</tr>
<tr>
<td>van der Ree (2002)</td>
<td>Population ecology of the squirrel glider in linear habitat, Victoria</td>
</tr>
<tr>
<td>Wormington et al. (2002)</td>
<td>Habitat preferences of arboreal mammals in south-east Qld; includes the squirrel glider (though few records)</td>
</tr>
<tr>
<td>Smith and Murray (2003)</td>
<td>Habitat preferences and response to fragmentation, NSW central coast</td>
</tr>
<tr>
<td>van der Ree and Bennett (2003)</td>
<td>Home-range in linear habitat, Victoria</td>
</tr>
<tr>
<td>van der Ree et al. (2003)</td>
<td>Movement potential in fragmented habitat, Victoria</td>
</tr>
<tr>
<td>Eyre (2004)</td>
<td>Review of the status of possums and gliders in southern Qld; includes the squirrel glider</td>
</tr>
<tr>
<td>Goldingay and Sharpe (2004a)</td>
<td>Population viability analysis in fragmented urban matrix of Brisbane, Qld</td>
</tr>
<tr>
<td>Goldingay and Sharpe (2004b)</td>
<td>Detection methods, comparing trapping and spotlighting</td>
</tr>
<tr>
<td>Rowston and Catterall (2004)</td>
<td>Examination of the effects of historic land clearing on the squirrel glider and the sugar glider in south-east Qld</td>
</tr>
<tr>
<td>Kavanagh (2004)</td>
<td>Review of the status of possums and gliders in NSW; includes the squirrel glider</td>
</tr>
<tr>
<td>Quin et al. (2004)</td>
<td>Habitat preferences in sympatry with the sugar glider, NSW mid north coast</td>
</tr>
<tr>
<td>van der Ree et al. (2004)</td>
<td>Review of the status of possums and gliders in Victoria; includes the squirrel glider</td>
</tr>
</tbody>
</table>

Table 1.3 (cont.)
<table>
<thead>
<tr>
<th>Publication</th>
<th>Focus of Study</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter et al. (2004)</td>
<td>Review of the status of possums and gliders in north Qld; includes the squirrel glider</td>
</tr>
<tr>
<td>Dobson et al. (2005)</td>
<td>Diet (observational study using radio-telemetry), Brisbane Qld</td>
</tr>
<tr>
<td>Goldingay et al. (2006)</td>
<td>Overview of squirrel glider research to date in Brisbane Qld</td>
</tr>
<tr>
<td>van der Ree (2006)</td>
<td>Effect of a road upgrade on mobility of squirrel gliders</td>
</tr>
<tr>
<td>van der Ree et al. (2006)</td>
<td>Longevity in the squirrel glider</td>
</tr>
<tr>
<td>Woodd et al. (2006)</td>
<td>Reproductive physiology (laboratory-based)</td>
</tr>
<tr>
<td>Holland et al. (2007)</td>
<td>Time budge and diet of the squirrel glider in Victoria</td>
</tr>
<tr>
<td>Sharpe and Goldingay (2007)</td>
<td>Home-range in north-east NSW</td>
</tr>
<tr>
<td>Ball and Goldingay (2008)</td>
<td>Use of gliding poles to reconnect habitat remnants, Qld</td>
</tr>
<tr>
<td>Beyer et al. (2008)</td>
<td>Den tree characteristics in north-east NSW and south-east Qld</td>
</tr>
<tr>
<td>Crane et al. (2008)</td>
<td>Den tree characteristics in south-west NSW</td>
</tr>
<tr>
<td>Flaherty et al. (2008)</td>
<td>Gliding performance</td>
</tr>
<tr>
<td>van der Ree and Suckling (2008)</td>
<td>General account of squirrel glider biology</td>
</tr>
</tbody>
</table>

**Fig. 1.1:** Current known distribution of the squirrel glider. Source: van der Ree and Suckling (2008).

however, a study of arboreal mammal distribution in the Grafton/Coffs Harbour area of the NSW north coast recorded it at only 3 of the 291 sites surveyed (Kavanagh et al. 1995). In
contrast, the sugar glider was recorded at 115 sites. A similar study in south-east Qld found the squirrel glider at only 4 of 38 sites (Wormington et al. 2002). In Brisbane and other parts of south-east Qld, its habitat continues to be threatened by fragmentation and urban expansion (e.g. Rowston et al. 2002). Thus, the squirrel glider may not be secure in these key areas of NSW and Qld. At the commencement of this thesis there were no studies that examined the impact of fragmentation or urbanisation on the squirrel glider.

Due to rarity and extreme habitat fragmentation, the squirrel glider is considered threatened in the southern half of its range. In Victoria, it is listed as endangered under the *Flora and Fauna Guarantee Act 1988*. It is listed as vulnerable with several endangered populations in NSW under the *Threatened Species Conservation Act 1995*, having originally been listed under the *Endangered Species (Interim Protection) Act 1992*. In Qld, the squirrel glider is considered common fauna under the *Queensland Nature Conservation Act 1992*, but this is in need of review (Eyre 2004). The squirrel glider is considered a priority species of management concern by Brisbane City Council (BCC 2000, 2005).

1.4. Objectives of and Rationale for this Study

The over-riding aim of this thesis was to conduct studies that extend our knowledge of squirrel glider ecology, focusing on aspects that will facilitate their management in coastal habitats subject to on-going human impacts. To do this required identifying significant gaps in knowledge (see below). The only detailed studies conducted on the squirrel glider prior to the commencement of this thesis (Table 1.2) had focused on population ecology (Quin 1995), distribution and habitat requirements (Menkhorst et al. 1988), and diet (Menkhorst and Collier 1987). It is important that species with a broad geographic range are studied at different locations throughout their distribution because it is likely that variation in key elements of a species’ ecology is driven by climatic variation. The geographic spread of squirrel glider study locations was extended in this thesis by examining the squirrel glider in north-east NSW and south-east Qld, adding to the detailed work conducted on the NSW central north coast (Quin 1995) and Victoria (Menkhorst and Collier 1987; Menkhorst et al. 1988) (Table 1.2). Moreover, the two study sites chosen for this thesis provided opportunities for insights into how different types of human disturbance affect the squirrel glider (previous logging, urban expansion; see above). Because my honours thesis described the home-range, den use and diet of the squirrel glider in north-east NSW, the present thesis sought to extent this work by studying other aspects of the squirrel glider’s behavioural ecology (vocal behaviour, time budget) and its population ecology.
At the commencement of this thesis, the population ecology of the squirrel glider had been described in detail at a single site on the NSW central north coast over a 2.5-year period (Quin 1995). Thus, there was an obvious need to conduct further studies of the squirrel glider’s population ecology in different parts of its range. The squirrel glider relies heavily on nectar at some sites (Quin 1995) and substantial year-to-year variation in nectar production is characteristic of eucalypt forests (Law et al. 2000; Law and Chidel 2008). This suggests that long-term studies will be required to adequately document variation in population size. Quin (1995) found that flower failure following a wildfire caused a squirrel glider population to reduce in size. While this finding was important, the duration of this study raises concerns that the extent of squirrel glider population fluctuations has not been adequately described. It is also unclear how food resources, and therefore populations, may vary in the absence of a severe catastrophic event (i.e. because a wildfire was involved in Quin’s observation). This has implications for the frequency of population fluctuations. It is important to understand the frequency and extent of population variability due to the substantial influence it has on extinction proneness (Reed et al. 2003; O'Grady et al. 2004). While further studies in relatively undisturbed habitat remain important to provide comparative data, it is also necessary to examine the population ecology of the squirrel glider in habitats subject to varying types of disturbance to understand the effects of different threatening processes. Ideally, quantitative estimates of life history parameters should be made to provide rigorous input into PVA studies. Preferably, these estimates should come from study systems that coincide with areas subject to development pressure where such viability analyses would take place in case there is variation in vital rates (e.g. due to fragmentation).

Previous authors have suggested that the squirrel glider is less vocal than other petaurids, indicating a lower degree of sociality (Menkhorst 1995; Traill 1998). However, other authors (e.g. Davey 1990) have suggested that vocalisations increased detection rates during spotlight surveys. Clearly, there is a need to better describe the vocal and social behaviour of the squirrel glider. Due to its conservation status in NSW and the Brisbane local government area, targeted surveys for the squirrel glider are required in relation to development proposals and prior to logging. Therefore, it would be useful if a characteristic call could be described for the squirrel glider that would facilitate its detection during fauna assessments and surveys.

Petaurid gliders are known to spend the majority of the activity period engaged in foraging behaviours (e.g. Goldingay 1989a, 1990). While this is generally true, Jackson and Johnson
(2002) suggested that the proportion of time spent foraging was positively related to body size within the genus. However, this analysis was conducted with few available data. At the commencement of this thesis, no time budget data were available for the squirrel glider. Animals that spend the majority of their activity period feeding may be time limited and have difficulty adapting to habitat disturbance (Goldingay 1989b). Therefore, it remains important to further assess the implications of an exudivorous diet on the time budgets of the petaurids and how this relates to body size.

1.5. Structure of the Thesis
This thesis is organised into five research chapters that focus on aspects of the squirrel glider’s behaviour and ecology that have hitherto been poorly described or have not been examined in the full range of habitats occupied (e.g. urban forest remnants). While each of these topics is of scientific interest in extending our understanding of the basic biology of the squirrel glider, they also provide important information that can be used to inform management decisions.

Chapter 2 reports on a six-year capture study on the squirrel glider in an area of continuous forest in north-east NSW. Chapter 3 describes the population ecology of the squirrel glider in contrasting habitat, a 47 ha urban forest remnant in Brisbane, over a four-year period. Chapter 4 subjects the mark-recapture data collected in Brisbane to statistical modelling to provide quantitative estimates of capture probability, survival and population density. Chapter 5 gives the first description of the vocal behaviour of the squirrel glider, providing insights into its social behaviour, describing a characteristic call that enables this species to be reliably detected during spotlighting activities. Chapter 6 describes the time budget of the squirrel glider in the same urban remnant in Brisbane used to describe population ecology.

1.6. Publications Arising from Thesis


These two publications are shown in Appendix 1.
2. **Effect of Flowering Patterns on a Population of Squirrel Gliders (Petaurus norfolcensis) in North-East New South Wales**

2.1. **Introduction**

Knowing the extent to which populations of a species fluctuate in size, and understanding the reasons why, is essential to any analysis of their viability (Vucetich and Waite 1998). Such considerations are particularly important for small populations, which are more prone to the effects of demographic stochasticity (McCarthy et al. 1994). Moreover, without appreciating changes in population size it may be difficult to determine the relationship between animal abundance and habitat type because such studies may be conducted over several months, or even years (e.g. Menkhorst et al. 1988; Bennett et al. 1991).

Previous studies on the population ecology of the squirrel glider (Petaurus norfolcensis) have been undertaken over a period of up to 2.5 years (Quin 1995; van der Ree 2002). These studies showed that the populations examined were relatively stable. Long-term monitoring of populations is required, however, to adequately document fluctuations in population size (Franklin 1988; Vucetich and Waite 1998). Understanding the extent and causes of fluctuations in the size of squirrel glider populations is important because in parts of its range its habitat has been reduced and fragmented (Menkhorst et al. 1988; Rowston et al. 2002; van der Ree 2000 2002). Consequently, many of its populations are likely to be small and vulnerable to extinction (e.g. Goldingay and Sharpe 2004a). The aim of this study was to provide long-term data on the population dynamics of the squirrel glider.

2.2. **Methods**

2.2.1. **Study Area**

This study was conducted in Bungawalbin Nature Reserve (NR), northern New South Wales (NSW) (29°10’S, 153°07’E). The dry eucalypt forests of this area appear to be an important stronghold for the squirrel glider (Quin et al. 1996). Bungawalbin NR is around 500 ha in area and is relatively flat. The study site is at 25 m elevation. The reserve is surrounded by private land, yet is part of a large area of relatively continuous forest that covers thousands of hectares. The squirrel glider appears to be widespread throughout this area (personal observations).

The dominant overstorey species at the study site were smudgy apple (Angophora woodsiana), swamp box (Lophostemon suaveolens), pink bloodwood (Corymbia intermedia),
northern grey ironbark (*Eucalyptus siderophloia*), narrow-leaved red gum (*E. seeana*), cabbage gum (*E. amplifolia* ssp. *sessiliflora*), grey box (*E. moluccana*), small-fruit grey gum (*E. propinquia*) and red mahogany (*E. resinifera*). Midstorey species include coast banksia (*Banksia integrifolia*), *Melaleuca* spp., curracabah (*Acacia concurrens*) and green wattle (*A. irrorata*). The feathertail glider (*Acrobates pygmaeus*), sugar glider (*Petaurus breviceps*) and the yellow-bellied glider (*P. australis*) also occur on the study site. Further details of the study area are provided by Sharpe and Goldingay (1998).

### 2.2.2. Glider Trapping, Assessment and Marking

A 30 ha trapping grid with 30 traps (in a 5×6 arrangement) at 100 m intervals was established at the study site in January 1996. The grid was trapped in most months for four consecutive nights from March 1996 until November 1996. The grid was then increased to 38 ha (38 traps) to encompass the home ranges of six groups, which radio-tracking had shown extended outside the original grid (Sharpe 1996). The new grid was trapped for 4–7 nights twice yearly (June/July and November/December) from July 1997 until December 1999. Trapping was extended for several days where possible when few gliders were captured over the first few days of a trip. The trapping periods were targeted to gather reproductive data, in addition to data on population size, because it was known that squirrel gliders reproduce at these times (Quin 1995; Sharpe 1996). The 38 ha grid was then trapped bi-monthly from March 2000 until October 2001.

Elliott type B traps (45×15×15 cm) were used in this study. These were attached to wooden platforms with rubber bands (made from tyre inner tubes) and set 2–4 m high on the tree >20 cm DBH nearest each grid intersection. All traps were baited with rolled oats, peanut butter and honey. A solution of diluted honey was sprayed on the trunk above the traps to a height of 6–8 m. The trapping technique follows that of Smith and Phillips (1984).

Captured squirrel gliders were weighed, sexed and assigned to age classes using aging characteristics, such as tooth condition and ventral fur colour, provided in the published literature (Suckling 1984; Quin 1995; Jackson 2000a). Gliders greater than one year old were considered adults because female gliders are able to reproduce early in their second year (Quin 1995; van der Ree 2002; Millis and Bradley 2001). The reproductive status of female gliders was assessed by inspecting their pouches to determine whether they were nulliparous, non-parous, pregnant, carrying pouch young or freely lactating (Quin 1995; Millis and Bradley 2001; van der Ree 2002). As I regularly worked alone, it was not possible to measure
pouch young to estimate their ages. Instead, characteristics relating to the development of the pouch young were noted according to descriptions provided by Smith (1979). These characteristics were used to estimate age and, hence, the month of birth. During 1996, monthly trapping ensured accurate estimation of the month of birth and enabled the characteristics of pouch young development to be verified in the field. The estimated weight of pouch young (Smith 1979) was then subtracted from the female’s weight. All captured gliders were fitted with numbered fingerling ear tags to which unique combinations of coloured reflective tape were glued. The reflective tape allowed individuals to be recognised during spotlighting (see below). Following the handling procedure, squirrel gliders were released at the point of capture.

The mean body weights of adult gliders captured during September 2000 (the month prior to the population decline when body weights were expected to decrease) were compared to the mean weight of gliders upon their first capture during the entire study period prior to that month using t-tests. This approach was adopted to enable statistical independence. A repeated measures ANOVA was not possible because individual gliders could not necessarily be captured in successive trapping periods. Furthermore, it was assumed that using glider weights at their first capture represented a random sample of body weights as initial captures occurred across a number of seasons and years.

2.2.3. Spotlighting
Spotlighting was undertaken at the study site during all trips from 1997 onwards (radio-tracking studies were conducted during 1996) to supplement the trapping data. Regular paths were taken that were designed to cover all habitat types and home-ranges that occurred on the trapping grid. To decrease the need to closely monitor the direction of travel with a compass the exact path taken was somewhat meandering. As nectar is the most important food resource at this site (Sharpe and Goldingay 1998), this approach also enabled flowering trees to be targeted. Spotlighting was undertaken at around 300 mhr⁻¹ using a 50 W light connected to a 12 V battery. Walking speed was calibrated by occasionally timing movement between trap stations. Gliders were observed with the aid of 10×50 binoculars and their feeding behaviour was recorded.

The identity of tagged gliders and the presence of untagged gliders were noted as they were encountered during spotlighting. Untagged gliders were added to the population counts obtained during a trapping period only if it could be ensured that these individuals were not
subsequently captured, i.e. they represented unique individuals (see also Suckling 1984). This could be achieved by determining sex and/or age class (adult males versus females/juvenile males), ventral fur colour (light versus discoloured) and position on the trapping grid (the spatial organisation of home-ranges was known: Sharpe 1996). Adult males could be distinguished by the well-developed gland on their forehead.

Because trapping was undertaken twice per year between 1997 and 1999, it was not always possible to distinguish transients from resident gliders. Transients were those gliders that were passing through the trapping grid and only captured once. However, Quin (1995) suggests that other classes of gliders, such as those living on the edge of the trapping grid or juvenile gliders, would have low capture probabilities. Therefore, all gliders were included in estimates of population density.

2.2.4. Population Estimates
In common with other studies on the squirrel glider (Quin 1995; van der Ree 2002), population size estimates were derived using the Minimum Number Known Alive method (MNKA) (Krebs 1999). The MNKA estimates incorporated both the trapping and spotlighting data (see above). Gliders that were not recorded on a particular trip, but were detected on the previous and subsequent trips, were assumed to have remained resident on the trapping grid. Following a radio-tracking study (Sharpe 1996), it was known that all glider home ranges were contained within the trapping grid, assuming that each trap represented a 1 ha area around each trap (i.e. 38 ha in total). Thus, glider density was estimated by dividing the estimated population size by 38.

2.2.5. Flowering
An assessment of flowering phenology was important because nectar is the dominant food resource at Bungawalbin NR (Sharpe and Goldingay 1998). The flowering of key nectar-producing tree species within the trapping grid was recorded during all field trips. Over the course of the study, this approach enabled the flowering period of these species to be determined. In addition to recording reproductive data, the field trips were timed so that the presence/absence of blossom in the winter/spring period could be determined in each year for each species that typically flowers at this time.
2.3. **Results**

2.3.1. **Glider Detection**

Between January 1996 and October 2001, there were 322 squirrel glider captures during 4012 trapnights, an overall trap success of 8.0% (Table 2.1). Ninety-seven individual squirrel gliders were captured during this time; 47 males and 50 females. Capture rates per census ranged from a low of 0.7% in March and August 2001 to a high of 25.0% in September 2000. The most consistently high trap success was from May to September 2000 (12.5 to 25.0%). Similarly high trap success was also obtained between March and July 1996. In contrast, the most consistently low trap success was during the twelve months from November 2000 until October 2001 (Table 2.1).

There were 100 records of squirrel gliders during 137 hr of spotlighting at Bungawalbin NR, a mean detection rate of 0.66 hr\(^{-1}\) (Table 2.2). Detection rates per trip ranged from a low of 0.0 hr\(^{-1}\) in January 2001 to a high of 1.67 hr\(^{-1}\) in November 1997. The detection rate from May to September 2000 ranged from 1.13 to 1.50 hr\(^{-1}\). In common with the trapping results, the spotlighting detection rate decreased substantially from November 2000 (Table 2.2).

2.3.2. **Population Size and Glider Condition**

The MNKA estimates revealed that the number of adult gliders typically resident on the trapping grid was 12 (6 males and 6 females). In some years, however, females early in their second year were also observed with pouch young, suggesting that they should be considered adults. The population reached peaks of around twenty as young gliders entered the trappable population (Fig. 2.1). These gliders appeared at about six months of age in November or as yearlings in July.

Population estimates commenced after March 1996 once the trapping program was well established. This was done because the trappability of gliders generally increases over the first few trips due to greater trap exposure. Similarly, trapping results from October 2001 were not included because the MNKA estimates are unreliable when there are no subsequent trips to confirm residency (e.g. Quin 1995; van der Ree 2002).

During the winter of 2000, the population of gliders was at a five year high and numbered over 30 individuals across all age groups. There appeared to have been considerable recruitment following breeding the previous year as most new individuals were young gliders around 12 months of age (Fig. 2.1). The estimated size of the aged component of the population is lower than the MNKA estimates because estimates of glider ages could only be
Table 2.1: Trapping data for the squirrel glider over a 6-year period at Bungawalbin Nature Reserve.

<table>
<thead>
<tr>
<th>Month/Year</th>
<th>No. Trapnights</th>
<th>No. Glider Captures</th>
<th>No. Individuals</th>
<th>Trap Success (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>January 1996</td>
<td>120</td>
<td>8</td>
<td>8</td>
<td>6.7</td>
</tr>
<tr>
<td>February 1996</td>
<td>120</td>
<td>4</td>
<td>4</td>
<td>3.3</td>
</tr>
<tr>
<td>April/March 1996</td>
<td>120</td>
<td>17</td>
<td>11</td>
<td>14.2</td>
</tr>
<tr>
<td>May 1996</td>
<td>120</td>
<td>22</td>
<td>13</td>
<td>18.3</td>
</tr>
<tr>
<td>June 1996</td>
<td>120</td>
<td>21</td>
<td>14</td>
<td>17.5</td>
</tr>
<tr>
<td>July 1996</td>
<td>120</td>
<td>6</td>
<td>5</td>
<td>5.0</td>
</tr>
<tr>
<td>August 1996</td>
<td>120</td>
<td>6</td>
<td>6</td>
<td>5.0</td>
</tr>
<tr>
<td>September 1996</td>
<td>120</td>
<td>1</td>
<td>1</td>
<td>0.8</td>
</tr>
<tr>
<td>October 1996</td>
<td>120</td>
<td>3</td>
<td>3</td>
<td>2.5</td>
</tr>
<tr>
<td>November 1996</td>
<td>120</td>
<td>10</td>
<td>10</td>
<td>8.3</td>
</tr>
<tr>
<td>July 1997</td>
<td>152</td>
<td>30</td>
<td>18</td>
<td>19.7</td>
</tr>
<tr>
<td>November 1997</td>
<td>152</td>
<td>16</td>
<td>10</td>
<td>10.5</td>
</tr>
<tr>
<td>June/July 1998</td>
<td>266</td>
<td>28</td>
<td>20</td>
<td>10.5</td>
</tr>
<tr>
<td>November 1998</td>
<td>152</td>
<td>14</td>
<td>7</td>
<td>9.2</td>
</tr>
<tr>
<td>July 1999</td>
<td>152</td>
<td>13</td>
<td>10</td>
<td>8.6</td>
</tr>
<tr>
<td>November/December 1999</td>
<td>266</td>
<td>7</td>
<td>6</td>
<td>2.6</td>
</tr>
<tr>
<td>March 2000</td>
<td>190</td>
<td>9</td>
<td>8</td>
<td>4.7</td>
</tr>
<tr>
<td>May 2000</td>
<td>152</td>
<td>32</td>
<td>24</td>
<td>21.1</td>
</tr>
<tr>
<td>July 2000</td>
<td>152</td>
<td>19</td>
<td>17</td>
<td>12.5</td>
</tr>
<tr>
<td>September 2000</td>
<td>152</td>
<td>38</td>
<td>24</td>
<td>25.0</td>
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<tr>
<td>November 2000</td>
<td>152</td>
<td>5</td>
<td>4</td>
<td>3.3</td>
</tr>
<tr>
<td>January 2001</td>
<td>114</td>
<td>1</td>
<td>1</td>
<td>0.9</td>
</tr>
<tr>
<td>March 2001</td>
<td>152</td>
<td>1</td>
<td>1</td>
<td>0.7</td>
</tr>
<tr>
<td>May 2001</td>
<td>152</td>
<td>6</td>
<td>4</td>
<td>3.9</td>
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<tr>
<td>July 2001</td>
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<td>2</td>
<td>2</td>
<td>1.3</td>
</tr>
<tr>
<td>August 2001</td>
<td>152</td>
<td>1</td>
<td>1</td>
<td>0.7</td>
</tr>
<tr>
<td>October 2001</td>
<td>152</td>
<td>2</td>
<td>2</td>
<td>1.3</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>4012</strong></td>
<td><strong>322</strong></td>
<td><strong>8.0</strong></td>
<td></td>
</tr>
</tbody>
</table>

Table 2.2: Spotlighting data for the squirrel glider at Bungawalbin Nature Reserve.

<table>
<thead>
<tr>
<th>Month/Year</th>
<th>No. Hours Spotlighting</th>
<th>No. Glider Detections</th>
<th>Detection Rate (No./hr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>July 1997</td>
<td>9.83</td>
<td>3</td>
<td>0.31</td>
</tr>
<tr>
<td>November 1997</td>
<td>7.42</td>
<td>12</td>
<td>1.62</td>
</tr>
<tr>
<td>June/July 1998</td>
<td>4.75</td>
<td>5</td>
<td>1.05</td>
</tr>
<tr>
<td>November 1998</td>
<td>4.25</td>
<td>3</td>
<td>0.71</td>
</tr>
<tr>
<td>July 1999</td>
<td>9.00</td>
<td>1</td>
<td>0.11</td>
</tr>
<tr>
<td>November/December 1999</td>
<td>10.92</td>
<td>6</td>
<td>0.55</td>
</tr>
<tr>
<td>March 2000</td>
<td>13.58</td>
<td>12</td>
<td>0.88</td>
</tr>
<tr>
<td>May 2000</td>
<td>9.75</td>
<td>11</td>
<td>1.13</td>
</tr>
<tr>
<td>July 2000</td>
<td>10.00</td>
<td>15</td>
<td>1.50</td>
</tr>
<tr>
<td>September 2000</td>
<td>10.67</td>
<td>14</td>
<td>1.31</td>
</tr>
<tr>
<td>November 2000</td>
<td>8.58</td>
<td>1</td>
<td>0.12</td>
</tr>
<tr>
<td>January 2001</td>
<td>4.17</td>
<td>0</td>
<td>0.00</td>
</tr>
<tr>
<td>March 2001</td>
<td>6.50</td>
<td>1</td>
<td>0.15</td>
</tr>
<tr>
<td>May 2001</td>
<td>10.17</td>
<td>9</td>
<td>0.88</td>
</tr>
<tr>
<td>July 2001</td>
<td>9.25</td>
<td>4</td>
<td>0.43</td>
</tr>
<tr>
<td>October 2001</td>
<td>9.25</td>
<td>4</td>
<td>0.43</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>138.09</strong></td>
<td><strong>100</strong></td>
<td><strong>0.66</strong></td>
</tr>
</tbody>
</table>
Fig. 2.1: Age structure of the squirrel glider population at Bungawalbin NR. The Minimum Number Known to be Alive (MNKA) estimate is also shown.

Based on trapping data (Fig. 2.1). During the study, glider density ranged between a low of 0.18 ha\(^{-1}\) from November 2000 to March 2001, and a high of 0.87 ha\(^{-1}\) in May and September 2000. Throughout much of the study, however, glider density was between 0.31 and 0.63 ha\(^{-1}\) (Fig. 2.2).

Fig. 2.2: Squirrel glider density (based on Minimum Number Known Alive) and adult body weight (± 1 s.e.), at Bungawalbin NR, March 1996 – October 2001.
The mean body weight of adult gliders appeared to be above the 4-year mean during most of 2000 (Fig. 2.2). Body weight slowly decreased over winter 2000 before going into a rapid decline in late winter/early spring. The mean weight of male (t=3.581, df=27, p=0.001) and female (t=6.688, df=35, p<0.001) gliders was significantly lower during September 2000 (185.3 g and 159.9 g respectively) than during the previous four years (210.1 g and 197.0 g respectively). This rapid decrease in weight immediately preceded the decline in population size (Fig. 2.1). Although few captures were obtained, glider weights appeared to increase from November 2000 onwards.

Other observations also suggested that the glider population was experiencing stressful conditions in the late winter/early spring of 2000. For example, an adult male glider was removed from a trap in a torpid condition during September 2000. This was the only glider observed in torpor during the entire study despite a wide range of environmental conditions. Moreover, in the four years prior to 2000, only one glider with a broken lower incisor tooth was captured. In September 2000, three gliders with broken lower incisors were captured including a young male weighing 106 g that was estimated to be about six months of age. These observations coincided with a period of low body weight and a heavy reliance on arthropods for food (see below). The broken teeth of these gliders were presumed to have been the result of chewing crevices in dead branches to access arthropods (personal observations).

The adult component of the population (i.e. those gliders greater than 12 months of age) was relatively stable over the first four years of the study. There appeared to be some rapid population turnover in 1997/1998, but the gliders that were lost were quickly replaced by gliders in their second year, resulting in a stable population (Fig. 2.1).

The population decline observed in 2000 extended simultaneously across all age groups. A minimum of 33 gliders was present on the trapping grid in September of that year, although four of these that were in the 1–2 year age group were only captured during that month. Only seven gliders were detected over the following six months, a decline of about 80%. It should be noted, however, that the total population fell by only 55% and the adult population by 42% when compared to their average sizes over the previous four years. The only untagged glider observed post-September was presumed to be a glider that remained untrapped prior to the decline.
Glider persistence following September 2000 was highest in the 2-3 year age class, with 50% of these individuals remaining resident on the trapping grid (Fig. 2.1). Survivorship in the 1-2 and the >3 year age classes was 7% and 20% respectively. The only glider within the population known to be less than 12 months of age in September 2000 did not survive. Moreover, 5 of the 7 surviving gliders were female, indicating a higher survivorship than for males. This is despite females having a larger loss of body weight.

In the winter of 2001, two additional untagged gliders were located on the trapping grid. These gliders appeared to be small and they may have been born to one (or more) of the adult gliders observed to be reproductively active in November 2000. Because these untagged gliders were not captured they were not added to the age class data, but were included in the MNKA estimate.

2.3.3. Reproduction

Over the six years of study, 37 litters were recorded from births that occurred during the autumn/winter period. A further six litters were born in spring over the same period. The mean litter size was 1.8 over this time, with no variation between seasons and little between years (Table 2.3). Female gliders in all age classes above one year were observed with pouch young during the autumn/winter period. However, of the five litters born in spring prior to 2000, four were born to females in their second year (i.e. 1–2 years). Only two females were observed with pouch young in consecutive breeding periods. Both gliders had bred for the first time in the 1–2 year age group during spring, breeding again the following autumn.

The mean size of litters born during the autumn/winter of 2000 was 1.8 (n=7), which was no different to the five-year mean. However, three females (43% of those observed with pouch young) are known to have lost pouch young in that year, two of which lost both pouch young. This was determined by repeat observations of these gliders in consecutive trapping periods. One of these females tried, unsuccessfully, to breed a second time. This female was observed with two small pouch young in both July and September 2000. She was not carrying pouch young in November 2000, nor was she freely lactating. These observations indicate that the pouch young had not survived, as the offspring would not have been weaned until about four months of age. Breeding success appeared to be low during the winter of 2000 due to the loss of pouch young, although it was not possible to compare this with previous years. In November 2000, two pregnant females were captured and a third had a single pouch young (Table 2.3).
Table 2.3: Mean size of autumn/winter (Au/W) and spring (Spr) litters (± s.e.) at Bungawalbin Nature Reserve. n=number of litters recorded.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Au/W Spr</td>
<td>1.6</td>
<td>2.0</td>
<td>1.9</td>
<td>2.0</td>
<td>1.9</td>
</tr>
<tr>
<td>± s.e.</td>
<td>0.49</td>
<td>-</td>
<td>0.33</td>
<td>0.33</td>
<td>-</td>
</tr>
<tr>
<td>n</td>
<td>6</td>
<td>1</td>
<td>8</td>
<td>2</td>
<td>8</td>
</tr>
</tbody>
</table>

2.3.4. Flowering Patterns

The flowering patterns at Bungawalbin NR indicate that nectar is potentially available throughout the year (Fig. 2.3). Most tree species that flower between autumn and spring were found to flower reliably each year. During May and July of 2000, *E. robusta* was observed flowering for the only time during the five-year study. In contrast, *E. siderophloia* flowered every year except 2000.

<table>
<thead>
<tr>
<th>Month</th>
<th>Year</th>
</tr>
</thead>
<tbody>
<tr>
<td>J</td>
<td>96</td>
</tr>
<tr>
<td>F</td>
<td>97</td>
</tr>
<tr>
<td>M</td>
<td>98</td>
</tr>
<tr>
<td>A</td>
<td>99</td>
</tr>
<tr>
<td>M</td>
<td>00</td>
</tr>
</tbody>
</table>

![Fig. 2.3: Flowering periods of key nectar-producing tree species at Bungawalbin NR. The years in which each species flowered are also shown.](image)

2.3.5. Feeding Observations

Nectar and pollen were consistently the most important feeding activities from late autumn to late spring from 1996 (Sharpe and Goldingay 1998) to 1999 (unpublished data). Squirrel gliders were also observed obtaining nectar and pollen from *E. robusta* and *B. integrifolia* in May and July 2000. There was also minor use of some other food resources (Table 2.4).

In September 2000, when *E. siderophloia* failed to flower, the only nectar feeding observed was of a sub-adult squirrel glider feeding on the few remaining inflorescences on a single *B.*
integrifolia on two consecutive nights. A further six observations of squirrel gliders arthropod searching were obtained (Table 2.4). Arthropod feeding was also the only feeding behaviour observed for the other three exudivorous glider species that occur at the study site, based on 11 additional observations during September 2000 (unpublished data). Although the abundance of exudates (e.g. honeydew, sap) was not measured, the feeding observations appear to indicate that they were not sufficiently available to exploit.

| Table 2.4: Feeding behaviours of the squirrel glider observed during 2000. |
|------------------|-----|-----|-----|-----|
| **Month**        | **March** | **May** | **July** | **September** |
| Nectar Feeding   | 0    | 4    | 7    | 2    |
| Arthropod Searching | 5    | 0    | 1    | 6    |
| Honeydew         | 0    | 0    | 1    | 0    |
| Acacia Seeds/Arils | 1    | 0    | 0    | 0    |
| Acacia Gum       | 0    | 1    | 0    | 0    |
| **Total Observations** | **6** | **5** | **9** | **8** |

2.4. Discussion

2.4.1. Glider Detection

The mean squirrel glider capture rate (8.0%) obtained in the present study is higher than the 5% stated by Millis and Bradley (2001) from south-east Queensland, but lower than the rates reported from the NSW mid-north coast (16.5%) (Quin 1995) and central Victoria (25.8%) (van der Ree 2000). Both Quin (1995) and van der Ree (2000) documented higher population densities than was the case at Bungawalbin.

There are few data to compare with the spotlighting detection rates obtained at Bungawalbin (mean 0.66 hr⁻¹). In general, the studies that are available have been conducted as part of broad scale surveys for the squirrel glider (e.g. Menkhorst *et al.* 1988) or as part of surveys for arboreal mammals in general (e.g. Davey 1984; Bennett *et al.* 1991). These sites were frequently only surveyed once each. Surveys undertaken in Victoria recorded the squirrel glider at mean rates of 0.02-0.31 hr⁻¹ (Meredith 1984; Menkhorst *et al.* 1988; Bennett *et al.* 1991). Davey (1990) recorded a mean of 0.08 hr⁻¹ on the NSW south coast. The high detection rates obtained at Bungawalbin may be due to a number of factors: i) only one site, which was known to support squirrel gliders, was included; ii) as nectar is the most important food resource at the site, flowering trees could be readily targeted (see Sharpe and Goldingay 1998); and iii) travel speed was slow (see Goldingay and Sharpe 2004c).
2.4.2. Population Size and Glider Condition

The squirrel glider population at Bungawalbin NR was relatively stable, both in numbers and in age structure, in the four years prior to 2000. The density of this population generally ranged between 0.31 and 0.63 ha\(^{-1}\), peaking at 0.87 ha\(^{-1}\) in 2000. These findings are consistent with other studies on the squirrel glider, except higher population densities of 0.89 – 1.54 ha\(^{-1}\) have been reported (Quin 1995; van der Ree 2000).

During 2000, there was a substantial increase in the size of the squirrel glider population under study at Bungawalbin. This increase appears to have been mainly due to the persistence of juvenile gliders from the previous years’ breeding and/or the dispersal of young gliders onto the trapping grid as most of the new gliders were aged 1 – 2 years. Squirrel gliders are known to disperse in this age group (Quin 1995). The influx of many new gliders into the trappable population may have been due to the flowering of an additional tree species, *E. robusta*, during the winter of 2000.

Between July and September 2000, there was a substantial decrease in the condition of the resident squirrel gliders, as indicated by the rapid loss of body weight (males –11.7%, females –18.8%). The population was large at the time, suggesting that there was likely to be a strongly competitive environment. Moreover, very dry conditions prevailed at the time (Bureau of Meteorology 2000), which may have affected the availability of food, such as nectar (e.g. Wooller et al. 1998). Quin (1995) reported a similar decline in body weights in his study population between August and October 1988 (males –11.1%, females –13.2%), which also appeared to be associated with a drop in population density.

Following the decline in body weight that was observed between July and September 2000, there was a large decrease in population size (about 80%) between September and November of that year. This corresponded to a fall of 42% (adults only) or 55% (total population) when compared to the four-year mean population size. In addition to the prevailing dry conditions, this period coincided with the failure of flowering by *E. siderophloia*. This species is regarded as important to nectarivores in north-east NSW because it is one of the few species that flowers reliably each year in late winter/spring (Law et al. 2000). *Eucalyptus siderophloia* is typically used extensively by squirrel gliders (and other exudivorous gliders) at this site (Sharpe and Goldingay 1998; unpublished data). The conditions that resulted in the decline of the Bungawalbin squirrel glider population were sufficiently severe that all age classes were
affected. However, despite a larger percent fall in body weight, survivorship was highest for females in the 2-3 year age class.

A decline of a similar magnitude was also apparent at another site within the Bungawalbin catchment, about 10 km from the nature reserve (unpublished data). At this second site, only 3 of 10 squirrel gliders captured in September 2000 were subsequently detected there. The apparent loss of about 70% of the gliders at this site corresponds with the 80% lost at Bungawalbin NR. Furthermore, nine squirrel gliders were subsequently known to be resident on a 40 ha trapping grid at the second site, which corresponds with the seven gliders that were resident on the 38 ha nature reserve grid. These data from the second site suggest that the observed decline in squirrel glider numbers was due to mortality, not emigration. It appears that late winter/early spring is a critical time for squirrel gliders in northern NSW and that they are vulnerable to flower failure at this time of year (see below).

In contrast to the present study, Davey (1990) found that squirrel glider numbers increased during drought and decreased during years of above average rainfall, with sugar gliders showing the reverse trend. Years of above average rainfall coincided with increased flower availability (Davey 1990). There could be regional differences in the response of squirrel glider populations to climatic variation, possibly because rainfall is distributed differently throughout the year (Linacre and Geerts 1997). Alternatively, differences in the floristic composition between Bungawalbin and Davey’s (1990) NSW south coast sites may explain the observed differences in the response of the respective squirrel glider populations.

Davey’s (1990) findings are curious as nectar appears to be an extremely important food resource in the coastal forests of NSW and south-east Queensland (Quin 1995; Sharpe and Goldingay 1998; Millis and Bradley 2001; Dobson et al. 2005; unpublished data). Quin (1995) also found that squirrel glider population dynamics were strongly influenced by the flowering patterns of key eucalypts and banksias. Whereas drought may have influenced the flowering failure in the present study, fire has also been shown to alter flowering phenology (Quin 1995).

In another example, exudivorous gliders in Victoria have been shown to be relatively immune to the effects of drought because they were able to switch their diet to honeydew, which became abundant during this time (Henry 1986). At Bungawalbin, the feeding observations obtained during September 2000 suggest that the supply of exudates was very low, resulting
in a focus on arthropods. Arthropods were sought from a variety of substrates, with fissures in dead wood being very important (personal observations). Several squirrel gliders, including an individual about six months of age, had broken lower incisor teeth possibly due to attempts to obtain arthropods from this substrate. These observations suggest that the supply of exudates, including honeydew, was very low and could not be efficiently exploited. No other glider species at this site was observed feeding on exudates at the time (unpublished data). However, the squirrel glider’s declining body weights and population decline suggest that arthropods were not sufficiently abundant to sustain them.

Squirrel gliders appear able to effectively exploit arthropods in early autumn and may ignore flowering trees. At this time, the weather is still warm and it is the NSW north coast wet season. Arthropod abundance is influenced by climatic conditions, which vary between seasons and years (Woinarski and Cullen 1984; Recher et al. 1996). The combination of season (early spring), drought (see below) and unseasonally hot conditions (personal observations) may have contributed to the inability of the squirrel gliders to subsist on arthropods in the early spring of 2000.

The only observation of torpor in this squirrel glider population occurred in September 2000, when food appeared to be in short supply and glider weights were low. There appears to be no record of torpor in the squirrel glider in the literature, although D. Quin (personal communication) has also observed torpid individuals. This record is consistent with the findings of Körtner and Geiser (2000), who found that free-living sugar gliders entered torpor more readily and for longer periods when food appeared to be limiting, when energy reserves were low and/or when foraging was uneconomic due to adverse weather conditions. Furthermore, the mortality of sugar gliders increased as these conditions became severe. While some deaths were attributed directly to starvation, other gliders were thought to have died due to predation, particularly as shifts in activity patterns caused some gliders to forage during the day, exposing them to daytime predators, such as raptors (Körtner and Geiser 2000).

2.4.3. Reproduction

The long-term mean litter size of 1.8, and evidence of two distinct breeding seasons per year at Bungawalbin, one in autumn/winter and another in spring, was no different to that reported in other studies (Quin 1995; Rowston 1998b; Millis and Bradley 2001; van der Ree 2002). Mean litter size was found to be relatively constant across years and between seasons. In
2000, several females lost pouch young and at least one of these attempted, unsuccessfully, to breed again later that winter. It is unclear whether the loss of pouch young was due to the onset of adverse conditions, was a density-dependent effect or was typical of other years.

In common with the mahogany glider (*P. gracilis*) (Jackson 2000a) and Leadbeater’s possum (*Gymnobelideus leadbeateri*) (Smith 1984), female squirrel gliders may only breed a second time if the first litter is lost. Throughout this study, there were only three records of consecutive breeding by the squirrel glider. The loss of pouch young may not be a common occurrence. This suggestion is supported by the generally close correspondence between litter size and natality rate (Rowston 1998b; Millis and Bradley 2001; van der Ree 2002), although Quin’s (1995) data were more divergent. Furthermore, two-thirds of spring births at Bungawalbin were to females early in their second year. If these gliders were born late in the previous years’ autumn/winter breeding season, they may not have been sexually mature during autumn/winter the subsequent year. Rather, they may have delayed the onset of sexual activity to the following spring.

### 2.4.4. Hypothesis to Explain the Population Decline

The observed decline in the Bungawalbin NR squirrel glider population is argued to be a consequence of several concurrent factors. An abundant food resource provided by flowering trees appears to have increased the population size above the usual carrying capacity, which was followed by the failure of a usually dependable floral resource. This occurred during a drought, so conditions were not favourable for switching to alternative food resources. Thus, the gliders experienced a rapid loss of condition, which was followed by high mortality. This population decline appears to have occurred over a large area because the glider habitat at Bungawalbin is part of a much larger area of suitable forest habitat. While large populations may have a low extinction risk, they are not immune from the impacts of adverse environmental effects acting across the landscape (Rosenzweig 1999). Declines in population size attributed to food resource failure have been observed in other petaurids (Smith 1984; Goldingay 1992; Quin 1995).

In winter 2000, the squirrel glider population was at a five-year high. Nectar is the most important food resource in the Bungawalbin area during the winter/spring period (Sharpe and Goldingay 1998; unpublished data) and the population appears to have increased in response to a period of high nectar availability (*B. integrifolia* was flowering plus *E. robusta* flowered for the first time in five years). Subsequently, the failure of *E. siderophloia* to flower in late
winter-early spring deprived the squirrel gliders of their major food resource at this time. Consequently, gliders were forced to find alternative food resources. The lack of sufficient alternative exudates and the apparent inability to subsist on arthropods in early spring reinforces the importance of nectar to squirrel gliders at this time. The scarcity of food may also have been exacerbated by the presence of three other exudivorous glider species.

There were extremely dry conditions on the NSW north coast during 2000. The area suffered a serious rainfall deficiency for at least the seven months from February to August 2000 (Bureau of Meteorology 2000). The lack of rainfall during 2000 was exacerbated during August and September by very hot temperatures and dry westerly winds. Temperatures above 30°C were consistently recorded in the field at that time (unpublished data). It is possible that the dry conditions lowered sap flows (e.g. Henry 1986), which resulted in the lower availability of alternative exudates. The sudden onset of hot conditions in the late winter of 2000 may have also affected the arthropod food resource (e.g. Woinarski and Cullen 1984).

The decline in squirrel glider abundance appears to have occurred across the Bungawalbin catchment (see above). Deaths due to a food shortage (reported to the author as flower failure) also seemed to extend into the adjacent Clarence catchment to the south, where a number of starving squirrel gliders were brought into care, a very unusual event (June Richards, wildlife carer, personal communication). *Eucalyptus siderophloia* did not flower in the lower Clarence catchment in 2000 (personal observations) and similar climatic conditions are likely to have prevailed. Recovery from population lows can be slow if the decline occurs over a broad area and those populations cannot rapidly recover by recruiting immigrants. There was little change in the size of Bungawalbin squirrel glider population ten months after its decline.

Predation upon individual gliders (e.g. Sharpe 1996; van der Ree 2000) is certainly likely at the time of the observed population decline. Possible alterations to activity patterns may have imposed an increased predation risk if gliders attempted to forage before dark, for example (see Körtner and Geiser 2000). It is unlikely, however, that predation alone can explain the correlated decline of squirrel glider populations that appears to have taken place in northern NSW during 2000 because this phenomenon was too widespread.

2.4.5. Management Implications

This study has several implications for management. Fluctuations in glider populations can be correlated across the landscape and cover a broad area of relatively continuous forest. This is
important to consider when population targets, and the area required to support them, are being devised for conservation purposes (Vucetich and Waite 1998). In smaller areas of habitat, the implications for genetic viability must also be considered (Nunney and Elam 1994). Furthermore, the interpretation of the results of broad-scale surveys should attempt to account for, or at least acknowledge, the influence that fluctuating population sizes may have on survey results if surveys are conducted across regions or over an extended period (e.g. Bennett et al. 1991). However, several coinciding factors acting together may be necessary to affect glider abundance. As such, the population fluctuations of the degree documented herein may not be common.

Law et al. (2000) highlighted the importance of *E. siderophloia*, which is widespread in northern NSW, as a late winter/spring nectar resource. This species is likely to be important to a range of nectarivores. For example, the yellow-bellied glider appears to associate strongly with *E. siderophloia* in coastal northern NSW (Mackowski 1986) and south-east Queensland (Eyre and Smith 1997), presumably because it is an important nectar and pollen resource (personal observations). The size of two yellow-bellied glider groups at Bungawalbin also seemed to decrease in late 2000 (personal observations) and the detection rate of feathertail gliders halved (Goldingay and Sharpe 2004c). The over-harvesting of *E. siderophloia* in timber production forests would have the potential to adversely affect nectarivorous species, such as the squirrel glider and the yellow-bellied glider, both of which are listed as threatened in NSW.

It is clear that stability cannot be necessarily inferred in populations of gliding possums from short-term studies. Effective population size decreases as estimates of fluctuations in population size increase. Therefore, a failure to account for fluctuating population size may result in population viability being over-estimated (Vucetich and Waite 1998). Further, long-term studies are required to elucidate effective population sizes for gliding possums.
3. **Population Ecology of the Squirrel Glider** (*Petaurus norfolcensis*) **in Remnant Forest in Subtropical Australia**

3.1. Introduction

Describing the population ecology of a species is fundamental to understanding its response to local resource availability over time. Dramatic population fluctuations over time are well recognised for some mammal species (e.g. *Microtus* spp., *Antechinus* spp.) (Magnusdottir *et al.* 2008; Inchausti *et al.* 2009). However, population variability is poorly documented for many species and studies are often of insufficient duration to shed much light on this issue. For threatened species, an understanding of population dynamics is fundamental from the point of view of knowing whether a population is still contracting (e.g. Tasmanian devil (*Sarcophilus harrisii*): Lachish *et al.* 2009) or whether management actions have arrested a decline (e.g. mountain pygmy-possum (*Burramys parvus*): Heinze *et al.* 2004).

The diets of some species may drive their temporal patterns of abundance due to a close coupling between local climate and food abundance, and hence reproductive output and survival. Potential examples of this are the non-flying mammal species that exploit nectar and pollen from flowering trees. Australia contains many such species (e.g. Carthew and Goldingay 1997) and so is a highly suitable location in which to investigate this issue. Evidence is accumulating that many flowering trees in eastern Australia undergo temporal variation in abundance, which may be linked to local rainfall patterns (e.g. Goldingay 1990; Pook *et al.* 1997; Law *et al.* 2000). Non-flying mammals that are dependent on nectar may be exposed to periodic food shortages, which may lead to variation in their own local abundance (e.g. Goldingay 1992; Chapter 2). The extent to which this is characteristic of nectar-feeding non-flying mammals is unknown (e.g. Fleming and Nicolson 2002), but this is an important area for further research because species such as the squirrel glider (*Petaurus norfolcensis*), mahogany glider (*P. gracilis*) and yellow-bellied glider (*P. australis*) that exploit flowering trees (Goldingay 1990; Sharpe and Goldingay 1998; Jackson 2001; Dobson *et al.* 2005) are listed as threatened in part or all of their range.

The squirrel glider is a small (180-300 g) arboreal marsupial that has an extensive geographic range extending about 3,000 km along eastern Australia (Eyre 2004; Kavanagh 2004; van der Ree *et al.* 2004; Winter *et al.* 2004). It is considered threatened in the southern half of its range (Kavanagh 2004; van der Ree *et al.* 2004), while its status in the northern part of its range is in need of review (Eyre 2004; Winter *et al.* 2004). The diet of the squirrel glider is comprised of exudates, arthropods and pollen (Menkhorst and Collier 1987; Sharpe and
The diet of some populations is dominated by nectar and pollen (Sharpe and Goldingay 1998; Dobson et al. 2005; Ball et al. 2009), which makes it a suitable species for examining the influence of variation in flower abundance on population dynamics.

The squirrel glider typically occurs in landscapes subject to historic and/or contemporary habitat fragmentation, and it is poorly represented in conservation reserves (Menkhorst 1995; Smith and Murray 2003; Claridge and van der Ree 2004; Goldingay et al. 2006). Previous studies of its population ecology have occurred in natural forest in north-east New South Wales (NSW) (Chapter 2), in a natural “island” of forest surrounded by low wet heath in midnorth-east NSW (Quin 1995) and in an extensive linear network of remnant forest along roadsides surrounded by open pasture in central Victoria (van der Ree 2002). Studies of its population ecology are now needed in the northern part of its geographic range in Queensland (Qld) to see whether there are regional differences in its population ecology.

South-east Qld is one of the fastest developing regions of Australia (Australian Bureau of Statistics 2009) and, as a consequence of extensive habitat fragmentation (Catterall et al. 1997), much of the remaining habitat of the squirrel glider is embedded within an urban matrix (Rowston et al. 2002; Goldingay and Sharpe 2004). When living in habitat remnants within an urban matrix some arboreal marsupials, such as the common brushtail possum (*Trichosurus vulpecula*) and common ringtail possum (*Pseudocheirus peregrinus*), may benefit from the complementary food and shelter resources available (e.g. Harper et al. 2008). However, the squirrel glider may derive little benefit from such resources, so it is possible that its population ecology in urban remnants may differ to that in native forest. Comparison of demographic parameters among locations can provide important insights into how these may respond to broad variation in resources and help to identify whether ecological processes have been disrupted (e.g. Martin and Handasyde 2007). Population studies of the squirrel glider are needed in south-east Qld because the findings will have direct management relevance.

The present study was conducted in south-east Qld and was able to address two separate aims: i) to describe the population ecology of the squirrel glider in remnant habitat surrounded by urban development, and ii) to broadly determine whether a diet of nectar and pollen may influence its population dynamics. To investigate whether an abundance of nectar and pollen in the diet influences population dynamics, this study was conducted over a 4-year period. It
was expected that this would be a sufficient period of time over which to observe a variation in the local abundance of flowering trees (e.g. Goldingay 1990; Law et al. 2000; Chapter 2).

3.2. Methods

3.2.1. Study Area

By 2006 about 991,000 people lived in the Brisbane City Local Government Area (1,367 km²), a population density of 725 persons/km² (BCC 2009). The squirrel glider is used as a flagship species by Brisbane City Council (BCC) to promote the conservation of urban bushland (BCC 2000). This study was conducted at Minnippi Parklands, an area containing remnant forest, pasture and recreational areas owned and managed by BCC. It is located within an urban matrix less than 10 km from Brisbane’s Central Business District (27°28’S 153°06’E). Major arterial roads and a freeway, medium-density housing, a shopping centre and an industrial estate surrounded the study site. Horse and cattle grazing occurred on the site during the first three years of the study.

Minnippi Parklands covers a total area of 323 ha. It consists of two disjunct forest remnants, one on either side of mangrove-lined Bulimba Creek, that are connected by a forested corridor and surrounded by open grassland. This study focused on a patchy forest block situated in the west of the reserve (the study site). The southern part of the study site consisted of several smaller patches of forest that were linked to a larger area in the northern section for a total forest area of 47 ha. About 20 tree species were present, all of which were in the Family Myrtaceae (Dobson et al. 2005). Common species within the remnant included brush box (*Lophostemon confertus*), forest red gum (*Eucalyptus tereticornis*), narrow-leaved red gum (*E. seeana*), northern grey ironbark (*E. siderophloia*), scribbly gum (*E. racemosa*), broad-leaved white mahogany (*E. carnea*), pink bloodwood (*Corymbia intermedia*), smooth-barked apple (*Angophora leiocalyx*) and broad-leaved paperbark (*Melaleuca quinquenervia*). There was an open understorey comprised of wattles (*Acacia* spp.) and the exotic species lantana (*Lantana camara*). Hollow-bearing trees did not appear to be limiting at the site, with a mean of about five den trees used per group (Dobson 2002).

3.2.2. Glider Trapping and Handling

In April 2002, 36 trap stations were evenly spaced throughout the 47 ha remnant at a mean spacing of about 100 m. Home-range estimates (adaptive kernel 95% for 12 gliders) at the study site averaged 6.7 ha (Dobson 2002), indicating that about 6 traps were available to each
From April 2002 to May 2006 19 field trips of 5 nights duration were conducted to census the local squirrel glider population. Between 30 and 36 traps were set during each census. Eleven field trips at a mean interval of 48 days occurred between April 2002 and November 2003. Trapping occurred at intervals of about six months for the remainder of the study. These latter censuses, conducted in April/May and November/December, were timed to coincide with times of reproductive activity based on the first two years of research (e.g. Chapter 2). An intervening five-night census was conducted in October 2005 and an additional three-night census occurred in July 2006. Some supplementary trapping was also conducted to manage concurrent radio-tracking studies in 2002 and 2003 (see Dobson et al. 2005; Beyer et al. 2008). This additional trapping was used to enhance several aspects of the research, namely the collection of reproductive data and to improve population estimates using the minimum number alive (MNA). Certain traps were occasionally closed to avoid repetitive captures of the common brushtail possum.

All trapping was conducted using Elliott type B traps (Elliott Scientific Co., Victoria) measuring 45×15×15 cm. Traps were placed 3–5 m high on wooden platforms permanently affixed to trees >20 cm DBH. Traps were covered with plastic bags to provide shelter from adverse weather and some dry leaves were added for insulation. Traps were baited with rolled oats, peanut butter and honey. A trail of diluted honey was sprayed on the tree above the trap to a height of about 7 m (e.g. Chapter 2).

Traps were checked daily, commencing at dawn. All captured gliders were removed from traps and weighed to the nearest 1 g (using a 300 g or 1000 g spring balance, Pesola AG, Baar, Switzerland), sexed, assigned to age classes and assessed for signs of reproductive activity. Upon initial capture, all gliders were fitted with numbered fingerling ear tags (Salt Lake Stamp Co., Salt Lake City, USA) in each ear. Squirrel gliders were subsequently released onto trees at the point of capture.

3.2.3. Age Estimation
Consistent with other glider studies, a number of characteristics were used to estimate the age of squirrel gliders (Suckling 1984; Quin 1995; Jackson 2000a; van der Ree 2002). Body weight (females <160 g; males <180 g) was a useful indicator of age of gliders to about 12...
months (Smith 1979). Wear on the upper incisors (Suckling 1984) was useful for young animals, but showed individual and temporal variation in older animals. Similarly, the condition of the lower incisors (lateral cracks and staining) progressed variably with age. Ventral fur colour was white in gliders up to about 6 months, thereafter becoming increasing discoloured, eventually becoming a deep mustard. This character also showed individual variation. Due to the difficulty in accurately aging older individuals, three age classes were recognised (<1, 1-2, >2 years). Gliders >12 months were considered adults as female squirrel gliders can breed early in their second year (Quin 1995; van der Ree 2002). Pouch young were examined and their developmental stage determined according to descriptions provided by Smith (1979). This enabled the weight of pouch young to be determined and subtracted from the female’s weight.

3.2.4. Population Size and Density

To enable comparison with other studies of petaurid gliders (Suckling 1984; Quin 1995; Jackson 2000a; van der Ree 2002), population size was estimated as the MNA. This estimator simply counts the number of individuals captured during a population census and adds these to individuals not captured in that census but known to be alive due to capture during previous and subsequent sampling sessions. The MNA is sensitive to the capture probability between individuals and sampling sessions (i.e. capture heterogeneity), potentially resulting in biased estimates. However, the MNA remains useful by providing a lower limit to population size (Jolly and Dickson 1983) and has been used in previous studies of petaurids (Suckling 1984; Quin 1995; Jackson 2000a; van der Ree 2002; Chapter 2). All trapping, including trapping conducted to manage concurrent radio-tracking studies, was used to produce the MNA estimates. Because the entire forest remnant was trapped, population density was determined by dividing the estimated population size by the area of the remnant (47 ha).

3.2.5. Reproduction

The reproductive status of female gliders was assessed by examining the pouch and allocating its condition to one of six categories (Quin 1995; Millis and Bradley 2001; van der Ree 2002): i) nulliparous (juveniles that had not previously bred), pouch small and tight with white hairs and teats <1 mm long; ii) pregnant, pouch lining thickening, pouch wall with white glands visible (may or may not have previously bred); iii) females carrying pouch young; iv) lactating females, pouch loose and with one or more large, lactating teats; v) females recently bred, pouch and teats large, but not lactating and vi) non-breeding, pouch larger and deeper
than virgin females but no reproductive activity apparent, hairs yellow/brown and black scale often present, teats >1 mm long.

The number of pouch young or the number of lactating teats was used to estimate litter size. The developmental stage of pouch young (Smith 1979) or the presence of lactating teats was used to infer the month of birth. Regular trapping during the first two years of research ensured that these estimates were highly accurate. The sex of pouch young was determined for young ≥1 cm in length. This protocol required two personnel.

3.2.6. Survival
Due to the difficulty of aging older gliders, survival estimates were based on following the fate of individuals <2 years old in 2002. The ages of these animals at the time of their disappearance from the trapping record (gliders were assumed to have disappeared when not captured on at least three field trips) was estimated. Survival for offspring born in 2002 was expressed as the numbers of individuals that disappeared at each age (in months) as a percentage of all individuals of that cohort that disappeared during the study. This approach does not distinguish between mortality and dispersal. It is also prone to bias due to unequal capture probability (Carothers 1973).

3.2.7. Index of Floral Abundance
Flowering trees are sources of nectar and pollen for non-flying mammals (Goldingay et al. 1991; Goldingay 2005; Law and Chidel 2008), so their abundance provides a useful index of the availability of nectar and pollen. Flowering by individual trees and tree species is highly dynamic (unpublished observations), so the number of trees in flower at any single point in time may not be representative of flowering across a whole year. Rather than score flowering tree abundance on a short temporal scale, I have simply done this for each 12-month period of our study. Extended feeding bouts by squirrel gliders were observed in all tree species that flowered at the study site (Dobson et al. 2005; Chapter 6), so all tree species were included in the assessment.

The study area was visited monthly between May 2002 and April 2003 to conduct extensive, detailed observations on gliders as they fed at night. This enabled us to document the period over which each tree species flowered (see Dobson et al. 2005) and enabled us to reliably estimate the percentage of trees that flowered. I was also able to obtain insights into the flowering intensity of individual trees. In 2003, quadrants of 50 m radius were established in
the core home-range of six glider groups in different parts of the study area, giving a total area sampled of 4.7 ha (10% of the forest cover at the study site). These quadrants were monitored monthly over a 4-month period from July until October. The number of trees that flowered during this time and the number of flowers per tree was summed for this period. The number of flowers per visit was assessed by counting the number present in a typical subunit of the canopy and extrapolating this value across the whole tree. The number of quadrants was increased to seven in early 2004 (sampled area = 5.5 ha), which were monitored every 4-8 weeks until July 2006. Collectively, these observations enabled us to categorise each year of the study according to the abundance of flowering trees on a 3-point scale from 1 (poor flowering) to 3 (heavy flowering).

3.3. Results

3.3.1. Glider Trapping

Between April 2002 and July 2006, a total of 3,729 trap-nights produced 708 captures of 201 individual squirrel gliders (102 females, 99 males) at an overall trap success of 19%. There was a mean of 27.2±1.7 s.e. individuals and 32.5±2.3 s.e. captures per 5-night census (n=19). Mean nightly trap success declined significantly over the course of a trapping session ($F_{1,3}=36.47$, $p=0.01$, $r^2=0.92$) (Fig. 3.1). The MNA estimates indicated that a mean of 62%±3.95 s.e. of the population was trapped during each 5-night census. The number of new gliders captured was high during the first few census periods, but quickly declined. Following the initial sampling, the majority of new captures were of gliders <18 months of age.

![Graph showing the relationship between mean number of captures per night and the night of trapping over a 5-night census (n=19).](image)

**Fig. 3.1:** Relationship between the mean number of captures per night and the night of trapping over a 5-night census (n=19).
3.3.2. Population Size and Structure

The low MNA estimates for the initial and final few trapping sessions (Fig. 3.2) are an artefact of the estimation technique because there were no prior sessions and insufficient subsequent trapping, respectively. The MNA estimates suggest that the glider population numbered between 28 and 76 individuals (Fig. 3.2). The MNA estimates correspond to glider densities between 1.62 ha\(^{-1}\) (August 2002) and 0.49 ha\(^{-1}\) (December 2005). Population density was consistently high (1.3–1.6 ha\(^{-1}\)) from May 2002 to March 2003 (Fig. 3.3). Glider density declined during 2003 before stabilising at ~0.8 ha\(^{-1}\) during 2004. Population density again declined during 2005 and 2006 (Fig. 3.3).

The squirrel glider population was comprised of three recognisable age classes, although the <1 year age class was not recorded in three sampling periods (September 2003, November 2003, May 2006) (Fig. 3.2). The <1 year age class was only prominent in the population during 2002 and early 2003. Gliders 1–2 years old comprised 40–55% of the population between June 2002 and March 2003 and declined substantially thereafter (Fig. 3.2). The number of adults aged >2 was stable (26–32) from 2002 until late 2004 before falling to about 20 during 2005 (Fig. 3.2).

**Fig. 3.2:** The minimum number alive estimate of population size divided into three age classes, April 2002 - July 2006.
Fig. 3.3: Estimated squirrel glider population density for the 47 ha forest remnant, April 2002 - July 2006. Estimates for males, females and the overall population are given.

The sex of 26 offspring from 15 females indicated a sex ratio at the pouch stage of 1:1 (13 of each sex). While the overall juvenile sex ratio appeared female biased (Table 3.1), the difference was not significant ($\chi^2=1.185$, $p=0.28$). The overall adult and combined age classes were also close to parity (Table 3.1). In any year, females usually out-numbered males in both age classes and when they were combined (Table 3.1), although there were no significant differences (for all $\chi^2$, $p >0.05$).

Table 3.1: Sex ratios (female:male) of juvenile (<1 year) and adult (>1 year) squirrel gliders.
The sex ratios were based on the MNA estimate for each trapping session except the overall sex ratio, which was based on the total number of gliders captured.

<table>
<thead>
<tr>
<th>Year</th>
<th>Juvenile</th>
<th>Adult</th>
<th>Overall</th>
</tr>
</thead>
<tbody>
<tr>
<td>2003</td>
<td>9:8</td>
<td>45:38</td>
<td>54:46</td>
</tr>
<tr>
<td>2004</td>
<td>5:4</td>
<td>21:22</td>
<td>26:26</td>
</tr>
<tr>
<td>2005</td>
<td>5:0</td>
<td>24:21</td>
<td>29:21</td>
</tr>
<tr>
<td>2006</td>
<td>1:0</td>
<td>14:16</td>
<td>15:16</td>
</tr>
<tr>
<td>Overall</td>
<td>31:23</td>
<td>89:92</td>
<td>102:99</td>
</tr>
</tbody>
</table>

3.3.3. Reproduction
Female squirrel gliders first bred early in their second year. Throughout the study, 204 pouch young were born in 122 litters, giving a mean litter size of 1.7. These offspring were born to 73 individual females and the mean annual natality rate was 1.9 (Table 3.2). There were 13 records of females producing a second litter in the same year, 8 of which occurred in 2002.
(Table 3.2). The mean sizes of the first (1.4) and second (1.3) litters born to each female that reproduced twice did not differ (paired Students t-test, $t_{12}=0.32$, $p=0.75$), but females that reproduced twice had smaller litters (1.3, $n=26$) than those that reproduced once (1.8, $n=96$) ($t_{120}=4.25$, $p<0.001$). However, the natality rate of females that reproduced twice (2.7) was significantly higher than of those that had a single litter (1.8) ($t_{107}=7.25$, $p<0.001$). Older females had a larger mean litter size ($t_{110}=2.11$, $p=0.04$), but age did not influence the natality rate ($t_{107}=1.18$, $p=0.24$) (Table 3.3). There was no effect of year on mean litter size ($F_{2,106}=1.35$, $p=0.26$) or natality rate ($F_{4,104}=1.05$, $p=0.39$).

The timing of breeding was variable among years. Breeding commenced in March/April in 2002, 2004 and 2006, but did not occur until June in 2003 (Fig. 3.4). The timing of breeding was variable in 2005. Although some breeding occurred in April/May of that year, births did not peak until July (Fig. 3.4). Over the course of the study, births were recorded in all months except December, January and February and there was a clear peak of births in late autumn/winter (April-July) (Fig. 3.4). There appeared to be a tendency for females aged >2 years to breed earlier than those aged <2 in any given year (Fig. 3.4a). Accordingly, earlier births tended to be associated with larger litters (Fig. 3.4b). Female gliders had a mean lifetime reproductive output of 2.7±0.18 offspring per individual. The maximum number of offspring produced by a single female was 10. This female was still alive at the end of the study.

Table 3.2: Annual reproductive performance of female squirrel gliders, 2002 - 2006.
All years were pooled to calculate the overall mean litter size and natality rate. Index of relative flower abundance: 1 = poor, 2 = moderate, 3 = high. # based on number of offspring recruited into trappable population divided by the number of pouch young observed in the previous year. † note, trapping ceased in July 2006. *this value is not a sum of the yearly values because some females bred in more than one year.

<table>
<thead>
<tr>
<th>Year</th>
<th>Flower Abundance</th>
<th>Females Breeding %</th>
<th>No. Litters</th>
<th>No. Offspring</th>
<th>Mean Litter Size</th>
<th>Natality Rate</th>
<th>% offspring recruited#</th>
</tr>
</thead>
<tbody>
<tr>
<td>2002</td>
<td>3</td>
<td>44 100</td>
<td>52</td>
<td>86</td>
<td>1.7</td>
<td>2.0</td>
<td>33</td>
</tr>
<tr>
<td>2003</td>
<td>1</td>
<td>25 100</td>
<td>26</td>
<td>46</td>
<td>1.8</td>
<td>1.8</td>
<td>13</td>
</tr>
<tr>
<td>2004</td>
<td>2</td>
<td>14 100</td>
<td>16</td>
<td>27</td>
<td>1.7</td>
<td>1.9</td>
<td>56</td>
</tr>
<tr>
<td>2005</td>
<td>2</td>
<td>16 100</td>
<td>17</td>
<td>29</td>
<td>1.7</td>
<td>1.8</td>
<td>38</td>
</tr>
<tr>
<td>2006†</td>
<td>2</td>
<td>10 100</td>
<td>11</td>
<td>16</td>
<td>1.5</td>
<td>1.6</td>
<td>-</td>
</tr>
<tr>
<td>Overall</td>
<td>73* 100</td>
<td>122 204</td>
<td>1.7</td>
<td>1.9</td>
<td>32</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

43
Table 3.3: The influence of age class on the reproductive performance of female squirrel gliders, 2002 - 2006.
*this value allows for some females that are counted in more than one age class.

<table>
<thead>
<tr>
<th>Age Class</th>
<th>Females Breeding</th>
<th>No.</th>
<th>%</th>
<th>No. Litters</th>
<th>No. Offspring</th>
<th>Mean Litter Size</th>
<th>Natality Rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-2</td>
<td>37</td>
<td>100</td>
<td></td>
<td>42</td>
<td>64</td>
<td>1.5</td>
<td>1.7</td>
</tr>
<tr>
<td>&gt;2</td>
<td>72</td>
<td>100</td>
<td></td>
<td>80</td>
<td>140</td>
<td>1.8</td>
<td>1.9</td>
</tr>
<tr>
<td>Overall</td>
<td>109*</td>
<td>100</td>
<td></td>
<td>122</td>
<td>204</td>
<td>1.7</td>
<td>1.9</td>
</tr>
</tbody>
</table>

3.3.4. Recruitment, Survival and Longevity

For the purposes of this study, recruitment was defined as the entry of gliders in the <1 and 1–2 year age groups into the trappable population. Older gliders captured for the first time after the initial stages of the study were not considered recruits because the relatively isolated nature of the study site suggested that they were more likely to be trap-shy individuals rather than immigrants. The nearest habitat patch where animals might disperse from was approximately 0.5 km away. Surrounding development would prevent gliders from entering the population from other directions. Moreover, adult gliders in established groups tend to have stable home-ranges (Sharpe and Goldingay 2007).

Two male gliders weighing 90 g were captured. Body weight/age regressions for developing squirrel gliders suggest that a 90 g male would be about 110 days old (Smith 1979). Thus, squirrel gliders began to enter the trappable population at around 4 months of age. During the study, 87 juvenile and sub-adult squirrel gliders (41 males and 46 females) were recruited into the population (Table 3.4). Of these, 64 were from pouch young born during the study. This indicates that a mean of 32% of offspring were recruited into the population, based on the number of young gliders subsequently captured (Table 3.2). The remainder were born prior to the commencement of the study and were recruited in the initial stage of trapping aged around 1 year. Recruitment was apparent in all seasons and overall recruitment did not differ between the sexes ($\chi^2_{1}=0.29$, p=0.59). The number of offspring recruited varied among years ($\chi^2_{3}=15.58$, p=0.001), however, this effect disappeared when the number of offspring produced in the preceding breeding period was used to generate expected frequencies ($\chi^2_{3}=5.63$, p=0.13). Thus, the number of gliders recruited was affected by the number of offspring produced in addition to the prevailing conditions at the time of recruitment.
Fig. 3.4: The estimated month of birth of 122 litters recorded at Minnippi Parklands, April 2002 – July 2006, showing a) the age of females and b) litter size (1 or 2 young).

It was not possible to distinguish between the survival and dispersal of sub-adult gliders in this study. While there were limited opportunities for immigration at the study site (see above), it is also known that dispersing gliders sometimes attempted to enter the urbanised areas around the study site where some tree cover was retained (Melton 2007). Therefore, the
Table 3.4: Annual recruitment of juvenile and sub-adult squirrel gliders by age and sex in the years 2002 - 2006.

<table>
<thead>
<tr>
<th>Year</th>
<th>Sex</th>
<th>Age Class</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>&lt;1</td>
<td>1-2</td>
</tr>
<tr>
<td>2002</td>
<td>M</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>2</td>
<td>12</td>
</tr>
<tr>
<td>2003</td>
<td>M</td>
<td>6</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>8</td>
<td>5</td>
</tr>
<tr>
<td>2004</td>
<td>M</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>2005</td>
<td>M</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>2006</td>
<td>M</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Total Male</td>
<td></td>
<td>16</td>
<td>25</td>
</tr>
<tr>
<td>Total Female</td>
<td></td>
<td>19</td>
<td>27</td>
</tr>
<tr>
<td>Overall Total</td>
<td></td>
<td>35</td>
<td>52</td>
</tr>
</tbody>
</table>

potential for gliders to emigrate from the site was greater than the likelihood of them immigrating into it. The loss of young gliders from the population appeared rapid between 10 and 15 months, with males seeming to disappear at a faster rate than females in the 2002 cohort (Fig. 3.5). However, the mean age of males (13.2±1.5 months, n=16) and females (10.8±1.0 months, n=20) for all cohorts disappearing from the population were not significantly different (t = 1.43, p=0.16).

There was no difference in the persistence of all male (31.6±2.5 months, n=55) and female (32.5±2.0 months, n=60) gliders first captured during 2002 (t = 0.27, p=0.79). During 2002 there were a large number of young gliders that mostly disappeared early the following year (Fig. 3.2), which will have truncated the mean ages at disappearance. Only three gliders (all female) first captured in 2002 were alive at the end of the study. Two of these were at least 2 years old (though possibly older) when initially captured, making them a minimum of 6 years of age in July 2006. No gliders born on the study site in 2002 were known to be alive at the end of the study (Fig. 3.5).

3.3.5. **Body Weight**

Between April 2002 and July 2006, the mean (± s.e.) body weight of adult squirrel gliders was 199±1.3 g for males and 181±1.0 g for females. Body weight was generally highest during summer and declined during winter. Both sexes displayed similar trends in body weight.
fluctuations (Fig. 3.6). A pronounced low in the mean body weight of males was recorded in September 2003. Female weights were also low at this time. However, the lowest mean female weight was in October 2005 and male weights were concurrently low (Fig. 3.6).

Fig. 3.5: Estimated survival (months) of male and female squirrel gliders showing data for all cohorts and the 2002 cohort.

Fig. 3.6: Mean body weight (±s.e.) for adult squirrel gliders (>1 year) during each census period, April 2002 – July 2006.
3.3.6. Flowering Tree Availability

The number of flowering trees was not specifically quantified in 2002, but I estimate that >60% of trees in the study area flowered during this 12-month period. Moreover, gliders were regularly observed feeding in trees that contained >10,000 flowers during the winter and spring of 2002 (Chapter 6) and that individual forest red gum and northern grey ironbark trees flowered for periods of >4 weeks. Therefore, 2002 was scored as a year of heavy flowering.

Pink bloodwood and broad-leaved paperbark flowered moderately early in 2003, which was followed by extremely poor flowering during winter and spring. Only 18 of the 177 (~10%) winter flowering trees represented in the six quadrants flowered during the period July-October. Individual trees flowered poorly, collectively producing about 70,000 flowers during this 4-month period. Thus, 2003 was classified as a year of poor flowering. Although flowering differed each year between 2004 and 2006, the intensity of flowering was intermediate between the year of high flower abundance (2002) and the poor flowering year (2003) (Table 3.2).

3.4. Discussion

3.4.1. Comparison of demographic parameters across studies

One of the aims of this study was to determine whether the demographic characteristics of squirrel gliders in our urban study area differed to those described elsewhere. Generalist arboreal marsupials may benefit from such an environment because the surrounding matrix may provide additional resources (see Harper et al. 2008). However, it was more likely that the urban setting would have a negative influence on the squirrel glider because urban remnants may have a lower abundance of hollow-bearing trees compared to natural forest (Harper et al. 2005), predation from native and exotic predators may be higher than in continuous forest and habitat quality may be lower (Goldingay et al. 2006). The findings reported herein suggest that the demography of the squirrel glider in this urban forest remnant was similar to that reported at other locations. The study site contained resources important to the squirrel glider, such as a high abundance of hollow-bearing trees (Beyer et al. 2008) and a large diversity of food species, including an abundance of winter/spring flowering trees (Dobson et al. 2005).

The population density in this study ranged between 0.49 and 1.62 ha\(^{-1}\). This compares to a population density of 0.89–1.54 ha\(^{-1}\) at Limeburner’s Creek on the NSW central north coast (Quin 1995) and 0.95–1.54 ha\(^{-1}\) in fragmented habitat at Euroa in northern Victoria (van der
In contrast, glider densities of 0.18–0.87 ha$^{-1}$ were recorded in natural forest in north-east NSW (Chapter 2), while densities of 0.4–0.5 ha$^{-1}$ were reported in continuous forest in north-east Victoria (Traill 1995). The sex ratio of adult and juvenile gliders did not differ from parity, which was similar to what has been reported from other populations (Quin 1995; van der Ree 2002). These findings suggest that the quality of the habitat at Minnippi was at least equivalent to any other location where the squirrel glider has been studied.

The similarity in the maximum density (1.5–1.6 ha$^{-1}$) reported at several sites suggests that there may be a maximum threshold beyond which social factors prevent further increases in density. Alternatively, squirrel glider populations may lag behind increases in resource availability and because resource levels decline sufficiently quickly that higher densities are unlikely. This is particularly likely at sites where nectar is a dominant food item (e.g. Sharpe and Goldingay 1998; Dobson et al. 2005) due to the temporal dynamics of this resource (Law et al. 2000). Further studies are needed to gain a better understanding of the influence of habitat quality on the population density of squirrel gliders.

The overall mean litter size (1.7) in this study was similar to that recorded at other locations (see Quin 1995; Millis and Bradley 2001; van der Ree 2002). While the overall natality rate (1.9) was similar to Euroa (van der Ree 2002), it was less than the 2.4 recorded at Limeburner’s Creek (Quin 1995). There was a peak of births between April and July, with births continuing through to spring. Births late in the breeding season occurred because some females bred a second time and some that were born late in the previous year were not sexually mature at the beginning of the breeding season. There was no evidence that the loss of pouch young was a pre-condition for the production of a second litter, as proposed by Goldingay and Jackson (2004), as a concurrent nest box study revealed that the first litter was successfully raised (R. Goldingay unpublished data). Food availability appeared to facilitate the production of a second litter as most were recorded in 2002 when heavy flowering occurred. The onset of breeding varied among years, as in other studies (see Quin 1995; van der Ree 2002), and this may also reflect variation in food availability. A delay of approximately 3 months in year 2 compared to year 1 was observed, which coincided with a decline in the abundance of flowering trees.

Squirrel gliders at Minnippi were recruited into the trappable population from about 4 months of age. Juvenile recruitment was influenced by the number of offspring produced in the previous breeding period (Quin 1995). The prevailing conditions when they become
independently active are also likely to be important. During 2002 there was a large number of gliders in the 1-2 year age group, which was not apparent during the remainder of the study. Quin (1995) also found that young gliders periodically comprised a large component of the population. In contrast, the age structure of population at Euroa was more even over time and gliders aged 1-2 never dominated the population’s age structure (van der Ree 2002). Honeydew dominated the diet at this site (Holland et al. 2007), which may be a more temporally stable food resource than nectar. The 1-2 year age group appears to be the most elastic in response to variations in food availability (Chapter 2).

Overall, the percentage of offspring recruited into the population at Minnippi was rather low. Survival at the nestling stage appears to be high (R. Goldingay unpublished data), suggesting that mortality must be high when gliders first emerge from the den (Quin 1995) prior to many of them being captured. The cause of this mortality is unknown. Predators appeared to be scarce at Minnippi (personal observations) and none of 27 gliders radio-tracked in 2002-3 (Dobson et al. 2005) were taken by predators (unpublished data). The boobook owl (Ninox novaseelandiae) was the only owl known to be present and it is not expected to prey on the squirrel glider (unpublished observations). The carpet python (Morelia spilota) will prey on gliders (e.g. Goldingay et al. 2001), but appeared to be present in low numbers (unpublished observations). The lace monitor (Varanus varius), a known predator of the squirrel glider (Sharpe 1996), was not seen at Minnippi. Exotic predators such as cats (Felis cattus) and foxes (Vulpes vulpes) were expected to be present but none were seen within the study area. In contrast, radio-tracking revealed predation of several gliders by owls and a feral cat at Euroa (van der Ree 2002).

The mean persistence time of squirrel gliders in this study was similar for males and females (32 months). The maximum longevity recorded in this study (6 years, i.e. 72 months) was comparable to that obtained in other studies (Quin 1995; van der Ree 2002; Chapter 2). However, these estimates may be an artefact of the difficulty in aging gliders reliably beyond 2 years and the relatively short duration of field studies (van der Ree et al. 2006). A female glider aged 1-2 years old in April 2002, was known to be alive in July 2009 (Goldingay and Sharpe unpublished data), indicating a maximum longevity of >8 years (i.e. 96 months) at this site. This compares to an estimated maximum age of 7 years 9 months (i.e. 93 months) reported by van der Ree et al. (2006).
3.4.2. Population dynamics

Extreme variation in squirrel glider abundance was observed over the course of the study. The highest density of gliders was observed in the first year (\(~1.6\) gliders ha\(^{-1}\)), and was followed by a marked decline in the second year (to \(~1.0\) gliders ha\(^{-1}\)). By the third year it had stabilised at \(~0.8\) gliders ha\(^{-1}\) before declining further in the fourth year (\(~0.5\) gliders ha\(^{-1}\)).

The only study of the squirrel glider of comparable duration to which this can be compared is that conducted at Bungawalbin Nature Reserve (Chapter 2). In the fifth year of that study, the population size increased to \(~0.9\) gliders ha\(^{-1}\), which was followed by a precipitous decline (\(~0.2\) gliders ha\(^{-1}\)) over a period of less than two months. Variation in abundance can be represented by the ratio of the maximum density divided by the minimum density. At Minnippi the ratio was 3.3 and at Bungawalbin it was 4.8 from a period of \(~6\) years (Chapter 2). Studies of shorter duration may not detect such variation in population density. For study periods of 2.0-2.3 years the ratio was 1.6 at Euroa (van der Ree 2002) and 1.7 at Limeburner’s Creek (Quin 1995). Clearly, there is an increased probability of encountering large fluctuations when studies extend over at least 4-6 years. However, substantial variation may not occur in populations such as Euroa where nectar and pollen were not dominant in the diet (Holland et al. 2007). Similarly, folivores feeding on predictable food resources also appear to have stable population numbers (e.g. Martin and Handasyde 2007).

In Chapter 2 the hypothesis was advanced that the dynamics of nectar-dependent squirrel glider populations were strongly influenced by variation in the abundance of flowering trees, and in particular the failure of one usually dependable flowering resource. Our scoring of the annual abundance of flowering trees at Minnippi was consistent with this hypothesis. The first year of this study coincided with an over-abundance of flowering trees, but was followed by a year in which flowering was very poor. The abundance in flowering during year 1 was not observed again in this study. Alternative hypotheses to explain the variation in glider abundance include: that the trappability (i.e. detectability) of gliders at the site decreased over the course of the study; that gliders emigrated from the study area, or that predators frequented the study area in 2003 and drove the population down (cf. Kavanagh 1988). A prolonged decline in the capture probability of gliders at the study area was not evident in our data (Chapter 4) and is not consistent with studies at other locations, where trappability remained high over time (Quin 1995; van der Ree 2002). While the overall mean trap success in this study (19%) was less than the 26% recorded by van der Ree (2002) at Euroa it is comparable to the 17% recorded by Quin (1995) at Limeburner’s Creek. Moreover, it was
much greater than the 8% reported in Chapter 2 or the 5% recorded by Millis and Bradley (2001). There was no evidence that gliders emigrated en masse from the study area. The semi-isolated nature of the study area limits the ability of animals to move into other areas of suitable habitat and nearby habitat areas are already occupied (Beyer 2003). There was no evidence that an increase in predation in the second year produced the decline in glider abundance. The study area appeared to have a low abundance of predators (see above) compared to that at other locations (see Quin 1995; Sharpe 1996; van der Ree 2002). Therefore, the hypothesis that the dynamics in the Minnippi population was mediated by inter-annual variation in flowering tree abundance seems the most plausible.

I postulate that this pattern of variation in glider abundance may be characteristic of non-flying mammal populations in which nectar and pollen are dominant food resources (e.g. Wooller et al. 1998). Goldingay (1992) documented a decline in abundance of yellow-bellied gliders in response to the failure of their main winter food resource of nectar and pollen over consecutive years. At another location where yellow-bellied gliders did not specialise on nectar, their abundance was lower and had greater temporal stability (Goldingay and Kavanagh 1990). The variation in abundance that is apparent in populations of non-flying mammals that specialise on nectar occurs because the floral resource undergoes substantial inter-annual variation driven by local climatic factors (e.g. Wooller et al. 1998; Law et al. 2000).

The population peak in year 1 at Minnippi appeared to be due to high recruitment from the previous year’s breeding, as there was a large pool of gliders aged 1–2 years at this time. Thus, increases in the size squirrel glider populations appear to be driven by an influx of young gliders, which may persist during periods of high resource availability (Quin 1995; van der Ree 2002; Chapter 2). This influence was heightened because these individuals were able to breed when about 12 months of age. Furthermore, most records of a second litter occurred during the year of heavy flowering. Although females that bred twice in a year had smaller litters than females that bred once, their annual reproductive output was higher (2.7 vs. 1.8). Thus, a second litter appears to improve the fitness of females and is a strategy that should be adopted whenever conditions permit, such as years of abundant flowering (e.g. Quin 1995).

The poor flowering in the winter of 2003 was associated with the population declining to ~0.8 ha⁻¹ by November 2003. This decline was mainly due to the loss of individuals in the 1–2 year age group, while the number of adults >2 years initially remained relatively stable but
eventually declined later in the study following several years of moderate flowering. Young gliders of both sexes are clearly less competitive than adults in established social groups (Chapter 2).

3.5. Conclusions
This study provides the first detailed account of the population ecology of the squirrel glider in an urban forest remnant. The demographic parameters were similar to those reported in other studies of this species. Despite this remnant being embedded within a matrix of residential and commercial development, the study site had a good number of hollow-bearing trees (Beyer et al. 2008) and had a high floristic diversity, including an abundance of winter/spring flowering trees (Dobson et al. 2005), suggesting habitat quality was good. Annual variation in flowering appeared to influence both population size and reproductive output. Changes in population size appear to be largely mediated by the number of young gliders (<2 years) entering or leaving the population. Adult gliders appear to be more robust to fluctuations in the level of food resources (Chapter 2).

It is likely that population size and reproductive output will vary amongst remnants that differ in the quality and abundance of food and shelter resources. This requires investigation in a representative sample of forest remnants, particularly in urbanising areas. The substantial variation in flowering intensity that occurred at the study site appears to have induced substantial variation in population size, which has also been reported in other petaurid populations (Goldingay 1992; Chapter 2). Further investigations of nectar feeding non-flying mammals over at least several years are needed to determine whether population fluctuations of such magnitude commonly occur.

While this study showed that an urban forest remnant was capable of supporting a high-density squirrel glider population, the absolute population size was rather small due to the limited amount of habitat available (47 ha). The propensity for nectar-dependent populations to regularly fluctuate in size has implications for their population viability (Vucetich et al. 2000; Reed et al. 2003), which is particularly critical in small populations (Reed et al. 2003). Active management will be needed to maintain habitat quality in urban forest remnants (Goldingay et al. 2006). It also remains necessary to provide connectivity via treed corridors to other local populations to achieve a meta-population structure (sensu Hanski 1994). Only by achieving such inter-population connectivity amongst a number of urban forest remnants will the viability of local squirrel glider populations be secured (Goldingay and Sharpe 2004).
As urban expansion continues in south-east Queensland and other parts of the squirrel glider’s range, this can best be achieved in the context of regional conservation plans that identify existing habitat elements (large and small remnants, existing corridors) to be protected and areas that can be used to enhance connectivity (e.g. Sharpe and Goldingay 2006).
4. **ESTIMATING DEMOGRAPHIC PARAMETERS OF A SQUIRREL GLIDER (PETAURUS NORFOLCENSIS) POPULATION IN AN URBAN FOREST REMNANT**

4.1. **Introduction**

The rate and variability of individual survival and population size are key parameters of interest in wildlife research (e.g. Lindenmayer *et al.* 1998; Broome 2001; O'Grady *et al.* 2004; McClintock and White 2009). These parameters can be estimated via mark-recapture studies that follow the fates of known individuals and for which a variety of statistical estimation techniques are now available (Lebreton *et al.* 1992; Schwarz and Arnason 1996; Schwarz and Seber 1999; Williams *et al.* 2001). Significantly for species of particular management concern, computer programs for the analysis of mark-recapture data enable the testing of hypotheses regarding the factors that may influence variation in the rate of survival and population size (e.g. Bailey *et al.* 2004; Ozgul *et al.* 2004; Getz *et al.* 2006). This is important because fluctuations in population size have a major influence on the effective population size ($N_e$) and extinction probabilities of animal populations (Frankham 1995; Vucetich *et al.* 2000; Reed *et al.* 2003).

The squirrel glider (*Petaurus norfolcensis*) is a small (180-300 g) arboreal marsupial that occurs along the Australian east coast and adjacent inland plains (Eyre 2004; Kavanagh 2004; van der Ree *et al.* 2004; Winter *et al.* 2004). It is poorly represented in conservation reserves and its habitat is prone to clearing and fragmentation, including for urban development in coastal areas (Smith and Murray 2003; Claridge and van der Ree 2004; Goldingay and Sharpe 2004a). Accordingly, the squirrel glider is considered threatened in the southern half of its range (Kavanagh 2004; van der Ree *et al.* 2004). While it is currently considered to be a common species in Queensland, its status is in need of review (Eyre 2004; Winter *et al.* 2004). Despite its Statewide status in Queensland, the squirrel glider is regarded as a species of conservation concern by Brisbane City Council (BCC) and it is used as a flagship species to promote the conservation of urban bushland (BCC 2000, 2005).

A Population Viability Analysis (PVA) was recently conducted on a potential squirrel glider metapopulation occupying a series of tentatively linked urban forest remnants in the south-east suburbs of Brisbane (Goldingay and Sharpe 2004a). This PVA highlighted a number of population parameters that required better estimation to increase confidence in model output. Quantitative estimates of survival and rigorous estimates of population size were considered to be particularly critical in this regard (Goldingay and Sharpe 2004a). Sensitivity analysis
conducted as part of this PVA indicated that model output was most sensitive to the adult survival rate, with small changes in this value (e.g. 0.05) producing disproportionately large variations in extinction probability (Goldingay and Sharpe 2004a). Current density estimates of the squirrel glider were based on the minimum number alive (Quin 1995; van der Ree 2002; Chapters 2 and 3), which is prone to bias due to capture heterogeneity (Jolly and Dickson 1983). Individual capture heterogeneity and a behavioural response to capture are both common in mammal trapping studies (Hammond and Anthony 2006). The statistical analysis of mark-recapture data using computer software is generally robust to sources of variation in capture probability (e.g. Cooch and White 2007). Moreover, if the original PVA model is to be refined, the required data should ideally be collected from within the target study system.

The aim of this study was to provide estimates of adult survival and population size and to examine some factors that may affect squirrel glider survival. Goldingay and Sharpe (2004a) conducted a PVA on the series of local remnants that included the study site using a survival estimate that was derived from longevity data provided in the published literature. Accordingly, a further aim was to provide a more rigorous estimate of survival that could be used in a future PVA study. It was also intended to provide a refined population size estimate for the study site. These aims were achieved by trapping the target population over a 4-year period and by modelling the mark-recapture data in program MARK (White and Burnham 1999) using the Cormack-Jolly-Seber (CJS) model (Lebreton et al. 1992).

4.2. Methods

4.2.1. Study Area

This study was conducted at Minnippi Parklands, a public reserve owned by Brisbane City Council located <10 km from the Brisbane CBD (27°28’S 153°06’E). The study focused on a 47 ha area of remnant forest located in the west of the reserve, which had a narrow connection to a smaller area of forest 0.5 km to the east across mangrove-lined Bulimba Creek (Goldingay et al. 2006). There is further, albeit tenuous, connectivity to several other forest patches within the Bulimba Creek catchment, forming a potential squirrel glider metapopulation (Goldingay and Sharpe 2004a; Goldingay et al. 2006). The study site had a high floristic diversity, including winter and spring flowering trees, and numerous hollow-bearing trees (Dobson et al. 2005; Beyer et al. 2008), indicating that it was highly suitable squirrel glider habitat (e.g. Sharpe and Goldingay 1998, 2007). Further details of the study site are given by Dobson et al. (2005) and Goldingay et al. (2006).
4.2.2. Population Census

Trapping was conducted at Minnippi Parklands between April 2002 and May 2006. There were 7 census periods in 2002, 6 in 2003, 2 in 2004, 3 in 2005 and 1 in 2006, making a total of 19 sampling occasions. Each census consisted of 5 nights trapping except for May 2006 when 4 nights were completed. Thirty-six Elliott type B traps (45×15×15 cm) were distributed throughout the remnant at a spacing of 60–100 m. The distribution of traps allowed the entire remnant to be surveyed. The mean adaptive kernel home-range estimate of the squirrel glider at this site was 6.7 ha (Dobson 2002), suggesting that on average at least six traps were available to each individual. Traps were placed on wooden brackets 3–5 m high on tree trunks and baited with rolled oats, peanut butter and honey. A trail of diluted honey was sprayed on the tree trunks above the traps as an attractant (e.g. Quin 1995; van der Ree 2002).

Traps were checked daily in the early morning. Captured gliders were identified, sexed and weighed. Gliders were aged using a combination of ventral fur colour, wear on the upper incisors and cracking on the lower incisors as previously described for petaurid gliders (Suckling 1984; Quin 1995; Jackson 2000a; van der Ree 2002). All captured gliders were fitted with a numbered fingerling ear tag in each ear when first encountered. During the early stages of the study, unique combinations of colour-coded reflective tape were glued to the ear tags to facilitate individual recognition during concurrent radio-tracking studies. Following the handling procedure, squirrel gliders were released at the point of capture.

4.2.3. Population Modeling

The CJS model was used to assess the survival of adult squirrel gliders (Lebreton et al. 1992) as the data were found to be insufficient to use more complex models. The CJS model estimates survival and recapture probabilities and assumes an open population between census periods (Lebreton et al. 1992). The CJS model was implemented in program MARK, which uses a maximum likelihood approach to estimate model parameters (Cooch and White 2007). The notation used herein follows that of Lebreton et al. (1992). As such, \( \phi \) is used to denote the survival rate, while \( p \) represents the capture probability. The CJS model is conditional on first capture and, therefore, does not model the initial capture of unmarked individuals. It follows that the first census is not modelled because all individuals are unmarked at capture and marked before release (Lebreton et al. 1992). Thus, the CJS model allows \( \phi \) and \( p \) to be estimated for each of \( k-1 \) sampling occasions, where \( k \) is the number of sampling occasions. The framework provided by Lebreton et al. (1992) allows a flexible approach to model
building, enabling single factor, additive and interactive models to be constructed. Group effects (e.g. gender) may be included. For example, the model $\phi_{g \times t} p_{g \times t}$ would model survival as an interactive function of gender ($g$) and time ($t$), while allowing the capture probability to vary as an additive function of $g$ and $t$.

A capture matrix, representing the capture history of each adult glider marked across the 19 sample sessions, was constructed to provide an input file for MARK (Cooch and White 2007). Because females breed early in their second year, all gliders >1 year were considered adults (Quin 1995; van der Ree 2002; Chapters 2 and 3). For each sampling occasion, an animal was assigned a “1” if it was captured at least once during the session (i.e. irrespective of the number of times it was captured), otherwise a “0” was entered. For example, an animal with the capture history 100110 was captured and marked on sampling occasion 1, not capture on occasions 2 and 3, captured on occasions 4 and 5, and not captured on occasion 6.

Goodness-of-fit testing for the CJS model type was conducted using the sub-routine RELEASE (Burnham et al. 1987; Lebreton et al. 1992), which is available in MARK (Cooch and White 2007). The tests were conducted on the most general model in the candidate model set (Cooch and White 2007), which was a fully time varying model with an interactive gender effect for both $\phi$ and $p$ (i.e. $\phi_{g \times t} p_{g \times t}$).

RELEASE tests the assumptions of the equal probability of survival and capture of all individuals regardless of capture history (Burnham et al. 1987). Test 2.C considers whether the probability of being captured at time $i+1$ is dependent upon being captured at time $i$ (Cooch and White 2007). In other words, is there an effect of previous capture on the probability of future capture given the animal survives (equal capture probability)? Test 3.SR determines how many of the individuals captured at time $i$ were seen again and also in which sampling session they were seen again. Because some animals were first marked at time $i$, while others were previously marked, it is possible to determine if whether they were seen again (i.e. survived) depends on these histories. Similarly, Test 3.Sm assesses whether recapture after time $i$ depends on being marked on or before time $i$. If survival is equivalent for animals marked on or before time $i$ there should be no difference in whether or when they were recaptured (Test 3.SR) or when they were marked given capture in a subsequent period (Test 3.Sm) (Cooch and White 2007). Each of the three tests is constructed as a contingency table for each sampling period assuming a $\chi^2$ distribution. Because each test is independent the constituent $\chi^2$ are additive, enabling a pooled goodness-of-fit statistic to be derived.
(Lebreton et al. 1992; Cooch and White 2007). If the model does not adequately fit the data, it is possible to adjust a variance inflation factor (denoted $\hat{c}$) to control for the effects of over-dispersion (Cooch and White 2007).

The “live recaptures” CJS model available in MARK (Cooch and White 2007) was used to model the squirrel glider mark-recapture data. The analyses were constructed in MARK by entering 19 sampling occasions and specifying the intervals between them in fractions of a year to generate annual survival estimates (Table 4.1). However, because there were 19 sampling sessions, only 18 recapture occasions were modelled.

In addition to deriving parameter estimates for survival (the parameter of primary interest), various models considered whether various combinations of time, year and/or season affected the survival of squirrel gliders (Table 4.1). These factors were also applied to the capture probability to optimise the modelling process. The number of trap nights (Table 4.1) was used as a co-variate to model the capture probabilities in some models. Gender was applied as a group effect to all models to assess whether this provided an additional interactive or additive effect. Due to the long sampling intervals in the latter part of the study, it was necessary to pool season into winter/spring and summer/autumn periods (Table 4.1). These intervals approximate the time when squirrel gliders are heavily dependent on nectar (winter/spring) (Sharpe and Goldingay 1998; Dobson et al. 2005; Chapter 2) and also divided the year into wetter (summer/autumn) and drier seasons (Bureau of Meteorology 2008). Whether the survival and capture probabilities varied between the seasons and between calendar years was tested (Table 4.1). These factors were then combined to assess whether the squirrel glider population was affected by season and year (i.e. a seasonal effect, which differed between calendar years) (Table 4.1). Models were systematically constructed that so that all combinations of potential explanatory factors were explored.

All analyses were constructed by manipulating the design matrix available in program MARK. This facility allows the construction and comparison of complex model structures. The number parameters in models containing time variation in both survival and/or capture were constrained according to the recommendations of Cooch and White (2007) to ensure these parameters were not confounded. Because the models were constructed using the design matrix, the logit link function was used (Cooch and White 2007).
Table 4.1: Factors used to parameterise models of squirrel glider survival and capture probability and the sampling periods to which each category applied.

Note: for convenience the sampling intervals are given in days, although annual intervals were input into MARK (see text for details). Yr/season = a combination of year and season.

<table>
<thead>
<tr>
<th>Census Period</th>
<th>First Date</th>
<th>Interval (days)</th>
<th>Nights</th>
<th>Trapnights</th>
<th>Season</th>
<th>Year</th>
<th>Yr/season</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>15/04/02</td>
<td>5</td>
<td>150</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td>13/05/02</td>
<td>28</td>
<td>162</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>3</td>
<td>21/05/02</td>
<td>8</td>
<td>157</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>4</td>
<td>13/08/02</td>
<td>84</td>
<td>180</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>5</td>
<td>24/08/02</td>
<td>11</td>
<td>175</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>6</td>
<td>9/11/02</td>
<td>93</td>
<td>185</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>7</td>
<td>7/12/02</td>
<td>28</td>
<td>185</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>8</td>
<td>11/02/03</td>
<td>66</td>
<td>185</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>9</td>
<td>18/03/03</td>
<td>35</td>
<td>179</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>10</td>
<td>20/05/03</td>
<td>63</td>
<td>175</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>11</td>
<td>15/07/03</td>
<td>56</td>
<td>175</td>
<td>2</td>
<td>2</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>12</td>
<td>16/09/03</td>
<td>63</td>
<td>175</td>
<td>2</td>
<td>2</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>13</td>
<td>18/11/03</td>
<td>63</td>
<td>178</td>
<td>2</td>
<td>2</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>14</td>
<td>18/05/04</td>
<td>182</td>
<td>152</td>
<td>1</td>
<td>3</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>15</td>
<td>2/11/04</td>
<td>168</td>
<td>180</td>
<td>2</td>
<td>3</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>16</td>
<td>26/04/05</td>
<td>175</td>
<td>174</td>
<td>1</td>
<td>4</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>17</td>
<td>18/10/05</td>
<td>175</td>
<td>171</td>
<td>2</td>
<td>4</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>18</td>
<td>13/12/05</td>
<td>56</td>
<td>173</td>
<td>2</td>
<td>4</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>19</td>
<td>13/05/06</td>
<td>151</td>
<td>138</td>
<td>1</td>
<td>5</td>
<td>9</td>
<td>9</td>
</tr>
</tbody>
</table>

Akaike’s Information Criterion (AIC) (Akaike 1973) was used for model selection. The AIC looks for the model with the best fit to the data (the highest likelihood), but includes a penalty for the number of parameters required by the model. MARK uses a modified form of the AIC, the quasi-AIC, which enables the variance estimates to be adjusted for lack of model fit (over-dispersion of data, estimated by \( \hat{c} \); see above) if applicable, and differences in effective sample size. The quasi-AIC takes the form

\[
\text{QAIC}_c = -2\ln(L) + 2K + \frac{2K(K+1)}{M-K-1},
\]

where \( L \) is the model likelihood, \( K \) = the number of parameters in the model and \( M \) = the effective sample size (Cooch and White 2007). The model with the lowest \( \text{QAIC}_c \) best explains the probability of survival and capture given the data. To account for uncertainty in model selection, MARK provides an estimated relative likelihood for each model by dividing the \( \text{QAIC}_c \) weight for the model under consideration by the \( \text{QAIC}_c \) weight for the best model in the candidate model set to obtain a value between zero (no support) and 1 (strongest support).
support). When several models are well supported, it is possible to obtain a weighted average of the parameter estimates (Cooch and White 2007).

The estimation of population size is sensitive to violations of the assumptions of the equal probability of survival and capture amongst individuals. Goodness-of-fit testing was used to test these assumptions (see above). Provided these assumptions are met, population size can be estimated by dividing the number of individuals captured in a census \((N_i)\) by the capture probability for that census \((N_i/p_i)\) (Seber 1992; Williams et al. 2001).

4.3. Results

4.3.1. Goodness-of-fit Testing

Goodness-of-fit testing in program RELEASE revealed that the global model met the assumptions underlying the CJS model. The individual tests were also non-significant for both males and females (Table 4.2). Thus, the global model adequately fitted the data, enabling the testing of further model structures without the need to adjust \(\hat{c}\). Moreover, this result enables an unbiased estimate of population size to be determined.

Table 4.2: Summary of goodness-of-fit testing in program RELEASE (Tests 2.C, 3.SR, 3.Sm). Because the tests are independent the \(\chi^2\) tests are additive, enabling an estimate of overall model fit.

<table>
<thead>
<tr>
<th>Gender</th>
<th>Test</th>
<th>(\chi^2)</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>2.C</td>
<td>3.934</td>
<td>17</td>
<td>0.999</td>
</tr>
<tr>
<td>Male</td>
<td>3.SR</td>
<td>3.841</td>
<td>16</td>
<td>0.999</td>
</tr>
<tr>
<td>Male</td>
<td>3.Sm</td>
<td>5.015</td>
<td>14</td>
<td>0.986</td>
</tr>
<tr>
<td>Male</td>
<td>Test 2 + 3</td>
<td>12.791</td>
<td>47</td>
<td>1.000</td>
</tr>
<tr>
<td>Female</td>
<td>2.C</td>
<td>28.562</td>
<td>23</td>
<td>0.195</td>
</tr>
<tr>
<td>Female</td>
<td>3.SR</td>
<td>5.658</td>
<td>14</td>
<td>0.974</td>
</tr>
<tr>
<td>Female</td>
<td>3.Sm</td>
<td>3.251</td>
<td>13</td>
<td>0.997</td>
</tr>
<tr>
<td>Female</td>
<td>Test 2 + 3</td>
<td>37.472</td>
<td>50</td>
<td>0.905</td>
</tr>
<tr>
<td>Total (M + F)</td>
<td>Test 2 + 3</td>
<td>50.263</td>
<td>97</td>
<td>1.000</td>
</tr>
</tbody>
</table>

4.3.2. Survival Estimates and Model Ranking

Between April 2002 and May 2006 there were 3,265 trapnights over 19 census periods. There was minor variation in trap effort between sampling sessions (Table 4.1). The trap effort resulted in 620 captures of 187 individual adult squirrel gliders (91 male, 96 female). There were no trap deaths, so all marked animals were released. There was occasional trap
interference by common brushtail possums (*Trichosurus vulpecula*), but this did not have a substantial effect on trap availability. No other species were captured.

A large number of models were run due to the number of parameter combinations, with the best-performing 20 shown in Table 4.3. Four models that involved variation in survival and capture probabilities between seasons and years, with or without gender effects, best explain the squirrel glider mark-recapture data (Table 4.3). Due to the similar QAICc weights, these models were averaged using the model averaging facility in MARK. This provided estimates for survival and capture probabilities that varied between season and year with a weighted additive gender effect. The annual survival rate and capture probability was higher for females than for males (Table 4.4).

**Table 4.3: Model ranks for the best 20 models estimated by MARK.**

<table>
<thead>
<tr>
<th>Rank</th>
<th>Model</th>
<th>QAICc</th>
<th>Delta QAICc</th>
<th>QAICc Weights</th>
<th>Model Likelihood</th>
<th>No. Par</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>$\phi(yrseas)p(yrseas)$</td>
<td>1281.650</td>
<td>0.000</td>
<td>0.265</td>
<td>1.000</td>
<td>18</td>
<td>814.500</td>
</tr>
<tr>
<td>2</td>
<td>$\phi(g+yrseas)p(yrseas)$</td>
<td>1281.765</td>
<td>0.115</td>
<td>0.250</td>
<td>0.944</td>
<td>19</td>
<td>812.420</td>
</tr>
<tr>
<td>3</td>
<td>$\phi(yrseas)p(g+yrseas)$</td>
<td>1282.988</td>
<td>1.339</td>
<td>0.136</td>
<td>0.512</td>
<td>19</td>
<td>813.644</td>
</tr>
<tr>
<td>4</td>
<td>$\phi(g+yrseas)p(g+yrseas)$</td>
<td>1283.546</td>
<td>1.896</td>
<td>0.103</td>
<td>0.387</td>
<td>20</td>
<td>811.995</td>
</tr>
<tr>
<td>5</td>
<td>$\phi(g+year)p(yrseas)$</td>
<td>1286.633</td>
<td>4.983</td>
<td>0.022</td>
<td>0.083</td>
<td>15</td>
<td>826.002</td>
</tr>
<tr>
<td>6</td>
<td>$\phi(t)p(yrseas)$</td>
<td>1286.895</td>
<td>5.245</td>
<td>0.019</td>
<td>0.073</td>
<td>27</td>
<td>799.588</td>
</tr>
<tr>
<td>7</td>
<td>$\phi(year)p(yrseas)$</td>
<td>1286.934</td>
<td>5.284</td>
<td>0.019</td>
<td>0.071</td>
<td>14</td>
<td>828.454</td>
</tr>
<tr>
<td>8</td>
<td>$\phi(g+t)p(yrseas)$</td>
<td>1287.460</td>
<td>5.810</td>
<td>0.014</td>
<td>0.055</td>
<td>28</td>
<td>797.856</td>
</tr>
<tr>
<td>9</td>
<td>$\phi(t)p(g+yrseas)$</td>
<td>1288.027</td>
<td>6.377</td>
<td>0.011</td>
<td>0.041</td>
<td>28</td>
<td>798.423</td>
</tr>
<tr>
<td>10</td>
<td>$\phi(year)p(g+yrseas)$</td>
<td>1288.507</td>
<td>6.857</td>
<td>0.009</td>
<td>0.032</td>
<td>15</td>
<td>827.876</td>
</tr>
<tr>
<td>11</td>
<td>$\phi(g+year)p(g+yrseas)$</td>
<td>1288.573</td>
<td>6.923</td>
<td>0.008</td>
<td>0.031</td>
<td>16</td>
<td>825.780</td>
</tr>
<tr>
<td>12</td>
<td>$\phi(g+yrseas)p(trapeffort)$</td>
<td>1288.973</td>
<td>7.324</td>
<td>0.007</td>
<td>0.026</td>
<td>12</td>
<td>834.765</td>
</tr>
<tr>
<td>13</td>
<td>$\phi(yrseas)p(trapeffort)$</td>
<td>1289.067</td>
<td>7.417</td>
<td>0.006</td>
<td>0.025</td>
<td>11</td>
<td>836.978</td>
</tr>
<tr>
<td>14</td>
<td>$\phi(g+t)p(g+yrseas)$</td>
<td>1289.089</td>
<td>7.439</td>
<td>0.006</td>
<td>0.024</td>
<td>29</td>
<td>797.176</td>
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<tr>
<td>15</td>
<td>$\phi(g+year)p(year)$</td>
<td>1289.723</td>
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<td>0.005</td>
<td>0.018</td>
<td>11</td>
<td>837.634</td>
</tr>
<tr>
<td>16</td>
<td>$\phi(yrseas)p(g+trapeffort)$</td>
<td>1289.788</td>
<td>8.139</td>
<td>0.005</td>
<td>0.017</td>
<td>12</td>
<td>835.580</td>
</tr>
<tr>
<td>17</td>
<td>$\phi(yrseas)p(t)$</td>
<td>1289.828</td>
<td>8.178</td>
<td>0.004</td>
<td>0.017</td>
<td>27</td>
<td>802.521</td>
</tr>
<tr>
<td>18</td>
<td>$\phi(year)p(year)$</td>
<td>1289.880</td>
<td>8.230</td>
<td>0.004</td>
<td>0.016</td>
<td>10</td>
<td>839.901</td>
</tr>
<tr>
<td>19</td>
<td>$\phi(g+yrseas)p(t)$</td>
<td>1289.925</td>
<td>8.276</td>
<td>0.004</td>
<td>0.016</td>
<td>28</td>
<td>800.321</td>
</tr>
<tr>
<td>20</td>
<td>$\phi(g+yrseas)p(g+trapeffort)$</td>
<td>1290.365</td>
<td>8.716</td>
<td>0.003</td>
<td>0.013</td>
<td>13</td>
<td>834.027</td>
</tr>
</tbody>
</table>
Table 4.4: Estimates of survival and capture probability for each sex using the weighted mean of the best four models, which contained variation by year and season with or without an additive gender effect (see Table 4.3). Numbers in brackets are ± s.e.

<table>
<thead>
<tr>
<th>Year/Season</th>
<th>Survival</th>
<th></th>
<th>Capture</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Males</td>
<td>Females</td>
<td>Males</td>
<td>Females</td>
</tr>
<tr>
<td>Sum/Aut 2002</td>
<td>0.11 (0.16)</td>
<td>0.13 (0.19)</td>
<td>0.42 (0.08)</td>
<td>0.43 (0.08)</td>
</tr>
<tr>
<td>Win/spr 2002</td>
<td>0.48 (0.12)</td>
<td>0.53 (0.13)</td>
<td>0.31 (0.04)</td>
<td>0.32 (0.04)</td>
</tr>
<tr>
<td>Sum/Aut 2003</td>
<td>0.28 (0.12)</td>
<td>0.33 (0.12)</td>
<td>0.30 (0.04)</td>
<td>0.31 (0.04)</td>
</tr>
<tr>
<td>Win/spr 2003</td>
<td>0.37 (0.16)</td>
<td>0.42 (0.17)</td>
<td>0.43 (0.06)</td>
<td>0.44 (0.05)</td>
</tr>
<tr>
<td>Sum/Aut 2004</td>
<td>0.57 (0.27)</td>
<td>0.62 (0.26)</td>
<td>0.29 (0.09)</td>
<td>0.30 (0.09)</td>
</tr>
<tr>
<td>Win/spr 2004</td>
<td>0.96 (0.37)</td>
<td>0.96 (0.34)</td>
<td>0.36 (0.10)</td>
<td>0.37 (0.10)</td>
</tr>
<tr>
<td>Sum/Aut 2005</td>
<td>1.00 (0.01)</td>
<td>1.00 (0.01)</td>
<td>0.22 (0.07)</td>
<td>0.23 (0.07)</td>
</tr>
<tr>
<td>Win/spr 2005</td>
<td>0.06 (0.03)</td>
<td>0.08 (0.03)</td>
<td>0.65 (0.09)</td>
<td>0.65 (0.09)</td>
</tr>
<tr>
<td>Mean</td>
<td>0.48 (0.12)</td>
<td>0.51 (0.12)</td>
<td>0.37 (0.05)</td>
<td>0.38 (0.05)</td>
</tr>
<tr>
<td>Overall Mean</td>
<td>0.49 (0.08)</td>
<td>0.38 (0.03)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The capture probabilities of the squirrel glider in the study population ranged from 0.22-0.65 under the weighted average models. Generally, however, the capture probability was between 0.3 and 0.4 (Table 4.4). There was little difference in the capture probability for males and females. The overall annual survival rate of the squirrel glider was 0.49±0.08 and was variable throughout the study (Table 4.4). The weighted mean survival rate was slightly higher for females (0.51±0.12) than for males (0.48±0.12) (Table 4.4). The survival rate was lowest during 2003 and in late 2005 and highest in late 2004/early 2005 (Table 4.4).

4.3.3. Population Size Estimates

The model $\phi_t p_{s+t}$, which held survival constant while allowing the capture probability to vary as an additive effect of time and gender, was used to generate the population size estimates. The number of squirrel gliders captured per census ranged from 13-35 individuals (Table 4.5). When these values are divided by the corresponding capture probabilities, the number of individuals present was estimated to be 26-90 (Table 4.5). The adult glider density averaged 1.32 ha$^{-1}$ (range 0.55-1.90 ha$^{-1}$). Population density was highest early in the study and gradually declined thereafter. There was generally little difference in the density of male and female gliders (Fig. 4.1).
Table 4.5: The number of glider captured, the capture probability and the estimated population size for each census period using model $\phi_{p_{e+i}}$.

M = male, F = female, T = total.

<table>
<thead>
<tr>
<th></th>
<th>No. Captured</th>
<th>Capture Probability</th>
<th>Population Estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M</td>
<td>F</td>
<td>M</td>
</tr>
<tr>
<td>May-02</td>
<td>13</td>
<td>11</td>
<td>0.21</td>
</tr>
<tr>
<td>May-02</td>
<td>20</td>
<td>14</td>
<td>0.46</td>
</tr>
<tr>
<td>August-02</td>
<td>14</td>
<td>17</td>
<td>0.32</td>
</tr>
<tr>
<td>August-02</td>
<td>15</td>
<td>20</td>
<td>0.38</td>
</tr>
<tr>
<td>November-02</td>
<td>9</td>
<td>13</td>
<td>0.26</td>
</tr>
<tr>
<td>December-02</td>
<td>6</td>
<td>10</td>
<td>0.22</td>
</tr>
<tr>
<td>February-03</td>
<td>11</td>
<td>11</td>
<td>0.23</td>
</tr>
<tr>
<td>March-03</td>
<td>8</td>
<td>17</td>
<td>0.35</td>
</tr>
<tr>
<td>May-03</td>
<td>9</td>
<td>10</td>
<td>0.24</td>
</tr>
<tr>
<td>July-03</td>
<td>13</td>
<td>13</td>
<td>0.38</td>
</tr>
<tr>
<td>September-03</td>
<td>13</td>
<td>16</td>
<td>0.39</td>
</tr>
<tr>
<td>November-03</td>
<td>9</td>
<td>13</td>
<td>0.36</td>
</tr>
<tr>
<td>May-04</td>
<td>6</td>
<td>7</td>
<td>0.27</td>
</tr>
<tr>
<td>November-04</td>
<td>12</td>
<td>12</td>
<td>0.45</td>
</tr>
<tr>
<td>April-05</td>
<td>10</td>
<td>10</td>
<td>0.37</td>
</tr>
<tr>
<td>October-05</td>
<td>11</td>
<td>10</td>
<td>0.49</td>
</tr>
<tr>
<td>December-05</td>
<td>6</td>
<td>11</td>
<td>0.44</td>
</tr>
<tr>
<td>May-06</td>
<td>11</td>
<td>15</td>
<td>1.00</td>
</tr>
<tr>
<td>Mean</td>
<td>10.8</td>
<td>12.9</td>
<td>0.39</td>
</tr>
<tr>
<td>s.e.</td>
<td>0.9</td>
<td>0.8</td>
<td>0.04</td>
</tr>
</tbody>
</table>

4.4. Discussion

4.4.1. Survival Estimates

This study has provided the first survival estimates for the squirrel glider based on mark-recapture data. It was based on four years of fieldwork, which compares to earlier studies of the squirrel glider that were conducted over periods of 2-2.5 years (Quin 1995; van der Ree 2002). Previous studies of the squirrel glider have shown that population size is variable among years, which occurred due to changes in survival and reproductive output (Chapters 2 and 3). Therefore, it is important that longer-term studies are used to generate survival estimates.

The probability of capturing an animal is dependent upon firstly the chances of encountering a trap and then the odds of entering it (Ball et al. 2005). The capture probability in this study was generally about 0.3-0.4, which equated to an average of 62% of known gliders that were trapped during each sampling period (Chapter 3). There was some support for a higher
Fig. 4.1: Estimated size of the squirrel glider population based on the number of captures per census divided by the capture probability derived from model $\phi p_{g+t}$.

capture probability for females compared to males. The percentage of known gliders captured in Brisbane was similar to the 60-90% of individuals reported in earlier studies (Quin 1995; van der Ree 2002). The only study that directly reports on the capture probability of an arboreal marsupial from mark-recapture data found a value of 0.80 for the bobuck (*Trichosurus caninus*; now *T. cunninghamii*) using program CAPTURE (Lindenmayer *et al.* 1998). However, a capture probability of 0.14 was estimated for northern flying squirrels (*Glaucomys sabrinus*) using MARK (Lehmkuhl *et al.* 2006). Thus, the capture probabilities in this study were sufficiently high for use in mark-recapture analysis (e.g. Hammond and Anthony 2006).

The survival of squirrel gliders was found to vary between seasons and years, presumably in response to variation in food availability (Chapters 2 and 3). There was also some support for models that included gender as an additive effect. Thus, survival is slightly higher for female (0.51) compared to male (0.48) squirrel gliders, which is consistent with the difference in the longevity for each sex (Chapter 3). Survival estimates for female and male bobucks were 0.71 and 0.73, respectively (Lindenmayer *et al.* 1998). This difference in survival in consistent
with differences in the maximum longevity reported for each species. The oldest reported bobuck lived for 15 years (Lindenmayer et al. 1998), whereas squirrel gliders may live to over 7 years (van der Ree et al. 2006; Chapter 3). The maximum longevity reported for the sugar glider (Petaurus breviceps) in the wild is 7 years (Suckling 1984), suggesting that a similar survival rate to the squirrel glider is likely.

The survival probability for female gliders revealed by this study is substantially lower than the value (0.65) assumed by Goldingay and Sharpe (2004a) for females in a PVA conducted on the local squirrel glider metapopulation. This is of particular concern as the output of the PVA model was most sensitive to variation in the rate of adult survival. Relatively small changes (0.05) in the adult survival rate were found to roughly double the probability of metapopulation extinction (Goldingay and Sharpe 2004a). Accordingly, this PVA over-estimated the viability of the metapopulation. However, the sensitivity analysis that was conducted on the adult survival rate indicated that the viability predictions should be viewed with caution (Goldingay and Sharpe 2004a).

The survival rate may be confounded to some degree by the dispersal of gliders early in their second year (e.g. Hanski et al. 2000). This may have occurred because the study area is tenuously linked to some additional habitat about 0.5 km to the east. Moreover, there is some evidence that gliders entered the matrix habitat that surrounded most of the study site (Melton 2007). However, because the matrix would be rather hostile to squirrel gliders, many of the dispersing gliders entering this area are unlikely to have survived. It is difficult to determine to what extent the survival rate should be discounted due to dispersal in a PVA study to avoid double-dipping (sensu Brook 2000).

4.4.2. Population Estimates

The size of the squirrel glider population ranged from a high of around 90 individual adults early in the study (May and August 2002) to a low of 26 late in the study (May 2006). After February 2003, the adult population went into a gradual decline that was generally maintained until the end of the study. A small population peak was apparent in early 2005, which may have been due to a high level of recruitment into the adult age class following breeding in 2004 (Chapter 3) and higher survival at this time.

The size of the squirrel glider population at Minnippi Parklands predicted by the capture probability approach averaged 1.4 times higher than that calculated using the MNA (Chapter
3). This occurred even though the capture probability estimate only included adult gliders (>1 year), whereas the MNA estimate was for the entire population. However, juveniles (<1 year) were a small component of the population (Chapter 3). As this study was conducted in a discrete habitat patch, it was easy to derive population density estimates without resorting to assumptions about the effective trap area (e.g. Corn and Conroy 1998). The range of density in this study ranged between 0.6-1.9 ha\(^{-1}\), which compares to the MNA approach of 0.5-1.6 ha\(^{-1}\). Although the absolute values differed, both estimators predicted a similar trend in the population trajectory (Chapter 3). The MNA estimator remains useful for comparison to other petaurid studies (Suckling 1984; Quin 1995; Jackson 2000a; van der Ree 2002).

4.4.3. Management Implications

The survival estimates found in this study were lower than that used in the PVA by Goldingay and Sharpe (2004a). This PVA was conducted across a series of remnants that included the study site. To ensure that management decisions are not made on the basis of an overly optimistic viability assessment, it will be necessary to redo the PVA in the future using updated survival estimates.

While this study provided survival estimates for adult squirrel gliders, these estimates were confounded to some extent by dispersal primarily in the 1-2 year age group (see Quin 1995). Moreover, changes in the number of individuals aged 1-2 years strongly influenced the overall size of the population at sites in northern NSW and south-east Qld (Chapters 2 and 3), suggesting that survival in this group may differ from gliders aged >2 years. PVA studies also require a value for juvenile (<1 year) survival (Lacy 1993; Possingham and Davies 1995). Thus, it will be necessary to conduct further survival modelling that includes additional age groups. This could be achieved by constructing a multi-state survival analysis that included states corresponding to three age classes (i.e. <1 year, 1-2 years, >2 years), provided the data are sufficient for this level of complexity. This would provide a separate survival estimate for each age class and allow movement between age classes as a one-way state transition probability (Williams et al. 2001).

It is likely that population density and the survival rate will vary from one location to another due to differences in habitat quality and predation pressure, for example. Accordingly, there is a need to replicate survival and population size estimates for other local populations to understand how these parameters may vary (e.g. Frederiksen et al. 2005). For example, Minnippi includes lower slope and floodplain habitats, which may be more productive than
the upper slope/ridge habitats that characterise most of the other local remnants (Goldingay and Sharpe 2004a). Moreover, apart from the carpet python (*Morelia spilota*), no glider predators were observed in Brisbane. This contrasts with the diversity of predators (reptiles and owls) found in natural forest (e.g. Sharpe 1996).

It will be important to have context-specific survival and density estimates to use as inputs wherever PVA studies may be conducted. It is also important to obtain survival and density estimates from large areas of natural forest to provide comparative data. This is likely to provide insights into how the squirrel glider is able to persist in fragmented landscapes. Because this study found that survival varied amongst years, it will be necessary to conduct future studies over periods of at least 3–4 years to ensure that variation in the survival rate is adequately represented.
5. Vocal Behaviour of the Squirrel Glider (*Petaurus norfolcensis*)

5.1. Introduction

Vocalisations are an important means of animal communication and are used by a wide range of taxa (e.g. Lair 1990; Blumstein and Armitage 1997; Tang *et al.* 2001; Rowe and Skelhorn 2004; Wong *et al.* 2004). Vocal information has some advantages over other forms of communication, such as olfaction, because it enables more complex and precisely timed information to be conveyed (e.g. Lameira and Wich 2008). Because there is a need to transmit different kinds of information in different contexts, it is common for animals to exhibit a variety of calling behaviours (Seyfarth and Cheney 2003; Simeonovske-Nikolova 2004; Bezerra and Souto 2008). Determining the function of vocal communication requires a description of the behaviour, the context in which it occurs, its frequency and the response of receiving animals (Lemasson *et al.* 2004; da Cunha and Byrne 2006; Geissman and Mutschler 2006). It may be difficult to obtain such information in field studies of small nocturnal mammals because they are difficult to observe (e.g. Fichtel 2007).

The use of vocal communication is widespread among primates and its role in the social organisation of many species is well documented (Waser 1975, 1977; Sekulic 1982; Raemaekers and Raemaekers 1985; Whitehead 1987; Wich and Nunn 2002; Oliveira and Ades 2004). The calling behaviour of some species (e.g. Bornean gibbons *Hylobates muelleri*) is so developed that mated pairs engage in interactive singing that may last up to 1 h (Mitani 1985). This performs a territorial role, which maintains intergroup spacing and reduces direct conflict over space. Therefore, primates provide an important model for understanding the calling behaviour of other mammal species.

Many Australian arboreal marsupials have well developed vocal behaviours, but there are few detailed studies (Biggins 1984; Goldingay 1994; Runcie 2004). This hampers a broader understanding of the evolution of their vocal behaviour, as exemplified by the petaurid marsupials. The vocal behaviour of the yellow-bellied glider (*Petaurus australis*) is well described, with studies suggesting that it makes greater use of calls than any other marsupial (Kavanagh and Rohan-Jones 1982; Russell 1984; Goldingay 1994). Accordingly, there is considerable relevance in documenting the calling behaviour of other petaurids. Although not purposely studied, the repetitive “yapping” of the sugar glider (*P. breviceps*) and its alarm call are well known (Fleay 1954; Biggins 1984; Suckling 1995; Traill 1998). Preliminary
descriptions of mahogany glider (*P. gracilis*) vocalisations have also been provided (Van Dyck 1993; Jackson and Johnson 2002).

In contrast, the vocal behaviour of the squirrel glider (*P. norfolcensis*) remains poorly known (e.g. Traill 1998), leading to suggestions that it is the least social petaurid (Menkhorst 1995). Nonetheless, vocalisations reportedly increase the detection of squirrel gliders during spotlight surveys (Davey 1990; Goldingay and Sharpe 2004b). Moreover, call playback is routinely employed during pre-logging surveys for the squirrel glider on the New South Wales (NSW) north coast (P. Meek, personal communication), but its utility has not been established.

The aims of this study were to describe the call types of the squirrel glider, their frequency and context, and some of the factors that influence calling. Call playback was conducted to provide an evaluation of the response of individuals to conspecific calls, but also to assess whether this method is a reliable survey technique for the squirrel glider. The frequency of squirrel glider and sugar glider calls in sympatric populations was compared.

**5.2. Methods**

**5.2.1. Study area**

This study was conducted at five separate sites. Bungawalbin Nature Reserve (BNR, 29°10′S 153°07′E), Bungawalbin National Park (BNP, 29°05′S 153°07′E) and Bungawalbin State Forest (BSF, 29°07′S 153°05′E) occur in north-east NSW. These sites are all located within the same area of contiguous forest within 8 km of one another. Minnippi Parklands (MP, 27°28′S 153°06′E) and Karawatha-Kuraby Bushland Reserves (KK, 27°37′E 153°05′S) occur within the greater Brisbane area in south-east Queensland (QLD). MP is a disturbed urban fragment (c. 47 ha) in south-east Brisbane, while KK (c. 800 ha) are adjacent urban forest remnants in south-west Brisbane. All study sites were located in floristically diverse dry eucalypt forests, each containing a suite of 3-4 tree species that provide overlapping flowering periods during winter and spring. This flowering sequence appears to characterise high quality squirrel glider habitat in this part of its range (Sharpe and Goldingay 1998; Dobson *et al.* 2005). Further details of the BNR and MP study sites are provided elsewhere (Sharpe and Goldingay 1998, 2007; Dobson *et al.* 2005; Goldingay *et al.* 2006, Beyer *et al.* 2008).
5.2.2. Calling Behaviour

Data were collected during extensive periods of spotlighting or radio-tracking (e.g. Dobson et al. 2005; Chapter 2). Radio-tracking at MP was conducted with a red-masked, 50W spotlight powered by a 12V battery. A 50W white light was used during spotlighting at all other sites. Visual observations of gliders were aided by 10 x 50 binoculars. It is noted that there was some variation in the methods and effort between study sites.

Radio-tracking, stratified by night length, moon phase and gender was conducted at MP. Six gliders of each gender were observed during each of three seasons in a repeating series of 1 h focal observations (i.e. a sequence of different focal animals was used). Six whole nights (sunset to sunrise) of radio-tracking were completed in June 2002 and eight whole nights occurred during November/December 2002 and March/April 2003.

Spotlighting was conducted at BNR in June/July and November/December from 1997 to 1999. Bi-monthly spotlighting was then conducted from March 2000 to October 2001 (Chapter 2). During each trip, 2–5 consecutive nights of spotlighting were conducted. Spotlighting occurred during the first half of the night, usually for 2.0–3.5 h. Spotlighting along regular transects was conducted monthly at BNP from June to November 2000 and in February, March, June and August 2001. Each survey was conducted in the first half of the night for four consecutive nights for a mean of 130 min. At BSF, spotlighting was conducted over four consecutive nights in August 2000. Seven transects 250–300 m long were spotlighted on two occasions each. Spotlighting was conducted along 36 transects (most 200 m in length) on five occasions at KK between May 2006 and March 2008.

Squirrel glider vocalisations were opportunistically detected during the spotlighting and radio-tracking activities. Each time a vocalisation was heard, the type of call (assessed phonetically) and its duration (generally to the nearest 0.5 min.) were documented. Contextual information was also recorded (e.g. emerged from hollow, in flowering tree, chasing another glider, gliding) whenever possible. The calls of any other gliders that may have responded to the focal individual (i.e. the first to call) were also documented and any associated behaviours recorded if observed. Gliders at BNR and MP had colour-coded reflective tape glued to their eartags (e.g. Chapters 2 and 6), making it possible to determine the identity of calling and responding individuals. Moreover, concurrent studies at these sites enabled the nature of many social relationships to be established (i.e. via home-range analysis, stagwatching and
nest box checks: Dobson 2002; Beyer 2003; Sharpe and Goldingay 2007). Thus, it could be determined whether nearby or interacting gliders belonged to the same or different groups.

The sugar glider was present at all sites except MP. This enabled comparison of the calling rates of both species. Sugar glider vocalisations were recorded and documented in the manner described above.

5.2.3. **Playback experiment**

Call playback experiments were conducted at all study sites except KK, plus an additional site on private land at Larnook, northern NSW. Calls were broadcast in known home-range areas, particularly within core areas when these were known (e.g. Sharpe and Goldingay 2007). The protocol for call playback consisted of a 2 min settling period followed by a 10 min listening period. Then 1–2 min of squirrel glider call broadcast (a repeated nasal grunt) was conducted using the commercial CD of Stewart (1998). This call was recorded in northern NSW about 8 km from BNR (D. Stewart, personal communication). These calls were broadcast through a 9 V megaphone at an intensity that would enable them to be audible to human listeners at a distance of about 50 m. This distance was chosen to target individual home-ranges, rather than the broader population. Following the broadcast, there was another 10 min listening period and then 5 min of spotlighting in the immediate area (i.e. about 30 m around the broadcast location). Any calls heard or gliders seen during these events were documented in relation to the playback sequence.

5.3. **Results**

5.3.1. **Call types**

A total of 208 squirrel glider calls were recorded during 465 h of observation across the five study sites (Table 5.1). A number of different vocalisations were produced, which could be readily distinguished and were mostly produced in different contexts (Table 5.1). Some calls were variable and their characteristics sometimes changed within the same call sequence.

The most common call produced by the squirrel glider at all study sites (e.g. 36% of calls at MP, 88% at BNR and 56% overall, including responses) was a monosyllabic or polysyllabic nasal grunt (Table 5.1). However, the nasal grunt occurred infrequently (about 0.3 h⁻¹ at BNR, BNP/SF, MP and 0.08 h⁻¹ at KK) (Table 5.1). During whole-night observations at MP, calls were only heard on 23% of nights from focal individuals and on 55% of nights (n=22) from the sampled population. Nasal grunts were heard on 26% (n=61) of nights at BNR.
Table 5.1: The frequency of different call types made by squirrel gliders at the five study sites.

Varied calls are described in text. Values show the number of calls (including multiple callers) of each type detected during observations at each site. Numbers in brackets are the overall rate of calls per hour. † Does not include calling during handling events. * Heard during a lace monitor predation event. MP=Minnippi Parklands, KK=Karawatha/Kuraby, BNR=Bungawalbin NR, BNP/SF=Bungawalbin NP and Bungawalbin SF.

<table>
<thead>
<tr>
<th>Call Description</th>
<th>Presumed Function</th>
<th>MP</th>
<th>KK</th>
<th>BNR</th>
<th>BNP/SF</th>
<th>Overall</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Hours of observation</td>
<td>160.5</td>
<td>90</td>
<td>138.0</td>
<td>76.8</td>
</tr>
<tr>
<td>“Na” (nasal grunt)</td>
<td>Individual spacing (inter-group)</td>
<td>46 (0.29)</td>
<td>7 (0.08)</td>
<td>44 (0.32)</td>
<td>20 (0.26)</td>
<td>117 (0.25)</td>
</tr>
<tr>
<td>“Chibur” (growl) †</td>
<td>Threat</td>
<td>22 (0.14)</td>
<td>0 (0)</td>
<td>3 (0.02)</td>
<td>4 (0.05)</td>
<td>29 (0.06)</td>
</tr>
<tr>
<td>Droning “rar-rar” †</td>
<td>Elevated threat</td>
<td>6 (0.04)</td>
<td>0 (0)</td>
<td>1 (0.01)</td>
<td>0 (0)</td>
<td>7 (0.02)</td>
</tr>
<tr>
<td>Hisses (“shhht”) †</td>
<td>Extreme threat</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>1 (0.01)*</td>
<td>0 (0)</td>
<td>1 (&lt;0.01)</td>
</tr>
<tr>
<td>“Tsk”</td>
<td>Intragroup contact</td>
<td>11 (0.07)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>11 (0.02)</td>
</tr>
<tr>
<td>Gliding Gurgles</td>
<td>Individual contact</td>
<td>2 (0.01)</td>
<td>0 (0)</td>
<td>1 (0.01)</td>
<td>0 (0)</td>
<td>3 (&lt;0.01)</td>
</tr>
<tr>
<td>Varied calls</td>
<td>Unknown</td>
<td>40 (0.25)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>40 (0.09)</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td>127 (0.79)</td>
<td>7 (0.08)</td>
<td>50 (0.36)</td>
<td>24 (0.31)</td>
<td>208 (0.45)</td>
</tr>
</tbody>
</table>

The more prevalent monosyllabic nasal grunt (Table 5.2) can be described as a nasal “na”. This form alone comprised 89% and 78% of all nasal grunt call events (excluding responses) at BNR and MP, respectively (Table 5.2). The nasal grunt also had a number of two-note variations (i.e. “na-na”, “na-when”, “na-twang”). The two-note calls sometimes comprised a complete call sequence, but were also heard in call sequences that began with the monosyllabic form (six times at MP, once at BNR) (Table 5.2). Rarely, the two-note variations extended into a short continuous staccato bark (i.e. “na-na-na-na”) that was repeated at least several times. The staccato bark was only ever heard as a transition (once each at both BNR and MP); it never comprised an entire call event (Table 5.2). Transitions were heard during 8% of occasions calls were heard at MP and 6% at BNR (Table 5.2). Nasal grunts ranged from a single call to a long sequence of up to 20 min repeated at intervals of 3–8 seconds, with occasional longer intervals. The mean duration of the grunt call and its polysyllabic variants at MP, where calls were timed with high accuracy, was 2.1±0.6 min (n=46) (Fig. 5.1).

At MP, 59% of 39 call events involving nasal grunts occurred when at least one other glider (up to four) was known to be present within 30 m of the calling individual. This includes four occasions a glider called when an individual nearby changed trees (three times into the focal animal’s tree and once adjacent to it). These interactions occurred between members of different groups, but did not involve aggression. No predators (e.g. owls) were ever observed.
Stationary gliders typically produced nasal grunt vocalisations \((n=13)\), but moving individuals also made this call \((n=3)\). Females at MP made 73% of the grunt calls where the gender of the individual was identified (Table 5.3) even though observational effort was roughly equivalent between the sexes.

**Table 5.2: Frequency of nasal grunt call variations and the number of times another glider responded at Bungawalbin NR and Minnippi Parklands**

Call events refers to the number of times a call variation was recorded irrespective of the number of gliders calling. Numbers in brackets refer to the number of gliders in multiple call events. * referred to as call transitions in text and represent a change between related calls within a call sequence by at least one glider. † only one glider made the complete transition between the three sub-forms.

<table>
<thead>
<tr>
<th>Site</th>
<th>Call Duration (min)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Fig. 5.1:</strong> The duration of nasal grunt calls produced by squirrel gliders at Minnippi Parklands. Call duration is shown to the nearest whole minute.</td>
<td></td>
</tr>
</tbody>
</table>
Table 5.3: Frequency of different call types by sex at Minnippi Parklands.
Unknown is where the gender of the caller was not known.

<table>
<thead>
<tr>
<th>Call Type/Presumed Function</th>
<th>Male</th>
<th>Female</th>
<th>Unknown</th>
<th>Total Detected</th>
</tr>
</thead>
<tbody>
<tr>
<td>“Na” (Individual spacing, between groups)</td>
<td>4</td>
<td>11</td>
<td>24</td>
<td>39</td>
</tr>
<tr>
<td>“Chibur” (threat)</td>
<td>3</td>
<td>1</td>
<td>15</td>
<td>19</td>
</tr>
<tr>
<td>“Tsk” (Individual contact, within group)</td>
<td>2</td>
<td>4</td>
<td>5</td>
<td>11</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>9</strong></td>
<td><strong>16</strong></td>
<td><strong>41</strong></td>
<td><strong>82</strong></td>
</tr>
</tbody>
</table>

The nasal grunt appeared to affect the behaviour of the receiving individual to distances of at least 30 m. On three occasions at MP a glider stopped feeding and listened when another glider began to call nearby, with one individual also leaving a flowering tree. While the onset of calling by one individual caused another to stop calling on one occasion, conspecifics responded five times (13%) at MP. Call responses occurred on three (9%) occasions at BNR. Call transitions appeared to be more likely when there were call responses, although the sample size was small (Table 5.2). On one occasion, two calling gliders approached to 3 m of one another before a chase occurred.

The next most common vocalisation was a droning call that could typically be syllabised as “chibur” and was heard on a total of 29 occasions (Table 5.1). On two of these occasions “panting” noises preceded this call (see also Kavanagh and Rohan-Jones 1982). The “chibur” call was usually repeated at least several times (mean duration at MP, 22 sec; range 1–120 sec, n=22). Squirrel gliders also produced a droning “rar-rar” lasting 2–10 sec, which was heard on seven occasions (Table 5.1). Both calls were typically accompanied by scuffles and/or chases between members of different groups (n=8, which was 100% of both calls when the interaction was clearly observed). During interactions involving these calls it was usually difficult to determine which (or whether both) gliders were making the calls and the caller was definitively identified on only four occasions (Table 5.3). Gliders used the “chibur” and droning “rar-rar” as responses to the alternate call on one occasion each at MP. Both calls, but particularly the droning “rar-rar”, were frequently heard when squirrel gliders were handled (>200 times) and when a squirrel glider was preyed on by a lace monitor (*Varanus varius*) at BNR. At these times, the calls were often interspersed with hisses (“shhht”). “Chibur” calls were heard on two occasions at MP and once at BNR just before gliders emerged from their dens.
A soft “tsk” was heard on eleven occasions at MP (Table 5.1), as both a single call (n=4) and a double call (i.e. “tsk-tsk”, n=7). This call was produced upon contact between group members. Three females, two males and one juvenile (gender unknown) were identified as callers. Soft gurgling calls were heard twice at MP and once at BNR while individuals were gliding between trees. No conspecifics were known to be present at BNR (within >30 m), but were present on both occasions at MP. At MP, gliders were observed to make a variety of soft calls a total of 23 times. These were described as “yips” or “yaps” (13 occasions), “squeaks” (4), “bleeps” (2), “buzzes” (2), a soft “wrrt, wrrr” (1) and a “gasp” (1). The significance of these calls is unclear. The soft “yap” calls were audible only over very short distances (about 20 m) and are unlikely to be confused with sugar glider vocalisations.

5.3.2. Factors influencing call frequency

At BNR, the rate of nasal grunt calls varied from 0 to 2.3 h\(^{-1}\) (overall 0.32 h\(^{-1}\)) within each survey period, with no calls detected in 50% of 16 survey periods over 5 years (Fig. 5.2). Glider density over the five years varied from 0.18 to 0.87 ha\(^{-1}\) (Chapter 2). The relationship between population density and the number of call events (i.e. the number of separate times at least one glider called) (F\(_{1,13}=6.23, \ p=0.03, \ r^2=0.32\)) and call rate (the total number of individuals calling, thus allowing for two or more gliders calling simultaneously) (F\(_{1,13}=5.61, \ p=0.03, \ r^2=0.30\)) were both significant.

![Call rate comparison](image)

**Fig. 5.2:** Comparison of the call rate between squirrel gliders (nasal grunt) and sugar gliders (“yap”) at Bungawalbin NR. Data were gathered during field trips of 3–7 nights, with 2.0–3.5 h of observation per night. All individuals were included when there were multiple callers.
BNR and MP had marked differences in population density (mean 0.42 ha\(^{-1}\) and 1.3 ha\(^{-1}\) throughout the respective survey periods: Goldingay et al. 2006; Chapter 2) and, accordingly, the number of nasal grunt calls per glider \(\chi^2_1=27.29, p <0.001\) and the corresponding number of call events \(\chi^2_1=20.99, p <0.001\) was markedly higher at BNR (Table 5.2). However, there was no difference in the nightly frequency of nasal grunt calls \(\chi^2_1=0.07, p=0.79\) or call events (i.e. when one or more gliders called together) \(\chi^2_1=0.05, p=0.82\) between these sites when observational effort was used to generate expected frequencies (Table 5.2). There was a significant difference in the frequency of aggressive calls (“chibur” and droning “rar-rar”) between these sites \(\chi^2_1=11.63, p=0.001\), with more such calls recorded at MP when expected frequencies were based on observational effort (Table 5.1). When density was considered instead, the difference between the sites was not significant \(\chi^2_1=2.09, p=0.15\).

Responses to nasal grunt calls were infrequent, being heard five times at MP (13\%) and three times at BNR (9\%). Five of the eight responses occurred at times when call transitions also occurred (Table 5.2). The occasions of multiple calls generally involved two individuals (four times), but up to four called at MP. Calling gliders were within 40 m of one another. At BNR, two gliders called simultaneously twice (spacing \(\leq 30\) m) and there was one occasion when at least eight (though probably more) gliders called concurrently from an area of at least 3 ha (Table 5.4). At the time of the latter event, the population density was at a five-year high (Chapter 2). Multiple callers (spaced \(\leq 50\) m apart) were heard at BSF on four occasions (Table 5.4).

Time of night did not appear to exert any clear influence on the frequency of nasal grunts or other calls at MP (Fig. 5.3). There were many periods of the night when no calls were emitted by the focal animal, and the hourly frequency of calls by focal and non-focal animals was highly variable. While there appeared to be some evidence that season may affect calling rates (Fig. 5.4), the high variance produced a non-significant result for both nasal grunts \(F_{26,266}=0.79, p=0.76\) and other calls \(F_{26,266}=1.20, p=0.23\). Eight of nine “tsk” call events occurred in November, coinciding with the period that juvenile gliders began to forage independently and frequent close social contact between group members outside the den was observed.
Table 5.4: Comparison of calls by squirrel gliders and sugar gliders in sympatry.  
The number of call events (scored as 1 irrespective of the number of calling individuals) and number  
of calling gliders (when >1 glider calling) are shown.

<table>
<thead>
<tr>
<th>Site</th>
<th>Squirrel Glider</th>
<th>Sugar Glider</th>
</tr>
</thead>
<tbody>
<tr>
<td>BNR</td>
<td>44</td>
<td>35</td>
</tr>
<tr>
<td>BNP</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>BSF</td>
<td>12</td>
<td>6</td>
</tr>
<tr>
<td>KK</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>Total</td>
<td>70</td>
<td>55</td>
</tr>
</tbody>
</table>

![Graph showing call events by hour of the day](image)

**Fig. 5.3:** Mean (+s.e.) number of calls per hour by time of night pooled across seasons at Minniippi Parklands. Data for nasal grunts and all other calls pooled are given. F=focal animal, NF=individuals other than focal animal. Note, sunset varied from 17:02 h to 18:14 h and sunrise varied from 4:58 h to 6:38 h.

5.3.3. **Comparison with sugar glider calls**

Sugar gliders were sympatric with the squirrel glider at BNR, BNP BSF and KK. The calls of both species were recorded at all four sites. Squirrel glider nasal grunts were more common than sugar glider “yaps” at most sites and more calls of the former were recorded overall (Table 5.4). Both species had numerous occasions where more than one individual called and the maximum duration of the “yap” call was also about 20 min (at BNR). Vocalisations involving more than one glider comprised 15% of all call events for the squirrel glider compared to 25% for the sugar glider. Highly synchronised calling from multiple individuals was recorded for both species (Table 5.4). The “yap” was the most common sugar glider call.
heard at BNR (95%). Other vocalisations included the droning “rar-rar” and “chibur” when removed from traps and during a second lace monitor predation event. The “chibur” call was heard spontaneously on one occasion.

The density of sugar gliders (mean MNA estimate 1996–2001: 0.18 ha\(^{-1}\), range 0.10–0.58 ha\(^{-1}\)) was known to be about one half that of squirrel gliders at BNR (Chapter 2). Squirrel glider nasal grunts occurred more frequently than sugar glider “yaps” at BNR (\(\chi^2=9.92, p=0.002\)), but there was no difference between the relative frequency of calls when the respective population sizes were accounted for (\(\chi^2=0.29, p=0.59\)) (Table 5.4). Unlike squirrel gliders, sugar glider call rates did not show a significant relationship with population density over the five-year study, although there was a weak trend in this direction (\(F_{1,12}=2.19, p=0.16, r^2=0.16\)). However, both species showed similar patterns of call frequency during the various survey periods (Fig. 5.2). The mean duration of sugar glider calls (6.0±2.6 min, \(n=7\)) was longer than for the squirrel glider (see above).

![Fig. 5.4: Mean (+s.e.) number of calls per night for months representing winter, late spring, and autumn at Minnippi Parklands. Night length varied by season: June (13.6 h), Nov (10.6 h), April (12.4 h). F=focal animal, NF=individuals other than focal animal.](image-url)
5.3.4. Call playback

Squirrel glider vocalisations were broadcast a total of 21 times across five sites. Only two (10%) broadcasts elicited a response, although gliders were observed immediately before or after the broadcast on 13 (62%) occasions (Table 5.5). Thus, the percentage of responses to call playback was similar to that observed from spontaneous calling. On one occasion, two squirrel gliders that were calling during the initial listening stopped for the duration of the broadcast. Both gliders recommenced calling about 3 min after the listening period finished.

Table 5.5: Responses of squirrel gliders to call broadcast.

* Two gliders calling before and after one playback experiment but stopped during the broadcast and listening period. Sqg=squirrel glider. The number of times at least one squirrel glider was visually observed during a survey is given. Core home-ranges at Minnippi Parklands and Bungawalbin NR were determined by radio-tracking (Dobson 2002; Sharpe and Goldingay 2007).

<table>
<thead>
<tr>
<th>Site</th>
<th>Context</th>
<th>No. Surveys</th>
<th>No. Responses</th>
<th>No. Times Sqg Observed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Minnippi Parklands, Brisbane</td>
<td>Near occupied nest boxes in core home-range</td>
<td>3</td>
<td>0*</td>
<td>3</td>
</tr>
<tr>
<td>Bungawalbin NR</td>
<td>Amongst flowering coast banksias in core home-range</td>
<td>6</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Bungawalbin NP</td>
<td>Near flowering trees</td>
<td>6</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Bungawalbin SF</td>
<td>Near flowering trees</td>
<td>4</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Private land, Larnook NSW</td>
<td>Near flowering tree</td>
<td>2</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td><strong>21</strong></td>
<td><strong>2</strong></td>
<td><strong>13</strong></td>
</tr>
</tbody>
</table>

5.4. Discussion

5.4.1. Call types and calling pattern

A nasal grunt was the most common vocalisation emitted by the squirrel glider at the study sites. This call has also been heard at a substantial number of additional sites (>15) across north-east NSW and south-east QLD (the authors’, unpublished observations), indicating that it is used widely in the region. The nasal grunt is likened to the short call of the yellow-bellied glider (Davey and Russell-Smith 1984; R. Goldingay unpublished observations). It may be heard over at least 200 m, qualifying it as a loud call (Goldingay 1994). This call may occur in monosyllabic and polysyllabic forms and have a duration ranging from 1 sec to 20 min. The nasal grunt of the squirrel glider is similar to the call of the mahogany glider (R. Goldingay, unpublished observations), described as “na-when” (Van Dyck 1993).

The nasal grunt was only emitted 0.5–2 times per night by a focal individual or an average of 0.3 times per hour by multiple individuals. Its use was highly variable among nights. Sugar
glider populations in this study produced no more than 1–2 “yap” calls per night during spotlighting, but these calls may occur much more frequently at some sites (Goldingay 1994; the authors’, unpublished observations). Mahogany gliders averaged one call per night during 455 h (36 nights) of focal animal observation (Jackson and Johnson 2002). In contrast, individual yellow-bellied gliders called over 60 times per night or 2–16 times per hour from multiple individuals (Goldingay 1994).

Responses to the nasal grunt occurred infrequently, though in some instances a number of squirrel gliders (up to at least eight) called. Transitions to double calls and staccato barks were more likely to occur when there were multiple callers, suggesting that these variations of the nasal grunt are reflective of a heightened emotional state in the caller (Seyfarth and Cheney 2003; Simeonovske-Nikolova 2004; Gros-Louis et al. 2008) rather than being distinct calls serving a different function. While mahogany gliders rarely answered conspecifics (Jackson and Johnson 2002), calling by the sugar glider can be highly synchronised at some sites (Goldingay 1994; unpublished observations). The yellow-bellied glider, however, frequently answers conspecifics and readily responds to call playback (Goldingay 1994). The calling behaviour of the three smaller petaurids has similarities that suggest their loud calls may perform a common function, which differs to that of the yellow-bellied glider.

The “chibur” and droning “rar-rar” calls were produced in situations that clearly involved threat. Transitions between these calls further suggest a common function. When it was possible to observe individuals emitting these calls at night, both types involved scuffles and/or chases between members of different groups. “Chibur” calls were heard several times just before emergence from the den, indicating that it is sometimes directed towards group members. The yellow-bellied glider’s “growl” is directed toward other gliders, including group members while entering or leaving the den (Kavanagh and Rohan-Jones 1982). Moreover, squirrel gliders and yellow-bellied gliders were both heard to use the “chibur” call to exclude sugar gliders from flowering swamp mahogany trees at BNR in July 2000 (D. Sharpe, unpublished observations). In southern NSW, a sugar glider emitted a droning “rar-rar” call after capture by hand at night and two conspecifics approached the location of the calling individual (R. Goldingay, unpublished observations). Whereas threatening calls were common while handling captured squirrel gliders (the authors’, unpublished observations), spontaneous threatening calls were infrequent. Further understanding of these calls may be obtained by playback experiments.
Minnippi Parklands had a high population density during this study and was the only site where threatening calls directed towards conspecifics were regularly heard during nocturnal observations. Pursuit coupled with tail and rump biting is a typical form of aggressive behaviour amongst petaurids (Smith and Lee 1984; Klettenheimer-Salamon 2000). At least 28 gliders at MP were found to have fur on the tail, sometimes extending to the rump, closely cropped in a manner consistent with biting during regular conflicts. The remainder of the fur appeared normal. Of these, 68% were >2 years old, with the remainder 1–2 years (D. Sharpe, unpublished data). Similarly cropped fur has not been observed at any other sites (authors’, unpublished observations).

A soft “tsk” was used at MP upon contact between gliders from the same social group and has also been reported in the common ringtail possum (*Pseudochirus peregrinus*) (Biggins 1984) and the greater glider (*Petauroides volans*) (Henry 1984). The group contact call of the yellow-bellied glider has been described as a clicking sound (Russell 1984).

5.4.2. Function of loud calls in the squirrel glider

Waser (1977) proposed a set of seven potential functions for the loud calls of primates, which can be used to investigate the potential role of the squirrel glider’s nasal grunt. The functions are: i) the maintenance of intragroup cohesion, ii) the maintenance of group size and composition, iii) the attraction of potential mates, iv) the maintenance of exclusive access to mates, v) to advertise the location of food resources to group members, vi) to coordinate group movements while foraging, and vii) to maintain territories or to provide other forms of inter-group spacing. A further function was added to this list, which is to alert conspecifics to the presence of a predator.

The squirrel glider loud call does not appear to maintain intragroup cohesion or group size and composition. Squirrel gliders live in small family groups that share communal tree hollows (Quin 1995; Traill and Lill 1997; van der Ree 2002; Sharpe and Goldingay 2007; Beyer *et al.* 2008). Males possess well-developed scent glands and transfer scent to other group members (D. Sharpe, unpublished observations) as occurs in the sugar glider (Schultze-Westrum 1969; Stoddart and Bradley 1991) and the yellow-bellied glider (Russell 1984). This gives rise to a group-specific scent that is postulated to create intragroup cohesion (Schultze-Westrum 1969; Russell 1984). Group size is determined by patterns of breeding (i.e. monogamous/polygamous) and juvenile dispersal (Quin 1995; van der Ree 2002; Chapter 2).
The primary function of the loud call is not to attract potential mates because it is emitted by individuals within stable breeding groups. If the function of the nasal grunt were to maintain exclusive access to mates, one would hypothesise that calls would be given more frequently by one sex and that individuals of the opposite sex would be observed approaching the callers (Mitani 1985a). Although females produced nasal grunts more commonly than males, they occurred irrespective of whether females were in oestrous. Moreover, it was rare to see other gliders closely approach calling individuals; indeed, the opposite seemed to occur.

The patterns of dispersion and rates of renewal of different food types suggest that loud calls do not serve to advertise the location of food resources to group members. Squirrel gliders feed on arthropods and plant and insect exudates (Menkhorst and Collier 1987; Sharpe and Goldingay 1998; Dobson et al. 2005; Holland et al. 2007). Arthropods are widely scattered and occur at relatively low local abundance, so it would be ineffective for gliders to use calls to advertise their location. Exudates, on the other hand, have highly clumped spatial distributions but relatively long periods of availability (e.g. many days or weeks) and so would not require calling on a nightly basis (Goldingay 1994). Calling rates of the squirrel glider were low (0.3 calls h\(^{-1}\), or calls on 23-55% of nights) but higher than would be needed to advertise the changing location of exudate food resources. There were no occasions when a calling individual attracted group members to food resources, such as flowering trees, although group foraging was observed (D. Sharpe, unpublished data).

The loud calls were given too infrequently to coordinate group foraging movements. Squirrel gliders may visit >6 flowering trees per night when nectar feeding (D. Sharpe, unpublished data), which would require more than 1–2 calls per night if coordinating the movements of group members through home-ranges that average about 7 ha (Sharpe and Goldingay 2007). Nasal grunts at BNR were strongly associated with the use of small stands of flowering coast banksia trees, which were often used concurrently by group members (Sharpe and Goldingay 2007). This would obviate the need for calling to coordinate movements. Moreover, on several occasions at MP the majority of gliders in a group moved quickly between flowering trees without vocalising (D. Sharpe, unpublished data).

Could loud calls function to alert conspecifics to the presence of a predator? The sugar glider “yap” call has been suggested to be a predator alarm call (Biggins 1984; Suckling 1995; Traill 1998), but this conclusion remains speculative. During the present study, owls were never observed while squirrel gliders were calling. The only owl detected at MP was the southern
boobook (*Ninox novaeseelandiae*). Squirrel gliders foraged unperturbed in close proximity to this species. In central northern Victoria, powerful owls (*Ninox strenua*) and barking owls (*Ninox connivens*) preyed upon squirrel gliders (van der Ree 2002), but nasal grunts were not reported (R. van der Ree, personal communication). Thus, the nasal grunt does not appear to function as an alarm call.

The final function hypothesised for loud calls is to maintain territories or to provide other forms of inter-group spacing. The yellow-bellied glider has large, exclusive home-ranges (up to 120 ha) (Goldingay and Kavanagh 1993; Goldingay and Quin 2004), while mahogany gliders have minimal overlap (11%) between group home-ranges which are about 23 ha (Jackson 2000b). This seems to suggest that these species are territorial. The smaller sugar glider and squirrel glider have home-ranges of only 2–7 ha that overlap considerably with adjacent groups (Suckling 1984; Quin 1995; Sharpe and Goldingay 2007). Home-range overlap in the squirrel glider is about 50%, but core areas are used exclusively (Quin 1995; Sharpe and Goldingay 2007).

Following squirrel gliders for whole-night periods at MP revealed that the nasal grunt was infrequent and interspersed throughout the night with no obvious period when calls were more likely. This pattern contrasts markedly with that of the yellow-bellied glider, which vocalises frequently throughout the night but has a heightened period of calling early in the night. The distribution of yellow-bellied glider calls is expected for a species that defends its entire home-range area (Goldingay 1994). Geissmann and Mutschler (2006) observed that calling by indris (*Indri indri*) was more frequent over a few hours early in the active period whereas calling by ruffed lemurs (*Varecia variegata*) was less frequent but spread more evenly across the day. They postulated that this supported a territorial function in indris, but an inter-group spacing, alarm or intra-group coordination role in ruffed lemurs. A more irregular distribution of calls would indicate less predictable stimuli such as associated with alarm or if foraging paths by conspecifics are not predictable. Irregular calling by squirrel gliders is not consistent with a territorial function.

When nasal grunts were produced it was typical to observe non-group members in the vicinity of calling gliders. This supports the hypothesis that this call regulates inter-group spacing by functioning as an immediate warning to facilitate mutual avoidance. Calling for this reason would not need to occur frequently or at any particular time as it would occur on the basis of need. At other times, scent marking or simply a physical presence may be sufficient to
maintain individual spacing. During call events, the recipient may respond by moving away from the calling individual, while more motivated recipients may react by calling in response. This latter situation can apparently lead to an escalation of emotional intensity resulting in call transitions. Furthermore, calling would be expected to be more frequent at higher population densities, due to the increased chance of encountering conspecifics.

If higher population density promotes higher rates of calling, why was there no difference in the rate of calling between two sites of contrasting density, BNR and MP? At MP, resources were spread relatively evenly throughout the remnant, whereas at BNR the winter nectar resource (coast banksia) was concentrated into a relatively small area, resulting in intensive use of this habitat and therefore high local population density while foraging (Sharpe and Goldingay 2007). Most of the nasal grunts at BNR were produced when gliders were using the banksia habitat and more calls per individual glider ensued.

At a high-density site in central Victoria (van der Ree 2002) squirrel glider calls were rarely heard (R. van der Ree, personal communication). The gliders in this population occupied relatively exclusive home-ranges (mean overlap 14%) that were mostly comprised of narrow linear habitat along roadside reserves (van der Ree and Bennett 2003). Such home-ranges would only require defence at each end, minimising contact between members of adjacent groups. Thus, there would be little need to regulate spacing via calls. The lack of reported calling at other Victorian sites (Traill 1998) may reflect low population densities (Menkhorst et al. 1988).

5.4.3. Conclusions

Detailed observational studies enabled the vocal behaviour of the squirrel glider to be described. This revealed a diverse vocal repertoire and provided contextual information used to infer the function of some call types. The squirrel glider has a vocal diversity similar to its congeners. This study found little support for the use of call playback to elicit calls and facilitate detection.

Sabatini and Ruiz-Miranda (2008) hypothesised for primates that some loud call types first evolved to mediate intra-group spacing and were later selected for territorial advertisement. The contrast in the pattern of irregular calling by the squirrel glider and no response to call playback, compared to the highly regular calling by the yellow-bellied glider and strong response to call playback, lends support to this hypothesis. The lack of calls by squirrel
gliders on some nights and the proximity of non-group individuals to calling individuals suggest that loud calls serve an inter-group spacing function. This function appears to be an evolutionary precursor to a more elaborate function of calling in territorial defence.
6. **TIME BUDGET OF THE SQUIRREL GLIDER (**Petaurus norfolcensis**) IN AN URBAN REMNANT, BRISBANE**

6.1 **Introduction**

Time budget studies examine the strategies used by an animal to acquire energy and nutrients for activities associated with survival and reproduction (e.g. Miller *et al.* 2006; Henry and Kalko 2007; Chipman *et al.* 2008). An animal’s diet has one of the most important influences on its time budget (Nagy and Martin 1985; Goldingay 1989a, 1990; Kenagy *et al.* 1989; Byrne *et al.* 1993; Gelatt *et al.* 2002). This is because different foods have different distributions in space and time as well as different nutritional and digestive properties (Hume 1999; Whelan and Brown 2005). Such factors suggest time budget studies should show the optimal strategy of time allocation for a specific diet (Schoener 1971).

Jackson and Johnson (2002) suggested that the proportion of time an arboreal marsupial devotes to feeding should increase with body weight amongst exudate/insect feeders, but decrease in folivores. Although not explained, the former may derive from the recognition that larger species have higher absolute energy requirements (McNab 1986a,b) and because body size may not confer a food harvesting advantage for an exudivore/insectivore (Smith and Russell 1982; Quin 1993). Amongst folivores, the reverse trend can be explained by the increased digestive efficiency of larger body size (Hume 1999). As further studies accumulate it remains worth asking whether larger exudivores spend a greater proportion of time feeding than smaller species or whether other factors mitigate the need for longer foraging bouts.

Petaurid gliders feed on plant and insect exudates, such as nectar, sap, *Acacia* gum and honeydew, while arthropods and pollen are consumed for protein (Smith 1982; Goldingay 1986, 1990; Menkhorst and Collier 1987; Howard 1989; Quin 1993; Sharpe and Goldingay 1998; Jackson 2001; Dobson *et al.* 2005; Holland *et al.* 2007). Previous studies have shown that feeding and associated behaviours dominate the time budgets of petaurid gliders (Jackson and Johnson 2002). The largest exudivore, the yellow-bellied glider, spends about 90% of its active time foraging, which is the highest foraging rate reported for any mammal species (Goldingay 1989a, 1990). There has been one time budget study completed on each of the other petaurids (Quin 1993; Jackson and Johnson 2002; Holland *et al.* 2007). None of the preceding time budget studies were designed in a way that was amenable to the quantitative analysis of factors that may affect behavioural decisions.
The only time budget study of the squirrel glider (Holland et al. 2007) was undertaken toward the southern extreme of its range and observations were not conducted over whole night periods. This study aimed to provide an additional time budget for the squirrel glider based on whole night observations in a different part of its range and to explore some factors that may influence time utilisation. The time budgets of the different-sized petaurid gliders was also examined in relation to the energetic constraints of exudivore/insectivore feeding niche.

6.2 Methods

6.2.1 Study Site

This study was conducted at Minnippi Parklands (27°28’S 153°06’E), a forest remnant located within an urban matrix <10 km from Brisbane’s CBD in eastern Australia (Goldingay and Sharpe 2004a). Minnippi Parklands totals 323 ha in area and is made up of several disjunct forest remnants separated by open grassland and mangrove-lined Bulimba Creek. Major roads, medium-density housing, a shopping centre and an industrial estate surround this area. This study focused on a 47 ha patch of open eucalypt forest in the west of Minnippi Parklands (Plate 1.3) containing about 20 tree species, all of which were in the Family Myrtaceae (Dobson et al. 2005). Common species included brush box (Lophostemon confertus), forest red gum (Eucalyptus tereticornis), narrow-leaved red gum (E. seeana), northern grey ironbark (E. siderophloia), scribbly gum (E. racemosa), broad-leaved white mahogany (E. carnea), pink bloodwood (Corymbia intermedia), smooth-barked apple (Angophora leiocalyx) and broad-leaved paperbark (Melaleuca quinquenervia). There was an open understorey comprised of wattles (Acacia spp.) and the exotic species lantana (Lantana camara). Horse and cattle grazing occurred on this site during the study. The population density of squirrel gliders was high (minimum number alive 1.3–1.6 ha⁻¹) during the study (Goldingay et al. 2006).

6.2.2 Sampling Strategy

Radio-collars were attached to the first six adult male and six adult female gliders captured prior to each seasonal study period, resulting in some overlap in individual gliders. Radio-collared gliders belonged to different social groups (achieved in all but two cases). These gliders were radio-tracked during each of three study periods: mid winter (June 2002), late spring (November 2002) and mid autumn (April 2003). This approach provided variation in night length across its maximum range by conducting sampling near the two solstices and near the autumn equinox. Within each of these study periods the sampling was also evenly divided between the new and full moon. Data on sunset, sunrise and moon phase times for
Brisbane were obtained from Geoscience Australia (2002). Data were collected on the reproductive status of radio-collared females. Although six males and six females were collared per season, collar failure (due to the gliders damaging their collars or battery failure) meant that there was the full complement of individuals in only 6 of the 12 sessions. Gliders were re-collared between the paired sessions, so only one session had <10 gliders (3 males, 5 females on the summer new moon).

Throughout the study, individual collared gliders were each followed for about one hour per observation period, but the final observation period of each night was longer to ensure retirement times were documented. The first glider to be radio-tracked on each night was randomly chosen and the sequence then alternated between male and female gliders. This approach was repeated over a total of six nights in winter and eight nights during the other two periods. Each night’s observations commenced with a den watch to determine the onset of the activity period and finished once it was assured that gliders had returned to their dens in hollow-bearing trees for the day, marking the end of the activity period. Den occupancy was confirmed by a diurnal den fix taken later that day. A red-masked spotlight and 10 × 50 binoculars were used to observe gliders.

To define the length of the activity period, the time gliders emerged from or retired to their dens was documented relative to sunset and sunrise respectively. The following behaviours were observed: feeding (nectar, honeydew/lerp, random arthropod searching: see Dobson et al. 2005), returning to the current diurnal den between feeding bouts, climbing, gliding between trees, resting grooming, social interactions (mutualistic, aggressive, calling) and disturbed from feeding by another species, such as possums and flying-foxes (i.e. time spent moving away or remaining stationary). Feeding and movement behaviours were collectively termed foraging (Goldingay 1989a, 1990; Jackson and Johnson 2002; Holland et al. 2007). During each observation period, one behaviour was exclusively assigned to each half-minute interval. Behaviours were documented on audiotape and later transcribed and tallied.

Instances of group foraging were recorded. Group foraging was defined as two or more gliders engaged in the same feeding behaviour in the same tree. The time squirrel gliders spent in individual trees was recorded. Although gliders were not always seen entering and/or exiting trees used for feeding due to a maximum of about 60 min continuous observation, this nonetheless provided a relative index of tree utilisation in relation to the food consumed. During the glider observations, the number of flowers per flowering tree (to the nearest 500
for <5,000 flowers and the nearest 1,000 for ≥5,000 flowers) was estimated. The size (diameter at breast height, DBH) of trees used for honeydew/lerp feeding was also estimated.

6.2.3. Comparison of Petaurid Time Budgets

Time budgets and concurrent home-range estimates of petaurid gliders were derived from Goldingay (1989a, 1990, 1992), Goldingay and Kavanagh (1993), Quin (1993), Jackson (2000b), Jackson and Johnson (2002), Dobson (2002), van der Ree and Bennett (2003) and Holland et al. (2007). The home-range areas and percentage of the activity period used for various behavioural categories were compiled, enabling comparisons across the four gliding species.

6.2.4. Statistical Analysis

To account for differences in the exact duration of each observation period and to enable comparisons between petaurid time budget studies, all half-minute observations were summed and the value for each behaviour was converted to a proportion of the total number of half-minute intervals in each observation period. Binary logistic regression models (Rasbash et al. 2002) were fitted to each of the response categories assuming an extra-binomial distribution using MLwiN 2.02 (http://www.cmm.bristol.ac.uk/index.shtml). Quasi-maximum likelihood methods (Goldstein 2003) were used to explore the data to assess the effects of night length, moon phase and gender using the behavioural categories described above. The parameter estimates and their standard errors from the resulting models were used to construct estimates of the probability of each behaviour for each of the three factors and their combinations with a 95% confidence interval.

Models were assessed by first examining the 3-way interactions (season, moon phase, gender) for significance. If the 3-way effect was not significant a reduced model was constructed using the following procedure: first the 3-way effect was removed and the procedure then applied to the 2-way interaction effects (removing the most non-significant effect first), and finally non-significant main effects were removed if necessary. In all cases, each of the possible parameterisations of an effect was tested for significance using the Wald test ($\chi^2_1=\left(\text{parameter estimate/s.e.}\right)^2$) (Goldstein 2003). If any one of the parameter combinations for an effect was significant the effect was retained in the model, otherwise it was removed. Once the candidate model was determined selected comparisons and tests of fixed factors were constructed as Wald tests using the intervals and tests procedure in MLwiN. Fixed factors were added (weighted as appropriate) and/or subtracted to construct the required tests.
Emergence and retirement times were log-transformed and tested using a General Linear Model (GLM) to assess the effect of season and moon phase. Tukey's honestly significant difference was used to make post hoc comparisons. Chi-squared analysis or a G-test was applied to the frequency of group foraging observations and used to test the effect of food type and season. To assess the influence of time of night on the incidence of group foraging, each night was divided into 6 equal proportions between sunset and sunrise, scaled to night length. The size of groups and the duration of tree occupancy when engaged in different feeding behaviours were both examined with a Kruskal-Wallis test. Pairwise Mann-Whitney U tests were used for post hoc testing (Dytham 2003). Linear regression was used to examine relationships between tree size (DBH) or the number of flowers and the length of time spent in trees. The tree duration, DBH and the number of flowers were log-transformed prior to analysis. The home-range, energetic and time budget comparisons, log-transformed as required, of the petaurid gliders were also analysed using linear regression. All these analyses were conducted with SPSS (11.01).

6.3. Results
6.3.1. Activity Patterns
Squirrel gliders were observed for 160.5 hours (Table 6.1). They were strictly nocturnal, emerging shortly after sunset and retiring before sunrise (Table 6.2). Thus, night length can be used to define the maximum period available for activity (Table 6.2). The dark phase varied by 181 min across the study (Table 6.2). A GLM revealed that there was no difference between mean emergence and retirement times ($F_{1,94}=1.63$, $p=0.21$) (Table 6.2) and this factor was deleted from the model. Both moon phase ($F_{1,95}=3.80$, $p=0.05$) and season ($F_{2,95}=4.78$, $p=0.01$) affected emergence and retirement times, occurring earlier/later on the new moon and in summer compared to the other two seasons. There was no difference between males and females as all group members tended to emerge within a period of several minutes. Retirement times were also somewhat coincident. An afternoon thunderstorm apparently delayed emergence by just over 1.5 h on one night in autumn although it had stopped raining before sunset.

During winter and to a lesser extent in autumn, gliders exhibited a bimodal activity pattern, returning to their diurnal dens during the night and re-emerging to resume foraging (see below). This behaviour was considered to be part of the activity period. Thus, a very high proportion of the dark phase, almost 90%, was used as the activity period in all seasons (Table 6.2).
Table 6.1: Time (hours) spent observing squirrel gliders at Minnippi Parklands.

<table>
<thead>
<tr>
<th>Season</th>
<th>Female</th>
<th>Male</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
<td>27.1</td>
<td>20.7</td>
<td>47.8</td>
</tr>
<tr>
<td>Spring</td>
<td>25.6</td>
<td>23.4</td>
<td>49.0</td>
</tr>
<tr>
<td>Autumn</td>
<td>31.3</td>
<td>32.4</td>
<td>63.7</td>
</tr>
<tr>
<td>Moon Phase</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>New</td>
<td>42.4</td>
<td>33.3</td>
<td>75.7</td>
</tr>
<tr>
<td>Full</td>
<td>41.6</td>
<td>43.2</td>
<td>84.8</td>
</tr>
<tr>
<td>Total</td>
<td>84.0</td>
<td>76.5</td>
<td>160.5</td>
</tr>
</tbody>
</table>

Table 6.2: Summary of squirrel glider activity patterns in relation to season.

The difference between feeding and foraging represents the time devoted to gliding and climbing. * percent of time between sunset and sunrise. # length of the activity period (emergence to retirement) minus the amount of time in the den during the night.

<table>
<thead>
<tr>
<th>Season</th>
<th>Winter</th>
<th>Spring</th>
<th>Autumn</th>
<th>Range</th>
<th>Mean</th>
<th>s.e.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean Sunrise</td>
<td>6:38</td>
<td>4:58</td>
<td>6:02</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean Sunset</td>
<td>17:02</td>
<td>18:14</td>
<td>17:39</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean Night Length</td>
<td>816</td>
<td>635</td>
<td>743</td>
<td>181</td>
<td>731.3</td>
<td>52.6</td>
</tr>
<tr>
<td>Mean Emergence</td>
<td>48.5</td>
<td>32.5</td>
<td>35.3</td>
<td>16.0</td>
<td>38.7</td>
<td>4.9</td>
</tr>
<tr>
<td>Mean Retiring</td>
<td>50.1</td>
<td>32.8</td>
<td>30.7</td>
<td>19.4</td>
<td>37.9</td>
<td>6.1</td>
</tr>
<tr>
<td>Percent Dark Phase Active</td>
<td>87.9</td>
<td>89.7</td>
<td>88.6</td>
<td>1.8</td>
<td>88.7</td>
<td>0.5</td>
</tr>
<tr>
<td>Percent Activity Period Feeding</td>
<td>73.5</td>
<td>82.8</td>
<td>78.6</td>
<td>9.3</td>
<td>78.3</td>
<td>2.7</td>
</tr>
<tr>
<td>Percent Activity Period Foraging</td>
<td>78.9</td>
<td>93.4</td>
<td>83.5</td>
<td>14.5</td>
<td>85.3</td>
<td>4.3</td>
</tr>
<tr>
<td>Estimated Time Active (min)</td>
<td>583</td>
<td>560</td>
<td>597</td>
<td>37</td>
<td>580</td>
<td></td>
</tr>
<tr>
<td>Estimated Feeding Time (min)</td>
<td>527.2</td>
<td>471.6</td>
<td>517.4</td>
<td>55.6</td>
<td>505.4</td>
<td>17.1</td>
</tr>
<tr>
<td>Estimated Foraging Time (min)</td>
<td>565.9</td>
<td>532.0</td>
<td>549.7</td>
<td>33.9</td>
<td>549.2</td>
<td>9.8</td>
</tr>
</tbody>
</table>

6.3.2. Female Reproduction

Examination of the females radio-tracked in June revealed four had given birth in March or April and two gave birth in May 2002. Thus, at least four females would have entered late lactation (i.e. when offspring remain in den during adult foraging) during June 2002. Only one female was reproductively active (late lactation with a second litter) during the late spring period of 2002. No reproductive activity by females was apparent during the autumn study period 2003.

6.3.3. Time Budget

Squirrel gliders fed upon exudates (nectar, honeydew, lerp) and arthropods during the study. These feeding behaviours dominated the activity period, occupying 78.3% of the available time averaged across the year (Tables 6.2 and 6.3). When this is added to gliding and
Table 6.3: Estimated percentage of time spent on different behaviours during the study. Values in brackets are the 95% confidence interval. The model that best explains variation in each behaviour is given. Note, because these values are estimates derived from the statistical analysis they total to slightly more than 100%.

S = season, M = moon phase, G = gender

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Overall</th>
<th>Winter</th>
<th>Late Spring</th>
<th>Autumn</th>
<th>New Moon</th>
<th>Full Moon</th>
<th>Females</th>
<th>Males</th>
<th>Candidate Model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nectar</td>
<td>29.6 (20-44)</td>
<td>58.6 (41-74)</td>
<td>28.5 (18-44)</td>
<td>1.6 (0-13)</td>
<td>38.4 (27-53)</td>
<td>20.7 (13-34)</td>
<td>34.6 (25-47)</td>
<td>24.5 (15-40)</td>
<td>S+M+G+SM+MG</td>
</tr>
<tr>
<td>Honeydew/lerp</td>
<td>33.5 (23-51)</td>
<td>0.9 (0-23)</td>
<td>43.3 (28-60)</td>
<td>56.2 (40-71)</td>
<td>30.3 (21-50)</td>
<td>36.6 (25-52)</td>
<td>29.7 (20-45)</td>
<td>37.3 (25-57)</td>
<td>S+M+G+SM+MG</td>
</tr>
<tr>
<td>Exudate</td>
<td>62.6 (43-79)</td>
<td>60.3 (40-78)</td>
<td>71.0 (51-86)</td>
<td>55.7 (39-72)</td>
<td>68.1 (48-83)</td>
<td>56.7 (38-74)</td>
<td>63.9 (45-79)</td>
<td>61.2 (41-78)</td>
<td>S+M</td>
</tr>
<tr>
<td>Arthropods</td>
<td>14.9 (7-33)</td>
<td>13.9 (6-30)</td>
<td>12.1 (5-28)</td>
<td>18.6 (9-41)</td>
<td>12.6 (5-28)</td>
<td>17.1 (8-38)</td>
<td>16.4 (8-31)</td>
<td>13.3 (5-35)</td>
<td>S+M+G+SM+MG</td>
</tr>
<tr>
<td>Feeding</td>
<td>78.3 (62-89)</td>
<td>73.5 (55-86)</td>
<td>82.8 (66-92)</td>
<td>78.6 (64-88)</td>
<td>80.2 (63-91)</td>
<td>76.5 (60-87)</td>
<td>79.3 (64-89)</td>
<td>77.3 (60-89)</td>
<td>S+M+G+SM+SG+MG+SMG</td>
</tr>
<tr>
<td>Gliding</td>
<td>1.5 (1-3)</td>
<td>1.2 (1-2)</td>
<td>2.1 (1-3)</td>
<td>1.1 (1-2)</td>
<td>1.4 (1-3)</td>
<td>1.5 (1-3)</td>
<td>1.3 (1-2)</td>
<td>1.6 (1-3)</td>
<td>S+M+G+SM+MG</td>
</tr>
<tr>
<td>Climbing</td>
<td>5.6 (3-9)</td>
<td>4.2 (2-7)</td>
<td>8.7 (6-13)</td>
<td>3.8 (2-6)</td>
<td>6.3 (4-10)</td>
<td>4.8 (3-8)</td>
<td>4.6 (3-8)</td>
<td>6.6 (4-11)</td>
<td>S+M+G+SM</td>
</tr>
<tr>
<td>Foraging</td>
<td>85.3 (67-94)</td>
<td>78.9 (59-90)</td>
<td>93.4 (76-98)</td>
<td>83.5 (67-92)</td>
<td>87.8 (70-95)</td>
<td>82.7 (65-92)</td>
<td>84.9 (68-93)</td>
<td>85.6 (67-94)</td>
<td>S+M+G+SM+SG+MG+SMG</td>
</tr>
<tr>
<td>Den Return</td>
<td>10.0 (4-31)</td>
<td>18.7 (8-42)</td>
<td>1.8 (0-26)</td>
<td>9.4 (4-27)</td>
<td>8.0 (3-31)</td>
<td>11.9 (5-32)</td>
<td>10.4 (4-29)</td>
<td>9.6 (3-34)</td>
<td>S+M+G+SM+SG+MG+SMG</td>
</tr>
<tr>
<td>Groom</td>
<td>1.9 (1-5)</td>
<td>0.7 (0-3)</td>
<td>2.6 (1-5)</td>
<td>2.4 (1-5)</td>
<td>1.7 (1-5)</td>
<td>2.0 (1-4)</td>
<td>1.8 (1-4)</td>
<td>1.9 (1-5)</td>
<td>S+M+G+SM+SG+MG+SMG</td>
</tr>
<tr>
<td>Rest</td>
<td>2.5 (1-7)</td>
<td>0.8 (0-28)</td>
<td>1.9 (0-12)</td>
<td>4.9 (2-13)</td>
<td>1.9 (0-21)</td>
<td>3.1 (1-14)</td>
<td>2.4 (1-12)</td>
<td>2.7 (1-23)</td>
<td>S</td>
</tr>
<tr>
<td>Social</td>
<td>1.5 (1-4)</td>
<td>1.8 (1-5)</td>
<td>1.4 (1-4)</td>
<td>1.4 (1-3)</td>
<td>1.6 (1-4)</td>
<td>1.5 (1-4)</td>
<td>1.5 (1-4)</td>
<td>1.5 (1-4)</td>
<td>S+M+G+SM</td>
</tr>
<tr>
<td>Disturbed</td>
<td>1.1 (1-2)</td>
<td>1.2 (1-3)</td>
<td>1.2 (1-2)</td>
<td>0.8 (0-1)</td>
<td>1.2 (1-2)</td>
<td>1.0 (1-2)</td>
<td>1.0 (1-2)</td>
<td>1.1 (1-2)</td>
<td>S</td>
</tr>
<tr>
<td>Total</td>
<td>102.1 (75-153)</td>
<td>102.0 (69-181)</td>
<td>103.6 (79-147)</td>
<td>100.2 (75-141)</td>
<td>102.2 (76-158)</td>
<td>102.2 (74-148)</td>
<td>102.0 (76-144)</td>
<td>102.4 (74-162)</td>
<td></td>
</tr>
</tbody>
</table>
climbing to represent foraging behaviour, 84.5% of the time budget is accounted for. Returning to the den between nocturnal foraging bouts averaged 10.0% of the time budget across the year (Table 6.3). Resting (2.5%) and grooming (1.9%) accounted for only a small part of the time budget (Table 6.3). Grooming occurred in short bouts and usually consisted of scratching or removing pollen from the face between nectar feeding bouts and then licking the paws. Most bouts of resting were of short duration (several minutes) and only two long periods of resting were observed outside the den (one male and one female in autumn). The amount of time spent in social activity was very minor (Table 6.3). Gliders also lost a small amount of feeding time (mainly nectar feeding) due to disturbance by other species, such as the grey-headed flying-fox (*Pteropus poliocephalus*) and common brushtail possum (*Trichosurus vulpecula*) (Table 6.3). The model that best explained variation in the proportion of time devoted to each behaviour is given in Table 6.3.

The proportion of the activity period spent feeding ranged from 73.5% in winter to 82.8% in summer, with an intermediate value (78.6%) in autumn (Table 6.3). When these percentages are converted to time values, squirrel gliders spent a mean of 505.4±17.1 min feeding per night (Table 6.2). They averaged an extra 56 min feeding in winter compared to late spring, while night length varied by 181 min. The remainder of the time difference between seasons was accounted for by time spent in the den during the night (a mean difference of 124 min between winter and late spring).

Variation in feeding time was best explained by the model containing the three-way interaction term (Table 6.3; Fig. 6.1). There were no gross differences between seasons (S1 v S2 χ²₁=2.26, p=0.13; S1 v S3 χ²₁=0.72, p=0.39; S2 v S3 χ²₁=0.53, p=0.47), moon phases (χ²₁=0.86, p=0.35) or genders (χ²₁=0.27, p=0.60). Neither gender showed seasonal differences in feeding intensity (χ²₁, p>0.05). Moon phase/gender combinations were explored in further detail for each season. Females engaged in more feeding on the winter new moon compared to the full moon (χ²₁=6.99, p=0.01), but there was no difference for males (χ²₁=0.17, p=0.68). There was no overall difference in the proportion of time spent feeding between the sexes in winter (χ²₁=0.86, p=0.35), however, the strong difference in female feeding intensity produced an overall difference between the moon phases (χ²₁=4.76, p=0.03). There were no differences between any moon phase/gender combinations in late spring when night length was at its minimum (χ²₁, p>0.05). The only difference during autumn was in male feeding intensity between the two moon phases (χ²₁=4.10, p=0.04).
Exudate feeding formed the major part of the squirrel glider’s time budget (Table 6.3). There was no difference in the percentage of time spent exudate feeding in any seasonal comparison except for late spring versus autumn ($\chi^2_1=5.98$, $p=0.01$) (Fig. 6.2). More time was spent exudate feeding on the new moon compared to the full moon ($\chi^2_1=6.86$, $p=0.01$). Gender was not a significant term in the model describing exudate feeding behaviour. No interaction terms were required to describe variation in exudate feeding (Table 6.3).

More effort was devoted to arthropod searching in autumn compared to late spring ($\chi^2_1=4.39$, $p=0.04$), while this effect was weakly non-significant when winter was compared to autumn ($\chi^2_1=3.24$, $p=0.07$) (Table 6.3; Fig. 6.3). Thus, there was more arthropod searching during autumn and they appeared to be more abundant at this time. For example, during autumn squirrel gliders were observed hunting within swarms of moths in *Acacia leiocalyx*. Overall, more effort was devoted to arthropod foraging on the full moon ($\chi^2_1=4.27$, $p=0.03$). Within the seasons, however, this only held for autumn ($\chi^2_1=7.63$, $p=0.01$), although late spring was weakly non-significant ($\chi^2_1=3.45$, $p=0.06$). Females influenced the propensity toward greater
Fig. 6.2: Proportion of time devoted to exudate feeding in the candidate model in different combinations of season, moon phase and gender. The candidate model was S+M. Codes as per Fig. 6.1.

Fig. 6.3: Proportion of time devoted to arthropod feeding in the candidate model in different combinations of season, moon phase and gender. The candidate model was S+M+G+SM+MG. Codes as per Fig. 6.1.
arthropod foraging on the full moon with two seasons showing significant differences (late spring $\chi^2_1=4.91, p=0.03$; autumn $\chi^2_1=7.73, p=0.01$); there were no differences between the moon phases for males in any season. There was no overall difference in the amount of time males and females devoted to arthropod searching ($\chi^2_1=0.14, p=0.71$).

Gliders were more likely to return to the current den during the night during winter (maximum night length) compared to late spring (minimum night length) ($\chi^2_1=5.67, p=0.02$) (Table 6.3; Fig. 6.4). Differences between the other seasonal combinations were not significant (S1 v S3 $\chi^2_1=1.50, p=0.22$; S2 v S3 $\chi^2_1=2.13, p=0.14$). The difference between winter and late spring was significant for males ($\chi^2_1=5.41, p=0.02$) but not for females ($\chi^2_1=0.74, p=0.39$). Gross differences between moon phases ($\chi^2_1=0.77, p=0.38$) and gender ($\chi^2_1=0.20, p=0.66$) were not significant. Females spent more time in the den on the full moon during winter ($\chi^2_1=5.36, p=0.02$), whereas males showed no difference ($\chi^2_1=0.02, p=0.90$). There was no overall difference between males and females in winter ($\chi^2_1=1.87, p=0.17$). Both sexes combined spent more time in the den on the full versus new moon during winter ($\chi^2_1=4.74, p=0.03$). No moon phase/gender combination produced a significant difference in late spring ($\chi^2_1, p>0.05$). During autumn, the only significant result was females spending more in the den on the new moon ($\chi^2_1=4.20, p=0.04$).

![Graph](image)

**Fig. 6.4:** Proportion of time spent returning to the diurnal den in the candidate model in different combinations of season, moon phase and gender. The candidate model was S+M+G+SM+SG+MG+SMG. Codes as per Fig. 6.1.
Gliding and climbing occupied only a small proportion of the squirrel glider’s time budget (Table 6.3), which was relatively consistent between the various combinations of season, moon phase and gender (e.g. Fig. 6.5). However, the amount of gliding and climbing conducted by males showed a sudden peak during the late spring new moon period. At this time the major exudate consumed was shifting from nectar to honeydew/lerp. In conjunction with this shift, males were observed to undertake home-range patrols by rapidly gliding and climbing through an area that roughly circled the locations of known den trees in habitat areas dominated by brush box (Dobson 2002). Brush box was the major source of honeydew (Dobson et al. 2005).

![Graph showing the proportion of time spent climbing in different combinations of season, moon phase, and gender.](image)

**Fig. 6.5:** Proportion of time spent climbing in the candidate model in different combinations of season, moon phase, and gender. The candidate model was S+M+G+SM. Codes as per Fig. 6.1.

6.3.4. Group Foraging

Squirrel gliders were observed group foraging on a total of 82 occasions (9% of all trees used), including 23 observations (2%) of >2 gliders (Table 6.4). Food type (nectar, honeydew/lerp, arthropods) influenced the frequency of group foraging ($\chi^2=176.48$, p < 0.001). Accordingly, the median number of gliders per tree varied with food type (Kruskal-Wallis $\chi^2=181.06$, p < 0.001). Larger groups occurred during nectar feeding compared to both honeydew/lerp (Z=6.27, p <0.001) and arthropods (Z=14.38, p <0.001) and honeydew feeding compared to arthropods (Z=7.03, p <0.001).
Table 6.4: Incidence of group foraging (≥2 gliders) in relation to feeding behaviour in individual trees.
Mean based on number of gliders observed per tree. Groups >2 indicates frequency of groups of three or more gliders. Numbers in brackets are the percentages of all observations.

<table>
<thead>
<tr>
<th>Food Type</th>
<th>No. Gliders: Mean</th>
<th>Honeydew/lerp</th>
<th>Arthropods</th>
<th>Overall</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>s.e.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nectar</td>
<td>1.73</td>
<td>1.17</td>
<td>1.02</td>
<td>1.12</td>
</tr>
<tr>
<td>Honeydew/lerp</td>
<td>0.11</td>
<td>0.03</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>Arthropods</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Frequency</th>
<th>Individual</th>
<th>48 (56%)</th>
<th>218 (87%)</th>
<th>576 (98%)</th>
<th>842 (91%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>All Groups</td>
<td>38 (44%)</td>
<td>34 (13%)</td>
<td>10 (2%)</td>
<td>82 (9%)</td>
<td></td>
</tr>
<tr>
<td>Groups &gt;2</td>
<td>17 (20%)</td>
<td>6 (2%)</td>
<td>0 (0%)</td>
<td>23 (2%)</td>
<td></td>
</tr>
</tbody>
</table>

| Total Observations | 86 | 252 | 586 | 924 |

6.3.5. Tree Utilisation

Squirrel gliders spent longer in trees when nectar feeding compared to the other two feeding behaviours and longer feeding on honeydew/lerp compared to arthropods (Kruskal-Wallis $\chi^2=525.50$, p <0.001) (Table 6.5). Despite the truncated observations, the mean time spent per tree nectar feeding (31 min) was over double that of honeydew/lerp feeding (14 min). Eight tree species were used for both food types (Table 6.5). The relationship between the number of flowers per feed tree and the amount of time in each tree during nectar feeding was significant in a combined analysis of forest red gum and narrow-leaved red gum ($F_{1,29}=15.94$, p <0.001, $r^2=0.36$) (Fig. 6.6). The relationship between tree size (DBH) and the time spent per tree during honeydew/lerp feeding was also significant ($F_{1,137}=18.86$, p <0.001, $r^2=0.12$) (Fig. 6.7). Thus, gliders spent longer feeding in larger trees and/or those with more flowers. Most tree species available were used for arthropod searching, with 1-3 min typically spent per tree (Table 6.5).

Table 6.5: Influence of food type on tree utilisation times.

<table>
<thead>
<tr>
<th>Food Type</th>
<th>No. Observations</th>
<th>No. Tree Species</th>
<th>Mean Duration (min)</th>
<th>s.e.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nectar</td>
<td>86</td>
<td>8</td>
<td>31.4</td>
<td>2.7</td>
</tr>
<tr>
<td>Honeydew/Lerp</td>
<td>252</td>
<td>8</td>
<td>14.3</td>
<td>1.0</td>
</tr>
<tr>
<td>Arthropods</td>
<td>586</td>
<td>19</td>
<td>1.7</td>
<td>0.1</td>
</tr>
<tr>
<td>Total</td>
<td>924</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
y = 0.32x + 0.24
\( R^2 = 0.36 \)

Fig. 6.6: The relationship between the number of flowers and the duration of visits to forest red gum (E. tereticornis) and narrow-leaved red gum (E. seeana).

y = 0.25x + 2.90
\( R^2 = 0.12 \)

Fig. 6.7: The relationship between the size (DBH) of brush box (L. confertus) and the duration of visits to obtain honeydew.
6.3.6. Time Budgets of Petaurids

Data on body weight, length of the activity period, feeding rate, foraging intensity and home-range area of petaurid gliders are available for the four species across six study sites (Table 6.6). There was no relationship between body weight and the length of the activity period \( (F_{1,2} = 0.13, p = 0.75, r^2 = 0.06) \) (Fig. 6.8), the proportion of time used for feeding \( (F_{1,4} = 3.23, p = 0.15, r^2 = 0.45) \) (Fig. 6.9) or the proportion of time used for foraging (feeding plus gliding and climbing) \( (F_{1,4} = 0.26, p = 0.64, r^2 = 0.06) \) (Fig. 6.10). Home-range area was significantly related to body size \( (F_{1,4} = 9.85, p = 0.04, r^2 = 0.71) \) (Fig. 6.11).

6.4. Discussion

6.4.1. Activity Patterns

Squirrel gliders emerged from their dens shortly after sunset and remained active for most of the night. The bimodal activity pattern observed during winter and autumn in this study was similar to that of captive sugar gliders fed \textit{ad lib} (Goldingay 1984). Food was thought to be abundant throughout this study due to heavy flowering and psyllid infestation (see Dobson et al. 2005). However, squirrel gliders emerged earlier from their dens, retired later and spent little time in the den during the night in late spring when night length was near its minimum. Similarly, yellow-bellied gliders may remain active past sunrise during summer to extend feeding time (Goldingay 1989a). It appears that short night length imposes a constraint on the time budgets of exudivorous gliders. Seasonal changes in the length of the activity period are known to affect the time budgets of a broad range of taxa (e.g. Cope 2003; Bertolino et al. 2004; Koprowski and Corse 2005; Hwang and Garshelis 2006).

Table 6.6: Body weight, the proportion of time spent feeding and foraging, and the home-range area of the four Australian petaurid glider species.

Estimated daily energy requirement based on a regression formula developed for the sugar glider (Nagy and Suckling 1985). Percentage values based on the proportion of the activity period used. Wt = weight, Hr = home-range. Sources: 1 Suckling (1984); 2 Körtner and Geiser (2000); 3 Quin (1993); 4 Quin et al. (1992); 5 Quin (1995); 6 this study; 7 Dobson (2002); 8 Holland et al. (2007); 9 van der Ree and Bennett (2003); 10 Jackson and Johnson (2002); 11 Jackson (2000b); 12 Goldingay (1989a); 13 Goldingay and Kavanagh (1993); 14 Goldingay (1990); 15 Goldingay (1992); 16 Henry and Craig (1984).

<table>
<thead>
<tr>
<th>Species</th>
<th>Wt (g)</th>
<th>Estimated Energy (kJ day(^{-1}))</th>
<th>Nightly Activity (min)</th>
<th>% Feeding</th>
<th>% Foraging</th>
<th>Hr (ha)</th>
<th>Sources</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sugar glider</td>
<td>100</td>
<td>141.3</td>
<td>370-770</td>
<td>55</td>
<td>83</td>
<td>0.5-5.4</td>
<td>1,2,3,4,5</td>
</tr>
<tr>
<td>Squirrel glider</td>
<td>230</td>
<td>222.1</td>
<td>560-597</td>
<td>63-78</td>
<td>73-85</td>
<td>3.1-6.7</td>
<td>5,6,7,8,9</td>
</tr>
<tr>
<td>Mahogany glider</td>
<td>400</td>
<td>329.0</td>
<td>480-606</td>
<td>58</td>
<td>71</td>
<td>19.8</td>
<td>10,11</td>
</tr>
<tr>
<td>Yellow-bellied glider</td>
<td>590</td>
<td>417.1</td>
<td>552-624</td>
<td>81-85</td>
<td>89-90</td>
<td>34.0-63.0</td>
<td>12,13,14,15,16</td>
</tr>
</tbody>
</table>
**Fig. 6.8:** The relationship between the size of petaurid glider species and the length of the activity period (this value is the midpoint of the values given in Table 6.6). Data sources are listed in Table 6.6.

**Fig. 6.9:** The relationship between the size of petaurid glider species and the estimated proportion of time spent feeding. Data sources are listed in Table 6.6.
Moon phase also influenced emergence and retirement times, with gliders emerging later and retiring earlier on the full moon. This effect has not been detected in previous studies of gliding possums.

6.4.2. **Time Budget**

In common with other petaurids (Goldingay 1989a, 1990; Quin 1993; Holland *et al.* 2007; Jackson and Johnson 2002), squirrel gliders devoted the largest proportion of their time
budget to feeding and associated behaviours (gliding, climbing). The proportion of the squirrel glider’s time budget devoted to feeding (78%) in this study is higher than that reported by Holland et al. (2007) (63%). It also exceeds the value reported for the larger mahogany glider (58%) (Jackson and Johnson 2002) and is only slightly less than the value (81%) for the largest petaurid, the yellow-bellied glider, obtained by Goldingay (1989a). Both Holland et al. (2007) and Jackson and Johnson (2002) suggested they had probably over-estimated the amount of time devoted to resting and grooming by including occasions when gliders had become disturbed by observer presence. Over-estimating such behaviours would result in a concomitant reduction in observed feeding time. In contrast, disturbance to glider behaviour was rare in this study because the urban location of the study site appears to have habituated animals to high levels of background noise and light, therefore allowing rapid habituation to the presence of an observer.

It is possible that the high population density during this study contributed to an unusually large proportion of the activity period being used for feeding due to heightened scramble competition (e.g. Fashing et al. 2007). However, the squirrel glider population examined by Holland et al. (2007) occurred at a similarly high density (van der Ree 2002). Moreover, heavy flowering and the large number of brush box trees containing honeydew in the study area suggest that food was abundant (Dobson et al. 2005). Accordingly, food limitation is unlikely to have caused the high feeding intensities that were observed.

Variation in the proportion of time used for feeding by the squirrel glider in Brisbane did not show any simple relationship with season, moon phase or gender, but there was a complex interaction between these factors. During winter, female feeding rates were very high on the new full and much lower on the full moon, while males showed no variation with moon phase. Rather than a moon effect per se, the period between the two sampling periods apparently coincided with many females entering late lactation. While the energy requirements of females increase in late lactation (Tyndale-Biscoe 2005), there are also increased demands on a female’s time from the need to feed offspring left in the den. Thus, despite the long night length during the peak breeding period, females may not have sufficient time to maintain high feeding rates. The intensity of feeding immediately prior to late lactation suggests females were attempting to maximise their condition before a period of stress resulting from higher energetic requirements and the demands of other activities.
Squirrel gliders were observed to feed upon the exudate most abundantly available, selecting individual trees with greater energetic returns. Less exudate feeding and more arthropod searching occurred on the full moon compared to the new moon. Squirrel gliders appear to be visual predators of arthropods and greater visibility may enhance hunting success. Arthropods were also more heavily targeted during autumn when they were more abundantly available. Thus, the squirrel glider adopts an optimal foraging strategy designed to maximise energy gain while minimising energy expenditure (see Goldingay 1990). A 210 g squirrel glider is expected to require 222 kJ day\(^{-1}\) to meet its energy requirements (Nagy and Suckling 1985). This energy was obtained during 8.42 h of feeding per night averaged across the seasons, suggesting a typical feeding rate of 26 kJ h\(^{-1}\). Rates of energy return would be higher for exudates and lower for arthropods.

Returning to the den between feeding bouts was a conspicuous component of the squirrel glider’s time budget and such a pronounced tendency has rarely been reported in petaurids (but see Quin 1993). Variation in the amount of time in the den during the night was related to night length, resulting in an inverse relationship with the proportion of time used for foraging. While in the den, squirrel gliders may feed developing offspring during late lactation (females only), thermoregulate developing offspring (e.g. Holloway and Geiser 2000), minimise energy expenditure and minimise predation risk (both sexes). Considering the small amount of time spent resting outside the den, predator avoidance may be an important reason for this behaviour. However, the maximum proportion of time spent in the den coincided with a peak in the number of females in late lactation. These offspring would require both feeding and thermoregulation.

6.4.3. The Value of Different Food Types
Petaurid gliders derive most of their energy from plant and insect exudates, consuming pollen and arthropods to meet their nitrogen requirements. Different exudates influence the amount of time gliders spend in individual trees, with the greatest durations associated with sap feeding (by the yellow-bellied glider) (Goldingay 1989a) and nectar feeding (Jackson and Johnson 2002). The least amount of time is spent in trees used for arthropod feeding (Goldingay 1989a, 1990; Jackson and Johnson 2002).

Although the observations of tree use were often truncated and the reported values are therefore under-estimates, squirrel gliders nevertheless spent longer in trees when nectar feeding and they also appeared to have the higher rates of food ingestion when feeding on
this resource compared to honeydew (personal observations). Food type influenced the frequency of group foraging by the squirrel glider (see also Goldingay 1990), with larger groups when nectar feeding compared to other food types. These observations suggest that nectar is a particularly valuable resource, which the squirrel glider relies heavily upon at sites where it is readily available (Sharpe and Goldingay 1998; Dobson et al. 2005; Chapter 2).

6.4.4. Comparison of Petaurid Time Budgets

Jackson and Johnson (2002) reviewed the time budgets of exudivorous and folivorous arboreal marsupials, postulating that feeding time increased with increasing mass in exudivorous species. However, this relationship was contingent on the values estimated in two studies where it was acknowledged that the disturbance of animals during observations had led to an over-estimation of grooming and resting (Jackson and Johnson 2002; Holland et al. 2007). The present study casts doubt on a relationship between body mass and percentage of the time budget devoted to foraging because it was estimated in this study that squirrel gliders devoted an average of 85% of their active time to foraging, a value similar to the 89% estimated for the yellow-bellied glider (Goldingay 1989a, 1990). Furthermore, it was calculated that squirrel gliders spent 560–597 min active per night, which is similar to the estimate of 520–770 min per night for sugar gliders at ambient temperatures >2°C (Körtner and Geiser 2000) and 552–624 min for the yellow-bellied glider (Goldingay 1989a). Thus, the larger petaurids do not spend longer active nor do they spend a greater proportion of time feeding or foraging.

The length of the activity period and the proportion of active time spent feeding and foraging are not the only factors to consider. While it is probably not possible to determine actual food ingestion rates in the field, the larger petaurids may concentrate on food resources that have higher returns per unit effort (e.g. sap feeding, arthropod searching amongst hanging or shedding bark rather than random searching (Goldingay 1986, 1989a) to meet their higher absolute energy requirements (Quin 1993). Moreover, larger species have larger home-range areas, less home-range overlap, occur at lower densities and have lower reproductive output (Goldingay and Jackson 2004). Bigger home-ranges would be required by the larger species to ensure there is a sufficient abundance of high quality feeding resources (e.g. sap trees, flowering trees (particularly early and late in the flowering period), bark tangles) within the annual home-range. Lower population densities would ensure that there was less competition for food resources. These factors would allow the larger petaurids to meet their greater
absolute energy requirements without spending a significantly higher proportion of the activity period feeding.

6.4.5. Implications of This Study

Gliding enables animals to move about quickly with a relatively low energy cost (Nagy and Suckling 1985; Dial 2003). Gliding is likely to be of benefit to an animal feeding on easily digested but widely dispersed foods. By lowering the energy required to move about, the amount of time required for feeding is decreased. Gliding is also a rapid form of locomotion, which enables animals to move quickly between dispersed food patches, enabling longer feeding times (Smith 1982). Therefore, gliding may be a necessary adaptation in species that have diets requiring a large portion of the active period to be spent harvesting food and that occupy open habitats. Thus, the exploitation of the exudivore niche in open eucalypt forest may have required the evolution of gliding (Goldingay 1989a, 2000). This is particularly likely to be true for mammals such as the petaurid gliders, where a diet of dispersed food resources has resulted in larger home-ranges than expected on the basis of body size (Jackson 2000b; Goldingay and Jackson 2004). Non-gliding petaurids either live in denser forests where gliding would not provide a benefit (Leadbeater’s possum Gymnobelideus leadbeateri) (Smith 1995) or are more dependent on wood boring and social insects (striped possum Dactylopsila trivirgata) (Rawlins and Handasyde 2002).

Severe constraints on the amount of time available for feeding may restrict the size of petaurid social groups (e.g. Teichroeb et al. 2003; Korstjens et al. 2006; Korstjens and Dunbar 2007; Lehmann et al. 2007). This is because group members are potentially in competition with each other for food resources. Petaurid gliders are highly social mammals with flexible group structures. However, groups are typically small and consist of an adult male and one or two breeding females (Goldingay 1992; Sadler and Ward 1999; Goldingay et al. 2001). It has been suggested that group size varies (i.e. monogamy versus polygyny) in response to resource availability within and between sites (Goldingay and Jackson 2004).

Animals that increase their feeding intensity due to increased competition or periods of low food availability often “borrow” the extra feeding time from other components of the time budget (e.g. resting, social interactions), increase home-range area (e.g. Fashing et al. 2007) or alter group size (e.g. Lehmann et al. 2007). Petaurids feed intensively and spend limited time in other activities. As a result, they have little scope to increase their foraging effort. Thus, lower food availability will not translate into increased foraging time (e.g. Gelatt et al. 2007).
2002), but would have direct influences on population density by lowering population size due to mortality (Chapter 2), causing polygynous groups to become monogamous (Goldingay 1990) or increasing home-range area (Quin 1995). This suggests that petaurid gliders will be sensitive to forms of anthropogenic disturbance such as selective tree removal. It is hypothesised that the petaurid gliders would respond to such disturbance by increasing home-range area with a concomitant decrease in population density. Because gliding is an efficient means of locomotion, the use of larger foraging areas could be achieved with negligible impact on feeding time.
7. **GENERAL DISCUSSION AND CONCLUSION**

7.1. **Introduction**

At the commencement of this thesis the squirrel glider was a poorly known species (Suckling 1995; Chapter 1). Thus, the overall aim of this thesis was to conduct further research on the squirrel glider that would contribute to its management and conservation, particularly at the population level. This was achieved by conducting research at two contrasting study sites, one located in an area of extensive, relatively natural forest (*albeit* subject to previous logging, but now Bungawalbin Nature Reserve) and the other located in an urban forest remnant in Brisbane.

As urbanisation is regarded as a significant threat to the squirrel glider in the coastal part of its range, Brisbane presents a model of the consequences of habitat fragmentation, particularly in an urban environment. Importantly, insights gained through the study of squirrel glider populations in Brisbane can provide management strategies also applicable to different parts of its range. Moreover, these findings will have relevance to the management of petaurids more broadly (e.g. mahogany glider). This Chapter discusses some of the implications of the research that were not fully explored earlier in the thesis and provides a synthesis of the major findings. An updated account of the aspects of the squirrel glider’s ecology covered in this thesis is then given before the management of squirrel glider populations is discussed.

7.2. **Population Viability**

One of the ways that information gained from population ecology studies can be used is in estimating population viability using computer simulation. Field studies that are directed by this use can provide many key inputs for viability models or refine inputs that are derived from earlier studies. Among many of the key inputs required are appropriate estimates for annual variation in population size and survival rates. Due to the fact that many field studies are typically of short duration these inputs are likely to be a best guess (e.g. Goldingay and Sharpe 2004a) and consequently may be greatly under-estimated. In turn, the viability of the populations under consideration would be over-estimated (e.g. Vucetich and Waite 1998; Katzner *et al.* 2006). This section reviews the population ecology of the squirrel glider before giving more detailed consideration to the importance of fluctuating population size and survival rates on population viability assessments.
7.2.1. Population Ecology

This section reviews the population ecology of the squirrel glider, based on published studies. These data are summarised in Table 7.1.

Squirrel gliders den in tree hollows in small groups of 2-9 individuals, usually consisting of at least one adult male, one or two adult females and their offspring (Quin 1995; van der Ree and Bennett 2003; Sharpe and Goldingay 2007). Occasionally, groups may contain multiple males (Quin 1995; van der Ree 2002), but the significance of this has not been clarified (Goldingay and Jackson 2004). Squirrel gliders, therefore, may have either a monogamous or polygynous group structure. The structure of social groups can vary from group to group and between years at a locality and between localities (Quin 1995; van der Ree and Bennett 2003; Sharpe and Goldingay 2007), which has also been reported in other petaurids (Suckling 1984; Goldingay and Kavanagh 1990; Goldingay 1992; Quin 1995; Sadler and Ward 1999; Goldingay et al. 2001; Goldingay and Jackson 2004). This is thought to be a response to changes in local food availability (e.g. Goldingay 1992).

Female squirrel gliders are sexually mature at around 12 months of age and are capable of reproducing twice a year (Quin 1995; van der Ree 2002; Chapter 3). Births may occur in most months of the year, although there is a major autumn/winter peak and a smaller late spring/early summer peak (Quin 1995; Millis and Bradley 2001; van der Ree 2002; Chapters 2 and 3). Breeding appears to be linked to periods of high food availability, such as flowering in eucalypts and banksias (Quin 1995; Chapters 2 and 3). One or two offspring are produced per litter, resulting in a mean litter size of 1.7-1.8. The natality rate (number of offspring per female per year) ranges between 1.8 and 2.4, indicating that not all females breed twice in each year (Quin 1995; Millis and Bradley 2001; van der Ree 2002; Chapters 2 and 3). The propensity to produce a second litter appears to be influenced by food availability and the size of the first litter. Although females that breed twice may have smaller litters, their overall reproductive output is higher (Chapter 3). Thus, a second litter should be produced whenever local conditions within an individual home-range permit.

Smith (1979) provided data on the development and growth of juvenile squirrel gliders, acquiring this information from a small captive population. These data have proved valuable in allowing the age of pouch young, and therefore birth dates, to be estimated in the field. The growth rate of the squirrel glider is similar to that of the smaller sugar glider over the first 100 days of development, but it keeps growing for a further 35 days to achieve its larger size.
Table 7.1: Demographic characteristics of squirrel glider populations, showing the sites at which they have been studied.

<table>
<thead>
<tr>
<th>Location</th>
<th>Density (ha⁻¹)</th>
<th>Group Structure</th>
<th>Breeding Period</th>
<th>Min. Breeding Age (months)</th>
<th>Females Breeding (mean %)</th>
<th>No. Litters per Year</th>
<th>Mean Litter Size</th>
<th>Natality Rate</th>
<th>Dispersal (months)</th>
<th>Max. Longevity (years)</th>
<th>Refs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Euroa, Vic</td>
<td>0.95-1.54</td>
<td>M,MF,MM</td>
<td>May-Dec (peak June-Oct)</td>
<td>12</td>
<td>100</td>
<td>1-2</td>
<td>1.7</td>
<td>1.9</td>
<td>7-8</td>
<td>1, 2</td>
<td></td>
</tr>
<tr>
<td>Limeburner’s Ck, mid north coast NSW</td>
<td>0.89-1.54</td>
<td>MF,MM</td>
<td>Most months, but variable between years (peak early winter)</td>
<td>12</td>
<td>78*</td>
<td>1-2</td>
<td>1.8</td>
<td>2.4</td>
<td>12-13</td>
<td>5-6</td>
<td>3</td>
</tr>
<tr>
<td>Bungawalbin, NE NSW</td>
<td>0.18-0.87</td>
<td>M,MM</td>
<td>Autumn/Winter; Spring</td>
<td>12</td>
<td>100</td>
<td>1</td>
<td>1.8</td>
<td>1.8</td>
<td>6</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>Minnippi Parklands, Brisbane</td>
<td>0.49-1.62</td>
<td></td>
<td>April-Nov (peak April-May)</td>
<td>12</td>
<td>100</td>
<td>1-2</td>
<td>1.7</td>
<td>1.9</td>
<td>7-8</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>SE Qld</td>
<td></td>
<td></td>
<td>April-May; July-Nov</td>
<td>12</td>
<td></td>
<td></td>
<td>1.7</td>
<td></td>
<td></td>
<td>6</td>
<td></td>
</tr>
</tbody>
</table>

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Despite the usefulness of these development data from captivity, further verification is needed because growth rates in the field are likely to be influenced by temperature and local food abundance.

Juvenile squirrel gliders are weaned and become active outside the den by about 4 months and disperse early in their second year (Quin 1995; Chapter 3). Young female gliders may also be incorporated into the maternal group (unpublished data). Mortality is presumed to be high in dispersing sub-adult gliders and their recruitment appears to be related to the flowering intensity of Eucalypts and Banksias (Quin 1995). Adult squirrel gliders may live for at least 6 years, although few gliders appear to reach this age (Quin 1995; van der Ree et al. 2006; Chapters 2 and 3), suggesting that predation rates may be high. While predation events were observed at Bungawalbin, none were recorded at Minnippi. Thus, the source of predation at Minnippi has not been established. Throughout its range, the influences on dispersal and mortality of both juvenile and adult squirrel gliders are, in general, currently poorly known and require further study.

The population density of the squirrel glider shows considerable variation. Population densities of 0.49-1.62 (Brisbane) (Chapter 3), 0.89-1.54 ha$^{-1}$ (mid north coast of New South Wales) (Quin 1995), 0.18-0.89 ha$^{-1}$ (northern New South Wales) (Chapter 2), 0.95-1.54 ha$^{-1}$ (central Victoria) (van der Ree 2002), 0.40-0.49 ha$^{-1}$ (central Victoria) (Traill 1995) have been reported. Habitat disturbance from natural (e.g. fire) or anthropogenic causes (e.g. selective tree removal) reduces food availability and lowers squirrel glider density (Quin 1995; Goldingay and Sharpe, unpublished data). Sugar gliders appear to recover more quickly from disturbance than do squirrel gliders, presumably due to their smaller size and lower absolute energy requirements (Quin 1995). Population density is an important input into PVA studies. Caution must be applied when assessing density information because the estimates include, or may include, juvenile animals. Only adult (breeding) individuals should be used to determine population density in the PVA process (e.g. Possingham and Davies 1995).

Habitat fragmentation does not appear to have much effect on the population ecology of the squirrel glider. The timing of reproduction, the proportion of females breeding, mean litter size and the natality rate at Brisbane (Millis and Bradley 2001; Chapter 3) and Euroa (van der Ree 2002) were all similar to that reported in areas of more natural habitat (Quin 1995; Chapter 2). Indeed, population density and longevity may be at the higher end of reported values. It is not clear whether greater longevity is because studies in fragmented habitats have
been of long duration, allowing individuals to be followed for longer periods and for age to be estimated more accurately (van der Ree et al. 2006; Chapter 3, but see also Chapter 2), or whether this reflects lower predation rates (but see van der Ree 2002). However, some species occur at higher density in habitat remnants (e.g. Reunanen and Grubb 2005) provided there is an adequate food supply throughout the year.

Dietary studies conducted in fragmented habitat have revealed a heavy reliance on insect honeydew during all (Holland et al. 2007) or part of the year (Dobson et al. 2005). Trees growing in remnants may be under greater stress than those in continuous forest due to factors such as altered climatic or soil conditions and changes in the composition of the bird community, predisposing them to attack by herbivorous and sap-sucking insects (Landsberg and Wylie 1983; Grey et al. 1998; Jurskis 2005). In the short-term, this can provide a substantial food resource for exudate/insect feeders, such as petaurids. However, a positive feedback loop can result in which affected trees become exposed to repeated biotic stress that chronically undermines tree health, ultimately resulting in dieback (Landsberg and Wylie 1983; Jurskis 2005). Therefore, there is some concern that dieback will eventually lead to a depletion of food resources, leading to population declines in exudivorous mammals in fragmented habitats (Goldingay et al. 2006).

7.2.2. Population Fluctuations

Field studies of animal populations can provide information that is of direct use in their management and conservation. Importantly, studies that follow marked individuals through time allow one to estimate the size of local populations, which may be vital to decisions about the need and urgency of local management actions. However, long-term studies of individual populations are required to describe the variation in population size over time (Vucetich and Waite 1998; Reed et al. 2003).

Fluctuating population size has a major bearing on population viability (Vucetich et al. 2000; Reed et al. 2003). Therefore, it is important to adequately describe variability in the size of squirrel glider populations. Previous studies on the squirrel glider were conducted over maximum periods of 2.3 years. Quin (1995) found that population size varied by a factor of 1.7 over 2.3 years, while van der Ree (2002) documented a change of 1.6 over 2.0 years. At Bungawalbin, the population varied by a factor of 4.8 over 5.8 years (Chapter 2), while in Brisbane the difference was 3.3 times over 4 years (Chapter 3).
Nectar is a highly variable food resource in space and time. Its availability is affected by climatic variation, fire and anthropogenic disturbance such as logging (Law et al. 2000; Law and Chidel 2008). Accordingly, petaurid populations that rely heavily on nectar for food may be the most prone to fluctuating population size. This includes the mahogany glider (Jackson 2001) and many squirrel glider populations (Menkhorst et al. 1988; Sharpe and Goldingay 1998; Dobson et al. 2005), in addition to some yellow-bellied glider (Goldingay 1990) and sugar glider (Howard 1989) populations. For example, yellow-bellied gliders at Bombala in southern NSW had small but relatively stable group sizes (2.6 individuals) over a 5-year period (Goldingay and Kavanagh 1990), whereas the mean group size at Kioloa (180 km away) was large (4.2) but more variable over 3 years (Goldingay 1992). Sap and honeydew formed the bulk of the diet at the former site (Goldingay 1986), while nectar dominated at the latter (Goldingay 1990). Goldingay (1992) found that group structure at Kioloa changed from polygyny to monogamy apparently in response to several years of flower failure during winter. Because yellow-bellied gliders occupy exclusive home-ranges (Goldingay and Kavanagh 1993), the change in group composition translated directly into a lowering of population density. It is likely that other small arboreal marsupials that specialise on nectar will be similarly affected (e.g. Ward 1990; Wooller et al. 2004).

Fluctuating population size is likely to be of most importance in squirrel glider populations inhabiting fragmented habitats. This is because population variability is greatest in smaller populations (Reed and Hobbs 2004), as occur in many forest remnants (e.g. van der Ree 2002; Chapter 3). Moreover, habitat fragmentation continues to threaten the squirrel glider in many parts of its range (Menkhorst et al. 1988; Rowston et al. 2002; Smith and Murray 2003; Claridge and van der Ree 2004; Goldingay and Sharpe 2004a; Ball and Goldingay 2008). Populations inhabiting habitat fragments are likely to be of greatest concern (e.g. Claridge and van der Ree 2004). While squirrel glider populations inhabiting fragmented habitats can reach high densities, the restricted amount of habitat available ultimately results in relatively small population sizes (e.g. van der Ree 2002; Chapter 3). Thus, management attention should be greatest for populations inhabiting habitat remnants (e.g. Claridge and van der Ree 2004; Goldingay and Sharpe 2004a). Although requiring less management attention, large populations must also be protected. The most efficient way to do this is at the planning stage where it is possible to retain large habitat blocks.
It is apparent that longer studies are required to assess the extent of population fluctuations. Despite the findings of this thesis, Reed et al. (2003) suggest that more than 12 generations are required to document the full range of population size variation (but see also Vucetich and Waite 1998). As squirrel gliders first breed at 12 months of age (Quin 1995; van der Ree 2002; Chapter 3), generations equate to one year. This would require at least 12 years of study of squirrel glider populations. Moreover, because food supply is one factor that appears to drive population variability in this species, longer periods may be required because of climatically determined links to food availability (e.g. Chapter 2). In this context, the variability of the squirrel glider populations examined in this thesis should be regarded as an important first step.

7.2.3. Survival Rates

The survival rate of adult animals is a key input into PVA models (Goldingay and Sharpe 2004a; Oli 2004). Chapter 4 estimated the probability of adult survival to be 0.51 for females and 0.48 for males. The female value is substantially less than the 0.65 entered into a PVA (only females were modelled) on the squirrel glider for a series of linked remnants that included the current study area (Goldingay and Sharpe 2004a). However, the magnitude of the discrepancy is unclear because the estimate in Chapter 4 is likely to include a small element of dispersal, particularly by individuals aged 1-2 years. This is because the mark-recapture analysis treats survival as all individuals that have not disappeared from the population. Those disappearing would include true deaths and animals lost to dispersal. Animals that disperse either die in the attempt or successfully establish themselves somewhere outside the limits of the sampled population. Either way, these individuals are never seen again. However, a strength of the current study was that it was conducted over a 4-year period, which allowed some yearly variation in apparent survival to be assessed.

PVA models are constructed to allow dispersal among subpopulations within a metapopulation and there is an independent mortality component associated with such movements. Therefore, animals that die during dispersal may effectively die twice in a PVA, once due to loss from the population if the survival rate is based upon all individuals disappearing from a population and again during dispersal if they do not reach another habitat patch. This “double-dipping” causes the viability of the metapopulation to be under-estimated, producing an overly pessimistic PVA (Brook 2000). Further research is needed to clarify the
effect of dispersal of recently matured individuals on the estimated survival rate of adult squirrel gliders.

7.3. Time Budget

7.3.1. Time as a Limiting Factor

The squirrel glider uses most (85%) of its nocturnal activity period for feeding and associated behaviours. This was particularly pronounced in summer. In contrast, during winter gliders fed proportionally less and were able to spend 18% of the night in the diurnal den (averaging 10% across the year) (Chapter 6). In Victoria, foraging was also the dominant feature of the time budget, with relatively less time being required in winter, but little time (2.5% across the year) was spent in the den (Holland et al. 2007).

Jackson and Johnson (2002) hypothesised that the amount of time required for feeding amongst gliding exudivores was positively related to body size. This conclusion was based on only two time budget studies of the yellow-bellied glider and one on each of the other petaurid gliders. Furthermore, two of these studies may have been confounded by observer disturbance to gliders, resulting in inflated values for resting and grooming behaviours (Jackson and Johnson 2002; Holland et al. 2007). It is likely that resting and grooming are very minor components of the time budget (Goldingay 1989a, 1990; Chapter 6). Accordingly, when the data from the present study were used to re-examine the hypothesis of Jackson and Johnson (2002) the relationship was not upheld. Thus, all the petaurid gliders appear to be time limited, which is most pronounced during summer when night length is at its minimum. Further time budget studies across all the petaurid gliders and in different parts of their ranges are required to fully resolve whether there is a relationship between size and foraging intensity. Alternatively, differences in habitat quality, and hence foraging efficiency, are sufficient to obscure any trends (Quin 1993).

The size of groups in which animals live represents a compromise between the costs and benefits of group living. Group living involves intra-group food competition, which is likely to increase as groups become larger (Clutton-Brock and Harvey 1977; Terborgh and Janson 1986; Janson and Goldsmith 1995; Teichroeb et al. 2003). Variation in food availability is an important factor influencing differences in group size and composition between sites and over time (Korstjens et al. 2006; Korstjens and Dunbar 2007).
A species’ diet will influence its time budget, but this influence may vary from site to site due to the precise nature of the foods available. For example, folivores may require inactive periods to digest their food, but this requirement may increase when there is a need to feed on foliage of low quality (e.g. Wong and Sicotte 2007). Time limitations have been proposed to limit group size in a number of primate species due to the influence of larger groups on the proportion of time spent feeding, resting while digesting food and travelling (e.g. Teichroeb et al. 2003; Korstjens et al. 2006; Korstjens and Dunbar 2007). The bulk of a petaurid glider’s diet consists of easily digested exudates and they spend little time travelling between food patches due to their gliding locomotion. However, the amount of time spent foraging is a dominant feature of their time budgets. Moreover, group foraging may be relatively common for some food types and/or at some sites (Goldingay 1989a, 1990; Quin 1993; Jackson and Johnson 2002; Holland et al. 2007; Chapter 6). These factors suggest that intra-group scramble competition has the potential to occur. This is likely to have implications for various aspects of their ecology, their tolerance of environmental variation and tolerance to anthropogenic disturbance (Goldingay 1989b).

Petaurids are highly social animals, living in family groups and communicate using olfactory and vocal behaviours (Biggins 1984; Russell 1984; Goldingay 1994; Chapter 5). However, group size is invariably small, generally containing 2-4 adult gliders plus their offspring (Suckling 1984; Goldingay and Kavanagh 1990; Goldingay 1992; Quin 1995; Sadler and Ward 1999; Jackson 2000a; Goldingay et al. 2001; van der Ree 2002; Sharpe and Goldingay 2007). The composition of groups can be variable within a site (Sadler and Ward 1999; Goldingay et al. 2001), which may reflect differences in the productivity of specific home-ranges. Goldingay (1992) found that the size of yellow-bellied glider groups decreased during several years of poor flowering in the key winter nectar resource, spotted gum (Corymbia maculata). Similar to primates, restricted group size and the vulnerability of group structure to the prevailing food supply is likely to be one consequence of the high feeding rates that need to be maintained by the petaurid gliders.

Another consequence of time limitation may be a limited tolerance to habitat disturbance. Animal populations that experience habitat disturbance frequently adjust some components of their time budget to cope with the change (e.g. Johns 1986; Li and Rogers 2004; Behie and Pavelka 2005). However, Colobus vellerosus living in small fragments were found to have similar time budgets to those living in large fragments due to reduced levels of scramble
competition resulting from lower population density (Wong and Sicotte 2007). Thus, for species that are unable to alter their time budget to accommodate disturbance, a reduction in population density is the inevitable result.

The high proportion of time spent feeding in the time budgets of petaurids suggests that they are likely to be vulnerable to the effects of habitat disturbance (Goldingay 1989b). One prediction arising from this insight is that petaurid populations that experience reduced food availability, whether due to natural (e.g. Chapter 2) or anthropogenic causes, will not be able to forage more intensively in compensation. Therefore, a consequence of anthropogenic disturbance (e.g. selective tree removal) for petaurids is likely to be a decrease in population density. However, habitat fragments that are able to maintain a sufficient abundance of high quality foods may still be able to support high population densities (van der Ree 2002; Chapter 3).

7.3.2. Implications for Reproduction

It has been postulated that the timing of reproduction in petaurids is strongly influenced by the availability of protein (Smith 1982; Suckling 1984; Goldingay and Jackson 2004). In this study, squirrel gliders bred when arthropods were low in abundance, but there was abundant pollen. It is possible for petaurids to obtain sufficient dietary nitrogen from pollen (Smith and Green 1987), so the relative unavailability of arthropods may not be of consequence. However, other explanations for the timing of reproduction that are not mutually exclusive are also possible. Other factors may include the influence of rainfall and night length on the time budgets of the petaurids. These factors are likely to be of significance due to the high feeding rates that are maintained by these species (Goldingay 1989a, 1990; Quin 1993; Jackson and Johnson 2002; Holland et al. 2007; Chapter 6).

The squirrel glider produces most litters in late autumn/early winter (Quin 1995; Millis and Bradley 2001; van der Ree 2002; Chapters 2 and 3). Offspring remain in the pouch for about 2 months, before being deposited in the den until weaning, which occurs about 2 months later. Squirrel gliders are known to associate closely with reliable winter flowering trees (Menkhorst et al. 1988; Quin 1995; Sharpe and Goldingay 1998; Dobson et al. 2005; Chapter 2), providing ready access to energy and nitrogen (nectar and pollen). Long winter nights appear to provide gliders with more foraging opportunity than required to maintain energy balance, suggesting that parental care can be provided without the loss of feeding time in this season. Thus, females have considerable time to visit the den at night during late lactation to
feed their offspring. Males also spent a significant proportion of their time in the den during winter and may help with the care of offspring by assisting thermoregulation, as observed in the sugar glider (Holloway and Geiser 2000).

Because night length influences activity patterns, long night length may explain the general trend for petaurids to breed in late autumn/winter (Goldingay and Jackson 2004) so that late lactation occurs during winter when night length is near its maximum. This would enable the adult gliders sufficient time to provide parental care to the dependent offspring. Breeding occurs throughout the year in the nectarivorous honey possum (Tarsipes rostratus), but with few births over the summer months when night length is at its minimum (Renfree et al. 2004). Phalangerids have a peak of births in autumn, but their longer lactation periods indicate that other factors may influence the timing of breeding in this group (Kerle 1984). It is notable that folivorous species, such as the phalangerids, do not spend the majority of their activity period feeding (Jackson and Johnson 2002). Moreover, due to the long period of pouch life, the offspring would remain with the mother during winter nights. These factors indicate that phalangerids may not be constrained by night length.

Most petaurids also appear to avoid breeding during the time of year of heaviest rainfall, at least in high rainfall areas (e.g. Jackson 2001) (Table 7.2). Presumably, this is related to the likelihood that exudates will be depleted during wet periods (e.g. Law and Chidel 2008), resulting in lower activity levels (due to thermal effects), energetic stress and ultimately higher rates of mortality (e.g. Körtner and Geiser 2000).

Thus, protein availability, night length and the distribution of rainfall may all contribute to the timing of reproduction in different glider populations. A further consequence of this is that the timing of reproduction in relation to various seasonal constraints may limit the number of litters that can be raised in a year (e.g. Suckling 1984; Quin 1995).

7.4. Social Behaviour

The squirrel glider has been regarded as exhibiting a lower degree of sociality than other petaurids. This view was largely based on the low incidence of calling at sites at which it had been examined, the lack of a description of a characteristic call and a tendency toward social monogamy (Menkhorst 1995; Traill 1998). These findings were largely based on research conducted in Victoria and may not be reflective of the squirrel glider’s behaviour in other parts of its range.
Table 7.2: Timing of reproduction in the Petauridae in relation to the period of greatest rainfall.
Rainfall data from the authors or Bureau of Meteorology (2008). Note: rainfall in Victoria and southern NSW falls more evenly throughout the year with a minor peak during winter. W = winter, Sp = spring, Su = summer, A = autumn, All = throughout year.

<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
<th>Peak Birth Season</th>
<th>Peak Rainfall</th>
<th>Annual Rainfall (mm)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sugar glider</td>
<td>Rosedale, Sth Victoria</td>
<td>Sp</td>
<td>All,W</td>
<td>750</td>
<td>Suckling (1984)</td>
</tr>
<tr>
<td>Limeburner’s Creek, Nth coast NSW</td>
<td>W,Sp</td>
<td>Su,A</td>
<td>1550</td>
<td>Quin (1995)</td>
<td></td>
</tr>
<tr>
<td>Bungawalbin, NE NSW</td>
<td>W,Sp</td>
<td>Su,A</td>
<td>1100</td>
<td>Sharpe (unpublished data)</td>
<td></td>
</tr>
<tr>
<td>Muller’s Creek, Nth QLD</td>
<td>W</td>
<td>Su,A</td>
<td>2150</td>
<td>Jackson (2000a)</td>
<td></td>
</tr>
<tr>
<td>Leadbeater’s possum</td>
<td>Cambarville, Sth Victoria</td>
<td>W,Sp</td>
<td>All,W</td>
<td>1000</td>
<td>Smith (1984)</td>
</tr>
<tr>
<td>Yellingbo, Sth Victoria</td>
<td>All</td>
<td>All,W</td>
<td>1100</td>
<td>Harley and Lill (2007)</td>
<td></td>
</tr>
<tr>
<td>Squirrel glider</td>
<td>Euroa, Nth Victoria</td>
<td>W,Sp</td>
<td>All,W</td>
<td>650</td>
<td>van der Ree (2002)</td>
</tr>
<tr>
<td>Limeburner’s Creek, Nth coast NSW</td>
<td>W</td>
<td>Su,A</td>
<td>1550</td>
<td>Quin (1995)</td>
<td></td>
</tr>
<tr>
<td>Bungawalbin, NE NSW</td>
<td>A,W,Sp</td>
<td>Su,A</td>
<td>1100</td>
<td>Chapter 2</td>
<td></td>
</tr>
<tr>
<td>SE QLD</td>
<td>W,Sp</td>
<td>Su,A</td>
<td>1200</td>
<td>Millis and Bradley (2001)</td>
<td></td>
</tr>
<tr>
<td>Minnippi Parklands, SE QLD</td>
<td>A,W,Sp</td>
<td>Su,A</td>
<td>1200</td>
<td>Chapter 3</td>
<td></td>
</tr>
<tr>
<td>Mahogany glider</td>
<td>Muller’s Creek, Nth QLD</td>
<td>A,W</td>
<td>Su,A</td>
<td>2150</td>
<td>Jackson (2000a)</td>
</tr>
<tr>
<td>Yellow-bellied glider</td>
<td>Southern Victoria</td>
<td>Sp</td>
<td>All,W</td>
<td>1860</td>
<td>Henry and Craig (1984)</td>
</tr>
<tr>
<td>Bombala, Sth NSW</td>
<td>W</td>
<td>All,W</td>
<td>1167</td>
<td>Goldingay and Kavanagh (1990)</td>
<td></td>
</tr>
<tr>
<td>Kioaoa, Sth NSW</td>
<td>A</td>
<td>All,W</td>
<td>1050</td>
<td>Goldingay (1992)</td>
<td></td>
</tr>
<tr>
<td>Nth QLD</td>
<td>W</td>
<td>Su,A</td>
<td>2200</td>
<td>Goldingay et al. (2001)</td>
<td></td>
</tr>
</tbody>
</table>
A characteristic call has now been provided for the squirrel glider, which can be described as a repeated nasal grunt, described as “na” (Chapter 5). This call appears to be widely used in north-east NSW and south-east Qld, occurring at a mean rate of 0.25 h\(^{-1}\) across four sites. A variety of other calls were also described in Chapter 5. Although the frequency of calling by squirrel gliders is much less than reported for the yellow-bellied glider (Goldingay 1994), it was higher than that of sympatric sugar gliders (Chapter 5). Sympatric squirrel gliders and sugar gliders were both observed to respond to conspecific calls, including some occasions of mass calling (Chapter 5). Mahogany gliders were also found to vocalise infrequently and rarely responded to conspecifics (Jackson and Johnson 2002). It was hypothesised that the frequency of calling in the smaller petaurids relative to the yellow-bellied glider was reflective of an evolutionary progression from the regulation of individual spacing to territoriality, the latter being associated with higher rates of calling (Chapter 5).

The structure of squirrel glider groups is variable within and between sites, with both monogamy and polygyny being common at different sites (Quin 1995; van der Ree 2002; Sharpe and Goldingay 2007). Similar variability has been reported for other petaurids (Suckling 1984; Goldingay and Kavanagh 1990; Goldingay 1992; Sadler and Ward 1999; Goldingay et al. 2001). Moreover, group foraging, mainly during exudate feeding, was common for the squirrel glider in Brisbane (Chapter 6) and in the yellow-bellied glider (Goldingay 1989a, 1990). In contrast, group foraging appears to be rare in the mahogany glider (Jackson and Johnson 2002). Both the squirrel glider and the yellow-bellied glider maintain intra-group contact outside the den, indicating these species have similar social behaviour.

The vocal behaviour of the squirrel glider is similar to that of the sugar glider and the mahogany glider, but contrasts with that of the yellow-bellied glider. It was suggested in Chapter 5 that the apparent lack of calling by gliders in Victoria (Menkhorst 1995; Traill 1998) was not reflective of a regional difference, but was likely due to lower population densities and/or the spatial configuration of habitat in a fragmented landscape (e.g. linear habitat elements). Group structure and the incidence of group foraging in the squirrel glider is similar to that reported in some other petaurid studies. Accordingly, the squirrel glider’s social behaviour should be regarded as the equivalent to that of its conspecifics.
7.5. Habitat Fragmentation

Squirrel gliders have been able to persist in the fragmented landscapes. However, many of these populations inhabit relatively small habitat patches that are poorly connected to other local habitat areas (Rowston et al. 2002; van der Ree 2002; Smith and Murray 2003; Claridge and van der Ree 2004; Goldingay and Sharpe 2004a; Sharpe and Goldingay 2006). The provision of adequate dispersal habitat in fragmented landscapes can render the impact of fragmentation on population dynamics insignificant (Wiegand et al. 2005). Accordingly, connectivity between remnant patches of bushland is critical to the squirrel glider’s persistence in remnant habitat (Goldingay and Sharpe 2004a).

Research on the squirrel glider’s use of corridors has shown that they are capable of inhabiting narrow linear strips of vegetation (van der Ree 2002; van der Ree and Bennett 2003), even in heavily urbanised landscapes (Grimson 2006; Melton 2007). In urban Brisbane, the squirrel glider’s presence in corridors appeared to be more influenced by floristic composition (known food trees) and the presence of hollows than by the structure of the corridor (e.g. corridor length and width, tree density) (Melton 2007). Some corridors occupied by squirrel gliders were only one tree wide and others had a low tree density (see Melton 2007 and the photos provided therein). Corridors appeared to be used as both living (particularly larger corridors) and dispersal habitat. The extensive use of narrow corridors by the squirrel glider indicates that they are not an edge-sensitive species (i.e. they do not avoid habitat edges) (see van der Ree 2002).

Squirrel gliders are known to cross roads of varying widths and traffic volumes, particularly if there are fringing trees to permit gliding (van der Ree 2006; Melton 2007). Squirrel gliders are also known to make some use of matrix environment (e.g. large trees in yards and trees along busy roads) (Melton 2007). These findings show that the squirrel glider is somewhat tolerant of the noise, light and activity levels that characterise an urban environment and that the density of the tree cover will determine the permeability of the landscape.

Tree gaps of variable widths characterise fragmented forest habitats. Squirrel gliders are known to glide at a mean angle of 28.5º (Goldingay and Taylor 2009), which is similar to the 28-29º reported for the sugar glider and mahogany glider (Jackson 1999). This enables them to cross gaps of up to 75 m (van der Ree et al. 2003), although it is not clear whether such a distance would require some movement across the ground (personal observations), which would pose some risk of predation. Mean glide angles reflect a variety of different variables
(e.g. tree density, glide distance, tree form) (Goldingay and Taylor 2009) and it is instructive to look at the limits to the squirrel glider’s gliding performance. Goldingay and Taylor (2009) found that 33% of glides occurred at an angle of <25º, while van der Ree (2006) reported a glide angle of <20º by a glider volplaning across a four-lane freeway. These data indicate that it may be reasonable to assume a minimum glide angle of 20º for the squirrel glider. However, at this time it is not clear whether all individuals are capable of achieving shallower glide angles and what factors (e.g. wind exposure) may mitigate against gliders attaining maximum gliding performance. To be conservative, therefore, the value of 28.5º should be used to assess the squirrel glider’s ability to glide across gaps with different combinations of tree spacing and height. Thus, it is possible to assess the squirrel glider’s ability to move through fragmented environments without the need to conduct site-specific studies (see Goldingay and Taylor 2009).

7.6. Management

Although the squirrel glider has an extensive distribution (see Chapter 1), many of its populations are becoming increasingly vulnerable to the effects of habitat loss and fragmentation. These populations will need specific management attention to ensure their viability (Claridge and van der Ree 2004; Sharpe and Goldingay 2006). This section outlines management actions arising from the findings of this thesis that will assist in the conservation of the squirrel glider in fragmented habitats.

7.6.1. Detection Techniques

The ability to detect threatened species is the most fundamental step toward their effective management (e.g. Burbidge et al. 2007). Trapping, nest boxes and spotlighting are established methods for detecting arboreal marsupials, including the squirrel glider (Smith and Phillips 1984; Davey 1990; Quin 1995; van der Ree 2002; Smith and Murray 2003; Goldingay and Sharpe 2004b; Beyer and Goldingay 2006; Chapters 2 and 3). Trapping and spotlighting have been employed in both short- (e.g. during distribution studies) and long-term studies (e.g. population ecology studies) of the squirrel glider.

Many territorial species use calls to advertise territory ownership, which may elicit a response from conspecifics (Waser 1977; Lameira and Wich 2008). This means that call broadcasts can be used to survey for the presence of these species (e.g. Goldingay 1994). The success of spotlighting surveys can be greatly enhanced by the detection of squirrel glider vocalisations
A characteristic call of the squirrel glider was described in Chapter 5. Familiarity with this call should be requisite amongst field workers using spotlighting to detect squirrel gliders. However, there appears to be little value in the use of call playback to detect the squirrel glider because of the irregular pattern of calling and the low probability of a response from conspecifics (Chapter 5). The main value of using call playback would be to familiarise personnel with the squirrel glider’s call.

7.6.2. Habitat Consolidation and Connectivity

Wildlife may persist in fragmented landscapes while sufficient habitat remains available. Without conservation planning, however, continued habitat loss and fragmentation would at some point reach a threshold that is no longer sustainable (Harveson et al. 2007). The need to consolidate existing habitat patches and establish connecting corridors has been recognised for the squirrel glider (Rowston et al. 2002; Smith and Murray 2003; Claridge and van der Ree 2004; Goldingay and Sharpe 2004a). To achieve this it will be necessary to ensure an adequate supply of key food species, such as winter flowering trees (see below). Planting trees within gaps, mechanisms to ensure the perpetuation of dry sclerophyll forest (e.g. fire management) and weed control are actions likely to be required. Gliding poles may represent an interim measure to consolidate gaps between habitat patches (Ball and Goldingay 2008) and may be required long-term to facilitate road crossings where it is not possible to provide fringing trees (Sharpe and Goldingay 2006).

7.6.3. The Importance of Nectar

Many squirrel glider populations are dependent on nectar as a major source of exudate, particularly during winter and spring (Sharpe and Goldingay 1998; Dobson et al. 2005). Squirrel glider populations appear to be sensitive to the loss or failure of key winter/spring flowering tree species because the supply of alternative exudate sources seems to be poor at this time (Chapter 2). An inadequate supply of nectar can affect the squirrel glider by causing increased mortality and lower reproduction, which cause populations to decrease in size (Chapters 2 and 3).

The importance of nectar in the diet of the squirrel glider suggests that a sufficient number of individual winter/spring flowering trees across a number of species with overlapping flowering periods will be necessary to maintain functioning populations at many locations throughout its range (e.g. Menkhorst et al. 1988; Quin 1995; Sharpe and Goldingay 1998;
This will be important to consider in impact assessments because an insufficiency of one or two key tree species may be enough to threatened squirrel glider populations even if the remaining habitat is unaffected (Sharpe and Goldingay 2007). This could occur, for example, in a development scenario that removed one habitat type while leaving other habitat types untouched. A list of winter/spring flowering trees that squirrel gliders have been observed using is given in Table 7.3.

Table 7.3: Flowering trees known to be used by the squirrel glider in north-east NSW and south-east Qld.

Sources: Quin (1995), Sharpe and Goldingay (1998), Dobson et al. (2005). Chapter 2 and unpublished data. Additional information on flowering times from Stanley and Ross (1983; 1986; 1989) and Law et al. (2000). 1, sp = spring; au = autumn; su = summer; wi = winter; * = flowering; - = not flowering; (each season is shown in three parts indicating "early/mid/late")

<table>
<thead>
<tr>
<th>Plant Species</th>
<th>Common Name</th>
<th>Flowering Season¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>Angophora leiocarpa</td>
<td>rusty gum</td>
<td>**- **- *** --- ---</td>
</tr>
<tr>
<td>Banksia integrifolia</td>
<td>coast banksia</td>
<td>*** --- .** --- ---</td>
</tr>
<tr>
<td>B. serrata</td>
<td>saw banksia</td>
<td>.** **- *** --- ---</td>
</tr>
<tr>
<td>B. spinulosa</td>
<td>hairpin banksia</td>
<td>.** --- .** --- ---</td>
</tr>
<tr>
<td>Callistemon salignum</td>
<td>white bottle brush</td>
<td>*** --- --- --- ---</td>
</tr>
<tr>
<td>Corymbia gummifera</td>
<td>red bloodwood</td>
<td>--- .** **- *** ---</td>
</tr>
<tr>
<td>C. henryi</td>
<td>spotted gum</td>
<td>*** --- .** --- ---</td>
</tr>
<tr>
<td>C. intermedia</td>
<td>pink bloodwood</td>
<td>--- .** *** --- ---</td>
</tr>
<tr>
<td>C. tessellaris</td>
<td>carbeen</td>
<td>.** *** --- --- ---</td>
</tr>
<tr>
<td>Eucalyptus acmenoides</td>
<td>white mahogany</td>
<td>.** **- --- --- ---</td>
</tr>
<tr>
<td>E. amplifolia sessiliflora</td>
<td>cabbage gum</td>
<td>.** *** --- --- ---</td>
</tr>
<tr>
<td>E. carnea</td>
<td>broad-leaved white mahogany</td>
<td>**- **- --- ---</td>
</tr>
<tr>
<td>E. crebra</td>
<td>narrow-leaved ironbark</td>
<td>*** --- --- --- ---</td>
</tr>
<tr>
<td>E. fibrosa</td>
<td>broad-leaved ironbark</td>
<td>*** --- --- --- ---</td>
</tr>
<tr>
<td>E. pilularis</td>
<td>blackbutt</td>
<td>--- --- .** --- ---</td>
</tr>
<tr>
<td>E. racemosa</td>
<td>scribbly gum</td>
<td>.** *** --- --- ---</td>
</tr>
<tr>
<td>E. resinifera</td>
<td>red stringybark</td>
<td>.** **- --- --- ---</td>
</tr>
<tr>
<td>E. robusta</td>
<td>swamp mahogany</td>
<td>--- --- .** *** ---</td>
</tr>
<tr>
<td>E. seeana</td>
<td>narrow-leaved red gum</td>
<td>.** *** --- --- ---</td>
</tr>
<tr>
<td>E. siderophloia</td>
<td>northern grey ironbark</td>
<td>*** <strong>- --- .</strong> ---</td>
</tr>
<tr>
<td>E. tereticornis</td>
<td>forest red gum</td>
<td>*** --- .** --- ---</td>
</tr>
<tr>
<td>E. tindaliae</td>
<td>Tindale’s stringybark</td>
<td>--- --- .** *** ---</td>
</tr>
<tr>
<td>Lophostemon confertus</td>
<td>brush box</td>
<td>.** **- --- --- ---</td>
</tr>
<tr>
<td>L. suaveolens</td>
<td>swamp box</td>
<td>.** **- --- --- ---</td>
</tr>
<tr>
<td>Melaleuca quinquenervia</td>
<td>paperbark tea tree</td>
<td>*** --- *** --- ---</td>
</tr>
</tbody>
</table>
7.6.4. Population Viability Assessment

One of the major findings of this thesis was the extent of large fluctuations in population size that characterise squirrel glider populations using nectar as a major food source (Chapters 2 and 3). Population fluctuations were observed at both study sites over a collective period of about 10 years, suggesting that such fluctuations may be relatively common. The population fluctuations arise because of the large temporal variations in the availability of the nectar resource, which may be related to climate (Goldingay 1990; Law et al. 2000). A key consequence of this finding is that viable populations may need to be larger than previously thought because of the influence fluctuating population size has on the effective population size ($N_e$) (Vucetich et al. 1997, 2000; Reed et al. 2003). It is then necessary to ensure that an appropriate level of variability is used to model squirrel glider (meta-) populations in PVA studies.

The need to obtain quantitative estimates of survival in the squirrel glider for use in PVA was recognised at the beginning of this thesis. An earlier PVA on the squirrel glider by Goldingay and Sharpe (2004a) used a main survival rate (0.65) that was too high, which would have over-estimated population viability to a substantial degree. Sensitivity analysis was conducted to moderate the uncertainty associated with this estimate and this would have facilitated a more cautious viability prediction. Chapter 4 revealed that a more appropriate value would be 0.51 (but see caveat above). The under-estimation of the survival rate may have been a common flaw in PVA studies conducted so far on arboreal marsupials (see above). It is important that accurate survival estimates are used in PVA to ensure that population viability is not over-estimated.

7.7. Conclusion

A major finding that emerged from this thesis is the frequency and extent to which squirrel glider populations fluctuate in size. These fluctuations appeared to be influenced by variation in their nectar food resource. Further long-term studies in habitats containing winter flowering trees are required to confirm the generality and frequency of population changes. Studies that examine populations that are not nectar-dependent (e.g. Holland et al. 2007) should also be conducted to determine the extent of variability in these populations. Ideally, studies that involve food supplementation experiments during periods of low food availability are required to conclusively demonstrate the influence of food availability on population processes.
The squirrel glider is able to maintain self-sustaining populations in fragmented habitats. However, many populations in remnant habitat are small in size and may not be viable without ensuring that there is adequate connectivity between habitat patches. Moreover, the high proportion of the time budget devoted to feeding suggests that the squirrel glider is likely to be vulnerable to population declines associated with habitat disturbance. There is often ongoing development pressure affecting remnant habitat in fragmented landscapes (Smith and Murray 2003; Goldingay and Sharpe 2004a). In highly impacted landscapes considerable effort and money may be required to restore corridor connections between habitat patches.

PVA studies can help to determine how much habitat could be lost to development while still maintaining population viability. PVA can also provide guidance in relation to the number of habitat patches that may need to be connected to restore population viability. While PVA is valuable in providing relative comparisons between different development scenarios, the absolute predictions of a PVA should be treated with some caution due to uncertainty associated with model inputs and output (McCarthy et al. 2003). This study has provided updated density and survival estimates for the study system in which Goldingay and Sharpe (2004a) conducted a PVA study. This PVA should now be updated using the new input values. Given the on-going threat of habitat fragmentation to the squirrel glider, there will be a need to conduct similar PVA studies in different parts of its range.
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APPENDIX 1: PUBLICATIONS ARISING FROM THE THESIS

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The publisher's version of this article is available at http://dx.doi.org/10.1071/ZO08075