Ecology of arboreal marsupials in a network of remnant linear habitats

by

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Submitted in fulfillment of the requirements for the degree of Doctor of Philosophy

Deakin University, June 2000
I certify that the thesis entitled ‘Ecology of arboreal marsupials in a network of remnant linear habitats’ submitted for the degree of Doctor of Philosophy is the result of my own research, except where otherwise acknowledged, and that this thesis in whole or in part has not been submitted for an award, including a higher degree, to any other university or institution.

____________________________
Rodney van der Ree
June 25th 2000
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TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Chapter 1</th>
<th>General Introduction</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Habitat fragmentation and species decline 3</td>
</tr>
<tr>
<td></td>
<td>Linear landscape elements 3</td>
</tr>
<tr>
<td></td>
<td>The loss and fragmentation of temperate woodlands in Australia 3</td>
</tr>
<tr>
<td></td>
<td>Objectives and thesis structure 3</td>
</tr>
</tbody>
</table>

Chapter 2
The arboreal marsupial fauna of a landscape dominated by remnant linear woodland in north-eastern Victoria, Australia

<table>
<thead>
<tr>
<th>Chapter 2</th>
<th>The arboreal marsupial fauna of a landscape dominated by remnant linear woodland in north-eastern Victoria, Australia</th>
</tr>
</thead>
<tbody>
<tr>
<td>Introduction</td>
<td>3</td>
</tr>
<tr>
<td>Methods</td>
<td>3</td>
</tr>
<tr>
<td>Euroa floodplains study area</td>
<td>3</td>
</tr>
<tr>
<td>Study design and site selection</td>
<td>3</td>
</tr>
<tr>
<td>Mammal survey</td>
<td>3</td>
</tr>
<tr>
<td>Measurement of habitat features at survey sites</td>
<td>3</td>
</tr>
<tr>
<td>Statistical analysis</td>
<td>3</td>
</tr>
<tr>
<td>Results</td>
<td>3</td>
</tr>
<tr>
<td>Shape and arrangement of woodland habitat in the Euroa floodplains</td>
<td>3</td>
</tr>
<tr>
<td>Attributes of overstorey vegetation</td>
<td>3</td>
</tr>
<tr>
<td>Comparison of the arboreal marsupial assemblage between linear and non-linear remnants</td>
<td>3</td>
</tr>
<tr>
<td>Comparison of the arboreal marsupial assemblage between different types</td>
<td>3</td>
</tr>
</tbody>
</table>
Chapter 3
Habitat use by arboreal marsupials in a highly-fragmented linear landscape

Introduction 3
Methods 3
Study area 3
Trapping and animal handling techniques 3
Animal abundance 3
Habitat assessments 3
Statistical analysis 3
  Identification of vegetation groups 3
  Determining habitat preferences 3
Results 3
Attributes of remnant vegetation 3
  Linear network 3
  Description of vegetation groups 3
  Spatial arrangement of vegetation groups 3
Arboreal marsupials 3
  Abundance in the linear network 3
  Effect of width of linear remnants 3
  Dispersion of captures 3
Discussion 3
  Linear habitat network 3
  Habitat preferences of arboreal marsupials 3
Conclusions 3
Chapter 4
Population ecology of the Squirrel Glider *Petaurus norfolcensis*, within a network of remnant linear habitats

Introduction 3
Methods 3
Study area 3
Trapping and animal handling techniques 3
Age estimation 3
Female reproductive condition 3
Survival and longevity 3
Population size and density estimates 3
Social organisation and group composition 3
Results 3
Trappability of gliders 3
Population size and density estimates 3
Population structure and sex ratio 3
Recruitment, persistence and transients 3
Reproduction 3
Body weight 3
Social organisation 3
Discussion 3
Abundance and density 3
Population structure and sex ratio 3
Longevity, survival and dispersal 3
Reproduction 3
Social organisation 3
Conclusions 3

Chapter 5
Spatial arrangement of the Squirrel Glider *Petaurus norfolcensis*, in a network of remnant linear habitats

Introduction 3
Chapter 6
Use of den trees by the Squirrel Glider *Petaurus norfolcensis*, in a network of remnant linear habitats
Chapter 7

Synthesis of results and implications for management

Introduction
Patterns in the spatial configuration of habitat
Linear landscape elements as habitat for fauna
Important landscape and habitat features
  Large diameter trees
  Understorey characteristics
  Position on productive soils
Spatial configuration of woodland habitat
  An interconnected network of linear remnants
  Paddock clumps
  Edge effects and width
Implications for management and conservation

References

Appendices
LIST OF FIGURES

Figure 1.1. Outline of thesis. Chapter numbers are given in parentheses. 3

Figure 2.1. Location of the study area near Euroa, north-eastern Victoria. The inset shows the location of Euroa (solid square) within Victoria. The main diagram shows details of the Euroa floodplains study area (hatched area) and major roads and streams. 3

Figure 2.2. Plains grassy woodland, with overstorey *Eucalyptus* trees, shrubby midstorey and a grassy and herbaceous understorey along a roadside strip near Euroa. Photo: R. van der Ree 3

Figure 2.3. Aerial view of the agricultural landscape in the Euroa floodplains. Photo: A. Bennett. 3

Figure 2.4. Size-class distribution of woodland habitat patches (> 1 ha in size) within the Euroa floodplains study area. 3

Figure 2.5. Location of 42 survey sites in relation to the first two principal components from an ordination based on the basal area of tree species in linear and non-linear remnants near Euroa, north-eastern Victoria. 3

Figure 2.6. Mean abundance (+ 1 s.e.) of arboreal marsupials in linear and non-linear woodland remnants near Euroa. 3

Figure 2.7. Mean species richness and total number of arboreal marsupials (+ 1 s.e.) observed at each site in linear and non-linear remnants. 3

Figure 2.8. Mean abundance (+ 1 s.e.) of arboreal marsupials per site in linear remnants. 3

Figure 2.9. Mean species richness and total number of arboreal marsupials (+ 1 s.e.) per site in linear remnants. 3

Figure 3.1. The location and details of the trapping grid study area near Euroa in north-eastern Victoria. 3

Figure 3.2. Diagram of a linear strip showing three trap stations (A, B and C), 50 m sampling units (area between two vertical lines) and pooled 100 m transects (diagonal hatching) for each trap station. 3

Figure 3.3. Mean basal area (+ 1 s.e.) of overstorey *Eucalyptus* species and dead trees within 14.55 km of linear habitat trapped for arboreal marsupials. 3

Figure 3.4. Spatial arrangement of vegetation groups in a linear roadside network near Euroa, north-eastern Victoria. 3

Figure 3.5. The number of arboreal marsupials trapped along 14.55 km of linear remnants near Euroa between February 1997 and June 1998. 3

Figure 4.1. The location and details of the trapping grid near Euroa in north-eastern Victoria. 3
Figure 4.2. Trappability of *P. norfolcensis* during censuses in linear remnants near Euroa, north-eastern Victoria.

Figure 4.3. Population size estimates (MNKTBA) for *P. norfolcensis* during each census in linear habitats.

Figure 4.4. Estimated density of *P. norfolcensis* in linear habitats using the MNKTBA estimates of population size.

Figure 4.5. Age-structure of the population of *P. norfolcensis* living in the network of linear habitats at Euroa. Data are based on numbers known to be alive in each trapping census.

Figure 4.6. Capture status of individuals of *P. norfolcensis* in trapping sessions between February 1997 and May 1998 in a network of linear habitats near Euroa.

Figure 4.7. Number of resident *P. norfolcensis* disappearing from the trappable population between February 1997 and February 1998.

Figure 4.8. Reproductive condition of female *P. norfolcensis* captured between December 1996 and November 1998.

Figure 4.9. Estimated month of birth for litters of one (solid bars), two (open bars), or three young (diagonal hatching) between October 1996 and November 1998, near Euroa.

Figure 4.10. Variation in mean body weight (± s.e.) of adult (> 1 yr of age) *P. norfolcensis* between December 1997 and November 1998.

Figure 5.1. The location and details of the linear woodland remnants near Euroa in north-eastern Victoria where *P. norfolcensis* were radiotracked.

Figure 5.2. A) Calculation of range length as the sum of the two solid lines and B) calculation of home range area using the grid cell method as the sum of all grid cells. Solid squares denote telemetry fixes, shaded areas denote remnant woodland habitat and white denotes cleared agricultural land.

Figure 5.3. Cumulative range length vs. number of consecutive fixes for (A) five randomly selected male *P. norfolcensis* and (B) five randomly selected female *P. norfolcensis* radiotracked during summer or autumn 1998 in linear remnants near Euroa, north-eastern Victoria.

Figure 5.4. Mean perpendicular distance from the nearest wooded linear remnant to fixes of *P. norfolcensis* in small patches of woodland (paddock clumps) in the agricultural matrix.

Figure 5.5. Radiotracking locations (solid black squares) for *Petaurus norfolcensis* (Male 9) occupying a straight section of linear remnant.

Figure 5.6. Radiotracking locations (solid black squares) for *Petaurus norfolcensis* (Female 70) occupying a straight section of linear remnant adjacent to an intersection.
Figure 5.7. Radiotracking locations (solid black squares) for *Petaurus norfolcensis* (Male 31) occupying an intersection of linear remnants.  

Figure 5.8. Radiotracking locations (solid black squares) for *Petaurus norfolcensis* (Female 93) occupying an intersection of linear remnants.  

Figure 5.9. Home range overlap between individuals of *P. norfolcensis* occupying a straight section of linear remnant.  

Figure 5.10. Overlap of home ranges between adjacent social groups of *Petaurus norfolcensis* occupying an intersection between five linear remnants.  

Figure 6.1. Number of den trees used by individual *P. norfolcensis* in linear habitats near Euroa, north-eastern Victoria, as determined by radiotelemetry (n = 51 individuals).  

Figure 6.2. The cumulative number of den trees used by four *P. norfolcensis* in relation to the number of den tree locations.  

Figure 6.3. Proportional use of different den trees by female *P. norfolcensis* radiotracked in linear woodland remnants near Euroa, north-eastern Victoria.  

Figure 6.4. Proportional use of different den trees by male *P. norfolcensis* radiotracked in linear woodland remnants near Euroa, north-eastern Victoria.  

Figure 6.5. Distribution of den trees (solid black squares) and the sequence of consecutive days (numbers) at each den tree for *P. norfolcensis* Female 17.  

Figure 6.6. Distribution of den trees (solid black squares) and the sequence of consecutive days (numbers) at each den tree for *P. norfolcensis* Female 93.  

Figure 6.7. Distribution of den trees (solid black squares) and the sequence of consecutive days (numbers) at each den tree for *P. norfolcensis* Male 32.  

Figure 6.8. Distribution of den trees (solid black squares) and the sequence of consecutive days (numbers) at each den tree for *P. norfolcensis* Male 1.  

Figure 6.9. The percentage of den trees used by *P. norfolcensis* (open columns) and available trees (shaded columns) of each species within (A) linear remnants (n = 120 den trees) and (B) paddock clumps (n = 23).  

Figure 6.10. The percentage of den trees used by *P. norfolcensis* (open columns) and available trees (shaded columns) in each size class category (diameter at breast height) within (A) linear remnants (n = 120 den trees) and (B) paddock clumps (n = 23).
### LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.1</td>
<td>Basal area ($m^2$ ha$^{-1}$) of overstorey tree species at survey sites in linear and non-linear remnants.</td>
<td>3</td>
</tr>
<tr>
<td>2.2</td>
<td>Vector loadings on the first five axes of a principal components analysis of basal area for thirteen overstorey species in linear and non-linear remnants. The most highly correlated variables are given in bold.</td>
<td>3</td>
</tr>
<tr>
<td>2.3</td>
<td>Numbers of arboreal marsupials detected within 1.0 ha survey plots during spotlighting censuses, 1996.</td>
<td>3</td>
</tr>
<tr>
<td>3.1</td>
<td>Trapping transects established to census arboreal marsupials along roadsides and unused road reserves near Euroa, 1997 to 1998.</td>
<td>3</td>
</tr>
<tr>
<td>3.2</td>
<td>Summary of the size-class distribution of <em>Eucalyptus</em> stems and the number of hollow-bearing trees in the linear network near Euroa, north-eastern Victoria.</td>
<td>3</td>
</tr>
<tr>
<td>3.3</td>
<td>Comparison of structural and floristic habitat variables between vegetation groups.</td>
<td>3</td>
</tr>
<tr>
<td>3.4</td>
<td>Correlation coefficients for the relationship between basal area ($m^2$ ha$^{-1}$) of six <em>Eucalyptus</em> species at 99 trap stations in the linear network near Euroa.</td>
<td>3</td>
</tr>
<tr>
<td>3.5</td>
<td>Vector loadings on the first three axes of a principal components analysis of basal area for six <em>Eucalyptus</em> species. The most highly correlated variables are in bold.</td>
<td>3</td>
</tr>
<tr>
<td>3.6</td>
<td>Trapping results for arboreal marsupials in 14.55 km of remnant linear woodland near Euroa, north-eastern Victoria.</td>
<td>3</td>
</tr>
<tr>
<td>3.7</td>
<td>Effect of linear remnant width within vegetation group one on abundance indices of arboreal marsupials.</td>
<td>3</td>
</tr>
<tr>
<td>3.8</td>
<td>Abundance indices for each species of arboreal marsupial and all arboreal marsupials combined, in 20 m wide linear strips in three vegetation groups.</td>
<td>3</td>
</tr>
<tr>
<td>3.9</td>
<td>Correlation coefficients between indices of arboreal marsupial abundance and habitat variables.</td>
<td>3</td>
</tr>
<tr>
<td>3.10</td>
<td>Significant structural and floristic habitat variables influencing arboreal marsupial abundance indices identified through multiple stepwise regression modeling.</td>
<td>3</td>
</tr>
<tr>
<td>4.1</td>
<td>Parameters used to estimate ages of <em>P. norfolcensis</em> (modified from Suckling 1984; Quin 1995; Jackson 2000).</td>
<td>3</td>
</tr>
</tbody>
</table>
Table 4.2. Sex ratio (males : females) of juveniles (< 1 yr), adults (> 1 yr) and all gliders in a population of *P. norfolcensis* in a network of linear habitats near Euroa, north-eastern Victoria.

Table 4.3. Recruitment of *P. norfolcensis* by age and sex into a population inhabiting a network of linear habitats near Euroa, north-eastern Victoria.

Table 4.4. Summary of reproductive data for adult *P. norfolcensis* occupying linear habitats near Euroa, between 1996 and 1998.

Table 4.5. Composition of social groups of *P. norfolcensis* in summer, 1997-1998.

Table 4.6. Comparison of the population dynamics of *P. norfolcensis* populations at Euroa and elsewhere in Australia.

Table 5.1. Summary of radiotracking effort for adult *P. norfolcensis* tracked in linear woodland remnants during each season in 1997-1998.

Table 5.2. Comparison of home range estimates for adult *P. norfolcensis* radiotracked during each season within a network of linear habitats near Euroa, 1998.

Table 5.3. Comparison of home range size (ha) of four adult *P. norfolcensis* radiotracked in three or four seasons in linear habitats near Euroa, 1998. Home range area was derived using the grid cell estimator with 95% of fixes.

Table 5.4. A comparison of home range estimates for adult *P. norfolcensis* occupying straight sections or junctions of linear habitats. All data are from animals radiotracked in autumn 1998.

Table 5.5. Summary of radiotracking effort for juvenile *Petaurus norfolcensis* radiotracked in linear habitats near Euroa, in autumn 1998. Includes all juveniles with more than 25 fixes collected over a minimum of 20 days.

Table 5.6. Characteristics of home ranges of juvenile *Petaurus norfolcensis* based on a minimum of 20 days of tracking and 25 independent fixes.

Table 5.7. Comparison of floristic and structural habitat variables within linear habitats positioned near (< 100 m) and far (> 500 m) from the intersection of linear habitats.

Table 6.1. Number of individuals and number of diurnal radio-tracking locations obtained for 51 *P. norfolcensis* radiotracked in linear remnants of woodland near Euroa, north-eastern Victoria.

Table 6.2. Characteristics of the denning range of *P. norfolcensis* in comparison with 95% home range estimates.

Table 6.3. Number of radiocollared *P. norfolcensis* occupying each den tree during 1997 - 1998 as determined by radiotelemetry.
Table 6.4. Number of denning records in each den tree by eight radio-tracked *P. norfolcensis* occupying a continuous 2.1 km section of roadside vegetation in summer 1997-1998.

Table 6.5. Characteristics of den trees utilised by *P. norfolcensis*
ABSTRACT

Linear strips of vegetation set within a less-hospitable matrix are common features of landscapes throughout the world. Depending on location, form and function, these linear landscape elements include hedgerows, fencerows, shelterbelts, roadside or streamside strips and wildlife corridors. In many anthropogenically-modified landscapes, linear strips are important components for conservation because they provide a large proportion of the remaining wooded or shrubby habitat for fauna. They may also function to provide connectivity across the landscape. In some districts, the linear strips form an interconnected network of habitat.

The spatial configuration of remnant habitat (size, shape and arrangement) may influence habitat suitability, and hence survival, of many species of plant and animal in modified landscapes. Near Euroa in south-eastern Australia, the clearing and fragmentation of temperate woodlands for agriculture has been extensive and, at present, less than 5% tree cover remains, most of which (83%) occurs as linear strips along roads and streams. The remainder of the woodland occurs as relatively small patches and single isolated trees scattered across the landscape. As an assemblage, arboreal marsupials are woodland dependent and vary in their sensitivity to habitat loss and fragmentation.

This thesis focusses on determining the conservation status of arboreal marsupials in the linear network and understanding how they utilise the landscape mosaic. Specifically, the topics examined in this thesis are: (1) the composition of the arboreal marsupial assemblage in linear and non-linear woodland remnants; (2) the status and habitat preferences of species of arboreal marsupial within linear remnants; and (3) the ecology of a population of the Squirrel Glider *Petaurus norfolcensis* in the linear network, focusing on population dynamics, spatial organisation, and use of den trees.

The arboreal marsupial fauna in the linear network was diverse, and comprised seven out of eight species known to occur in the district. The species detected
within the strips were *P. norfolcensis*, the Sugar Glider *Petaurus breviceps*, Common Brushtail Possum *Trichosurus vulpecula*, Common Ringtail Possum *Pseudocheirus peregrinus*, Brush-tailed Phascogale *Phascogale tapoatafa*, Koala *Phascolarctos cinereus* and Yellow-footed Antechinus *Antechinus flavipes*. The species not detected was the Feathertail Glider *Acrobates pygmaeus*. Survey sites in linear remnants (strips of woodland along roads and streams) supported a similar richness and density of arboreal mammals to sites in non-linear remnants (large patches or continuous tracts of woodland nearby). Furthermore, the combined abundance of all species of arboreal marsupials was significantly greater in sites in the linear remnants than in the non-linear remnants. This initial phase of the study provided no evidence that linear woodland remnants support a degraded or impoverished arboreal marsupial fauna in comparison with the non-linear remnants surveyed.

Intensive trapping of arboreal marsupials within a 15 km linear network between February 1997 and June 1998 showed that all species of arboreal marsupial (except *A. pygmaeus*) were present within the linear strips. Further analyses related trap-based abundance estimates to measures of habitat quality and landscape structure. Width of the linear habitat was significantly positively correlated with the combined abundance of all arboreal marsupials, as well as with the abundance of *P. norfolcensis* and *T. vulpecula*. The abundance of *T. vulpecula* was also significantly positively correlated with variation in overstorey species composition, *Acacia* density and the number of hollow-bearing trees. The abundance of *P. norfolcensis* was positively correlated with *Acacia* density and canopy width, and negatively correlated with distance to the nearest intersection with another linear remnant. No significant variables were identified to explain the abundance of *P. tapoatafa*, and there were insufficient captures of the remaining species to investigate habitat preferences.

*Petaurus norfolcensis* were resident within the linear network and their density (0.95 - 1.54 ha⁻¹) was equal to the maximum densities recorded for this species in continuous forest elsewhere in south-eastern Australia. Rates of reproduction were also similar to those in continuous forest, with births occurring between May and December, a mean natality rate of 1.9, and a mean litter size of 1.7. Sex ratios
never differed significantly from parity. Overall, the population dynamics of *P. norfolcensis* were comparable with published results for the species in contiguous forest, clearly suggesting that the linear remnants currently support a self-sustaining, viable population.

Fifty-one *P. norfolcensis* were fitted with radio transmitters and tracked intermittently between December 1997 and November 1998. Home ranges were small (1.3 - 2.8 ha), narrow (20 - 40 m) and elongated (322 - 839 m). Home ranges were mostly confined to the linear remnants, although 80% of gliders also utilised small clumps of adjacent woodland within farm paddocks for foraging or denning. Home range size was significantly larger at intersections between two or more linear remnants than within straight sections of linear remnants. Intersections appeared to be important sites for social interaction because the overlap of home ranges of members of adjacent social groups was significantly greater at intersections than straight sections. Intersections provided the only opportunity for members of three or more social groups to interact, while still maintaining their territories.

The 51 gliders were radiotracked to 143 different hollow-bearing trees on 2081 occasions. On average, gliders used 5.3 den trees during the study (range 1 - 15), and changed den trees every 4.9 days. The number of den trees used by each glider is likely to be conservative because the cumulative number of den trees continued to increase over the full duration of the study. When gliders shifted between den trees, the mean distance between consecutive den sites was 247 m. Den trees were located throughout a glider's home range, thereby reducing the need to return to a central den site and potentially minimising energy expenditure. Dens were usually located in large trees (mean diameter 88.5 cm) and were selected significantly more often than expected based on their occurrence within the landscape.

The overall conclusion of this thesis is that the linear network I studied provides high quality habitat for resident populations of arboreal marsupials. Important factors influencing the suitability of the linear remnants appear to be the high level of network connectivity, the location on soils of high nutrient status, the high
density of large trees and an acacia understorey. In highly fragmented landscapes, linear habitats as part of the remaining woodland mosaic have the potential to be an integral component in the conservation of woodland-dependent fauna. The habitat value of linear strips of vegetation should not be underestimated.
CHAPTER 1
GENERAL INTRODUCTION

Habitat fragmentation and species decline

The loss, fragmentation and degradation of natural habitat and the alteration of ecological processes that follow are considered primary threats to maintaining biological diversity (Harris 1984; Wilcox and Murphy 1985; Wilcove et al. 1986; Saunders et al. 1991; Hobbs 1993b; Houghton 1994; Collinge 1996; Bennett 1999). Habitat fragmentation is the process of dividing a once continuous habitat into smaller pieces, resulting in the loss of habitat, a reduction in the size of remaining habitat patches, and an increase in the isolation of the patches as the matrix expands (Andren 1994; Collinge 1996; Forman 1997; Bennett 1999). While generalised models of habitat fragmentation have been proposed, a wide range of land conversion patterns based on the spatial configuration (i.e. amount and arrangement) of remnant habitat are also evident (McIntyre and Barrett 1992; Collinge and Forman 1998; Hobbs and Wilson 1998). Landscapes fall into a continuum from intact through variegated, fragmented and relictual, with each level containing decreasing proportions of natural vegetation and concomitant increases in the modification of what remains (McIntyre and Hobbs 1999). In these anthropogenically-modified landscapes, regular shapes predominate, and linear strips of vegetation characterise many agricultural landscapes throughout the world (Burel 1996; Forman 1997).

Regardless of the spatial configuration of habitat, the biological consequences of habitat fragmentation are potentially widespread and pervasive (Harrison and Bruna 1999). They include the loss of species, changes to the composition of faunal assemblages and the alteration and disruption of ecosystem processes (Saunders et al. 1991). After the initial clearing ceases, fluxes of radiation, wind, water and nutrients across the landscape may be altered, and it is these changes
that may cause further degradation of habitat resulting in the loss of species (Hobbs and Saunders 1993).

Two major ecological paradigms have dominated approaches to understanding the effects of habitat fragmentation on the biota (Harrison and Bruna 1999). The first, island biogeography theory (MacArthur and Wilson 1967) was developed for oceanic islands and explored the role of island size and distance from the mainland on species richness. The theory was later applied to habitat patches in fragmented terrestrial systems (Diamond 1975). The second, metapopulation dynamics (Levins 1969; Hanski and Gilpin 1991), considers the spatial structure of sub-divided populations and the dynamics of extinction and recolonisation in sub-populations, and their combined effect on the persistence of the overall metapopulation. Consequently, much research investigating the impacts of habitat fragmentation has focussed on discrete patches of habitat, often block-shaped, with special consideration given to patch size and level of isolation. Research has demonstrated that the consequences of habitat loss and fragmentation for fauna differ according to the amount and spatial configuration of the remaining habitat (Franklin and Forman 1987; Rolstad and Wegge 1987; Opdam 1991; Harper et al. 1993; Ims et al. 1993; Wiens et al. 1993; Hanski 1995; Collinge 1996; Forman and Collinge 1997; Collinge and Forman 1998). Therefore, when habitats are arranged in novel spatial configurations, such as networks of linear strips, it is imperative that landscape-specific studies be undertaken to investigate the effects of habitat loss and fragmentation.

A major driving force in fragmented landscapes appears to be the direct or indirect impact on remnants of processes originating in the surrounding structurally-dissimilar matrix (Janzen 1986; Saunders et al. 1991; Gascon et al. 1999). As a result of habitat clearing there is an increase in the amount of edge, defined as the junction of two different landscape elements (Yahner 1988), which exposes a greater proportion of the remnant vegetation to a diverse array of biotic and abiotic effects (Laurance and Yensen 1991; Collinge 1996). Changes at edges often have negative impacts on biodiversity conservation and can extend for large distances into remnants depending on habitat type, time since disturbance and the type of process being considered (Murcia 1995). Such 'edge effects' include the
alteration of microclimatic conditions (Kapos 1989; Turton and Freiburger 1997; Esseen and Renhorn 1998), elevated rates of nest predation (Paton 1994; Major et al. 1999b), changes to the structure and composition of the vegetation (Chen et al. 1992; Laurance 1997a), and increased soil nutrient levels (Cale and Hobbs 1991). The size and shape of a patch determine the amount of 'core' area that remains unaffected from edge effects because they influence the length of edge exposed to the matrix (Laurance and Yensen 1991; Collinge 1996). For example, with an edge effect that extends for 20 m, the amount of core area within a 1.0 ha linear strip of less than 40 m in width will be zero; the amount of core area in a circular patch of the same size will be 42% of the total area. Consequently, remnant habitats that are small or linear in shape will contain a lower proportion of core habitat than larger or block-shaped patches, and hence may be sub-optimal habitat for many species (Laurance and Yensen 1991; Collinge 1996).

**Linear landscape elements**

Linear landscape elements are common features in human-modified landscapes throughout the world, including urban, rural, and forest-dominated areas (Forman 1997; Bennett 1999). In urban areas, linear strips of vegetation often occur along streams, roads, railway reserves, other utility rights-of-ways and recreational paths (Hay 1991; Low 1991; Cilliers and Bredenkamp 1998, 2000). In forest-dominated landscapes, linear landscape elements may be openings in the forest canopy associated with roads and utility easements (Askins 1994; Rich et al. 1994; Ferris-Kaan 1995; Reed et al. 1996), or, they can be buffer strips of trees or reserved forest between adjacent clearcuts (Claridge and Lindenmayer 1994; Hagar 1999). In agricultural landscapes, linear landscape elements include hedgerows and fencerows (Burel and Baudry 1990; Watt and Buckley 1994; Burel 1996), riparian vegetation (Keller et al. 1993; de Lima and Gascon 1999), vegetation along roadsides (Bennett 1991), and planted shelterbelts or windbreaks (Yahner 1983; Schroeder et al. 1992). Depending on form and location, linear strips of vegetation fulfill a variety of functions that include the provision of recreational opportunities, improved landscape aesthetics, enhanced agricultural
productivity, maintenance of ecosystem processes and the conservation of biodiversity (Forman 1997).

In this thesis, references to linear landscape elements, such as linear habitats, linear remnants or linear strips, refers primarily to relatively narrow rows of trees or shrubs that enclose or separate cleared land used for agriculture (Forman and Baudry 1984; Burel 1996). Their distribution, floristic composition and structure has been studied in Sweden (Sarlöv Herlin and Fry 2000), Canada (Fritz and Merriam 1994), Great Britain (Helliwell 1975; Conyers 1986), France (Burel and Baudry 1990; Burel 1996), USA (Riffell and Gutzwiller 1996) and Australia (Hibberd and Soutberg 1991; Hussey 1991; Lamont and Blyth 1995). Their origins are diverse, and include vegetation remaining after clearing, plantings for a range of purposes, or spontaneous growth at the less-cultivated margins of fields (Burel 1996). The occurrence, structure and composition of the linear strips is largely dependent on surrounding land-uses and the level of human intervention (Forman and Baudry 1984; Burel 1996). In Europe, certain hedgerows may even date back hundreds of years to Roman times (Morgan Evans 1994; Kotzageorgis and Mason 1997).

In highly cleared landscapes, linear strips of vegetation are likely to be important for conservation because they may represent the last remaining examples of certain floristic communities. Numerous studies have documented that linear strips of vegetation may provide permanent or occasional habitat for a wide range of species of fauna, including birds (Osborne 1984; Arnold and Weeldenburg 1990; Cale 1990; Saunders and de Rebeira 1991; Parish et al. 1994; Parish et al. 1995; Hagar 1999), mammals (Yahner 1983; Bennett 1990a; Merriam and Lanoue 1990; Downes et al. 1997a; Kotzageorgis and Mason 1997; Laurance and Laurance 1999), amphibians (de Lima and Gascon 1999) and invertebrates (Eversham and Telfer 1994; Hill 1995; Major et al. 1999c). The abundance and richness of species within linear strips has been related to structural or floristic characteristics of the habitat (Yahner 1983; Osborne 1984; Arnold and Weeldenburg 1990; Merriam and Lanoue 1990; Parish et al. 1994; Parish et al. 1995), measures of isolation from other habitat patches (Yahner 1983; Arnold and Weeldenburg 1990; Kotzageorgis and Mason 1997), habitat width (Arnold and
Weeldenburg 1990; Cale 1990; Parish et al. 1995; Hagar 1999; Laurance and Laurance 1999), or the rate of predation (Major et al. 1999b).

Linear strips of habitat may also fulfill a conduit role and assist in allowing the movement of biota across the landscape (Beier and Noss 1998; Bennett 1999). However, the effectiveness of wildlife corridors as pathways for movement in fragmented landscapes is scant and subject to ongoing debate (Simberloff and Cox 1987; Bennett 1990b; Hobbs 1992; Simberloff et al. 1992; Hess 1994; Simberloff and Tebo 1994; Wilson and Lindenmayer 1995; Rosenberg et al. 1997; Beier and Noss 1998; Hobbs and Wilson 1998; Bennett 1999). The major constraint in ascertaining the biological value of movement corridors is the difficulty associated with designing and implementing rigorous studies in real landscapes (Nicholls and Margules 1991; Inglis and Underwood 1992; Beier and Noss 1998). Nonetheless, a recent review of corridor studies (Beier and Noss 1998) concluded that of the 12 studies that allowed meaningful inferences of their conservation value, 10 offered persuasive evidence that corridors provided adequate levels of connectivity to improve the viability of the connected populations. Further, none of the studies reviewed by Beier and Noss (1998) offered any evidence documenting the negative impacts from corridors.

However, the conservation potential of linear strips of vegetation as habitat may be limited by the constraints of patch size and shape, the influence of edge effects and ongoing habitat loss or degradation. Consequently, linear strips may be unable to support the full assemblage of species that occurs in continuous tracts of similar habitat (Arnold and Weeldenburg 1990; Cale 1990; Hill 1995; Laurance and Laurance 1999; Major et al. 1999c). Furthermore, the presence and abundance of common or generalist species may increase. Clearly, there is still a dearth of information on the occurrence and ecology of species utilising linear strips. Moreover, a thorough understanding of the ecological processes and ecosystem function of linear strips, and their effect on the conservation of biodiversity, is also currently lacking.
The loss and fragmentation of temperate woodlands in Australia

In Australia, the clearing of forests and woodlands for agriculture since European settlement has caused profound changes to the extent and structure of the vegetation (Graetz et al. 1995; Norton 1997). The temperate woodlands of eastern and south-western Australia have been drastically modified and, at present, there is an estimated 10 - 15% of such woodland remaining (Robinson and Traill 1996). Moreover, much of the remaining temperate woodland now occurs as small and often isolated remnants (Woodgate and Black 1988; Prober and Thiele 1993; Saunders et al. 1993; Bennett et al. 1994b; Robinson and Traill 1996; Bennett and Ford 1997; Norton 1997; Fisher and Harris 1999). Degrading processes have continued since the initial clearing and, consequently, many remnants are now highly disturbed due to grazing by domestic stock and introduced herbivores, cultivation, mining, weed invasion, nutrient input, or altered fire regimes (Prober and Thiele 1993; Muir et al. 1995; Robinson and Traill 1996; Norton 1997; NRE 1997; Raven 1997; Bennett et al. 1998). The general prediction for the temperate woodlands of Australia, and indeed in fragmented landscapes internationally, is that small reserves and linear habitats and much of the fauna contained within, are unlikely to be viable in the long-term (Hobbs 1993a; Goldney et al. 1995; Harrison and Bruna 1999).

In the Northern Plains region of Victoria, there is now less than 6% tree cover (Bennett and Ford 1997), and much of what remains occurs as small patches (<30 ha) or linear strips along roads and streams (Bennett et al. 1994b). However, at least eight species of arboreal and scansorial marsupial still occur in this region (Bennett et al. 1991). Arboreal mammals are an appropriate group to investigate the impacts of habitat fragmentation because they are woodland dependent (Tyndale-Biscoe and Calaby 1975) and display a suite of traits that increases their proneness to extinction (Laurance 1991a). These interacting factors may include body size, longevity, fecundity, mobility, trophic level, dietary specialisation, natural abundance or density, abundance in the cleared matrix and ubiquity (Laurance 1991a; Mac Nally and Bennett 1997). In the Northern Plains, the assemblage of arboreal marsupials includes species that range from being common and widespread, such as the Common Brushtail Possum Trichosurus
vulpecula, to the rare and localised Brush-tailed Phascogale *Phascogale tapoatafa* (Bennett *et al.* 1998).

As a group, the ecology and biology of many species of arboreal marsupial have been relatively well-studied (e.g. Smith and Hume 1984; Menkhorst 1995; Lindenmayer 1996). However, the majority of studies have been undertaken in large patches or forest-dominated landscapes and in a comparative sense, there is little knowledge or understanding about the distribution or ecology of species within fragmented landscapes. The paucity of knowledge in rural landscapes is of particular concern because the preferred habitat of some species (e.g. *P. norfolcensis*) coincided with prime agricultural land (Menkhorst *et al.* 1988). Consequently, the conservation of such species will depend upon the appropriate management of the remaining small fragments of habitat scattered within a cleared agricultural matrix.

To develop an effective conservation strategy for arboreal marsupials in fragmented landscapes, a thorough understanding of their conservation status and the factors that influence their distribution and abundance is required. To achieve this, we need species-specific information gathered from within fragmented landscapes as well as continuous tracts of habitat. In the first instance, landscape scale patterns of species distribution and abundance need to be elucidated. Once populations have been identified and located, the dynamics of the population, including rates of reproduction, longevity and mortality, need to be measured and described to determine if populations are self-sustaining. This will allow the identification of habitat patches that are critical to species persistence. In addition, detailed assessments of movement patterns will assist in the identification of other important landscape elements (Merriam 1988; Ims *et al.* 1993; McIntyre and Wiens 1999). Finally, critical habitat components or resources need to be recognised and managed in order to ensure an adequate supply into perpetuity.
Objectives and thesis structure

The overall aim of this thesis is to investigate the ecology of arboreal marsupials in a network of remnant linear wooded habitats. The specific objectives are:

1) to determine the distribution and abundance of arboreal marsupials in linear and non-linear remnant woodland at a landscape scale;
2) to identify landscape and habitat features that influence the distribution and abundance of arboreal marsupials within linear remnants; and
3) to investigate the ecology of *P. norfolcensis* within linear remnants to determine if the population was self-sustaining.

This thesis is divided into seven chapters (Fig. 1.1), of which five (Chapters 2 - 6) that outline results of field investigations have been written as self-contained manuscripts to facilitate subsequent publication. Consequently, these chapters contain separate introductions, methods, results, discussions and conclusions. Repetition between chapters has been reduced by compiling single abstract, bibliography and acknowledgements sections.

The first results chapter (Chapter 2) takes a landscape scale approach to investigating the distribution and abundance of arboreal marsupials within remnants of different size and shape. The focus of this chapter is to compare the arboreal marsupial assemblage occurring within linear remnants and larger blocks of habitat. After identifying a geographically smaller study area, the distribution and abundance of arboreal marsupials within a network of linear remnants is described (Chapter 3). In subsequent chapters, the results of an investigation of the ecology of one species, *P. norfolcensis*, in the linear network, is detailed. *P. norfolcensis* was selected for study because in south-eastern Australia, it mostly occurs in many small, linear and isolated fragments of woodland and is consequently rare and threatened with extinction (NRE 1999). The population dynamics of *P. norfolcensis* is detailed in Chapter 4, followed by an investigation of the species' spatial organisation and movement patterns (Chapter 5), and their utilisation of den trees (Chapter 6). The thesis concludes with a general
discussion that provides a synthesis of the results and their implications for management (Chapter 7).
Figure 1.1. Outline of thesis. Chapter numbers are given in parentheses.
CHAPTER 2
THE ARBOREAL MARSUPIAL FAUNA OF A LANDSCAPE DOMINATED BY REMNANT LINEAR WOODLAND IN NORTH-EASTERN VICTORIA, AUSTRALIA

INTRODUCTION

The clearing and replacement of natural habitats with human-modified landscapes is a widespread phenomenon around the world (Houghton 1994). The loss and fragmentation of natural habitats by anthropogenic causes typically creates a mosaic of fragments of natural habitat of varying size, shape, and spatial arrangement, set within a modified matrix (Forman 1997). Linear strips of vegetation are conspicuous components of many landscapes, including both urban and rural areas (Bennett 1999). Linear landscape elements are common in agricultural regions and include hedgerows (e.g. Burel 1996), fencerows (e.g. Fritz and Merriam 1993), vegetation along roadsides (e.g. Lynch et al. 1995) or streamsides (e.g. Hill 1995), as well as linear plantations to enhance agricultural productivity or provide movement corridors for fauna (e.g. Haas 1995). In some landscapes, linear strips make up a large proportion of the natural or semi-natural wooded vegetation and may form an interconnected network of habitats (e.g. Forman and Baudry 1984; Burel and Baudry 1990).

In many developed landscapes, the conservation of biodiversity is reliant on fragments of natural vegetation. In landscapes dominated by linear strips of wooded or shrubby vegetation, species occupying these habitat types must be able to survive within narrow, elongated habitats. However, linear habitats have been predicted to be sub-optimal for many species because of a variety of deleterious effects associated with the proximity of the modified matrix, often termed 'edge effects' (Murcia 1995). Linear fragments are spatially limited, and species with large area requirements or low levels of mobility are likely to be disadvantaged (Laurance 1991a). Other factors impacting on species survival within narrow
linear habitats are common to many fragmented landscapes and include the overall amount of suitable habitat in the landscape (Andren 1994) and the level of connectivity with other populations (Fahrig and Merriam 1985). Consequently, it has been predicted that not all species of fauna can survive in small patches or linear strips of habitat (Hobbs 1993a; Goldney et al. 1995; Harrison and Bruna 1999). Therefore, it is essential that the efficacy of linear strips as habitat for fauna be assessed and compared with that of larger patches of habitat.

This study examines the use of linear wooded habitats by arboreal marsupials in a rural environment in north-eastern Victoria. Arboreal marsupials were selected for study because they are widespread across the temperate Eucalyptus woodlands of south-eastern Australia (Menkhorst 1995c). As an assemblage, they are woodland dependent and are not able to persist in completely cleared landscapes (Tyndale-Biscoe and Calaby 1975). Furthermore, each species of arboreal marsupial may be expected to display different responses to habitat loss and fragmentation because of specific ecological and biological traits that will influence their proneness to extinction (Pahl et al. 1988; Laurance 1991a).

The ecology of arboreal marsupials within continuous tracts of forest and woodland has been studied extensively in eastern Australia (e.g. Smith and Hume 1984; Goldingay and Kavanagh 1991; Quin 1995; Lindenmayer 1997). However, we know less about the response of arboreal marsupials to habitat loss and fragmentation due to a paucity of ecological studies addressing this issue. The few studies investigating this have been undertaken in Victoria (Suckling 1984; Downes et al. 1997a) and north Queensland (Pahl et al. 1988; Laurance 1990; Laurance and Laurance 1999). While linear habitats or corridors were part of the survey design in all these studies (except Pahl et al. 1988), none were undertaken in landscapes with less than 5% tree cover; or, where the majority of suitable habitat was arranged as a network of linear strips. As the autecology of some species may vary according to landscape type (e.g. Barbour and Litvaitis 1993; Harper et al. 1993; Wauters et al. 1994; Major et al. 1999), it may be inappropriate to extrapolate the findings from forest-dominated landscapes to those dominated by linear habitats (Wilson and Lindenmayer 1995).
This chapter has two broad aims: first, to describe the spatial configuration of remnant woodland within the study area in north-eastern Victoria, and second, to describe broad patterns in the distribution and abundance of arboreal marsupials in woodland remnants within the study area. The specific objectives of this study were:

1) to measure and describe the amount, shape and arrangement of remnant woodland in the Euroa floodplains study area; and

2) to survey the composition of the arboreal marsupial assemblage in linear and non-linear woodland remnants, and to compare the richness and abundance of arboreal marsupials at survey sites in linear and non-linear remnants.

METHODS

Euroa floodplains study area

The *Eucalyptus* woodlands of temperate Australia formerly extended across a vast portion of south-eastern and south-western Australia (Robinson and Traill 1996). There is now, at a continental scale, approximately 10 - 15% of tree cover remaining in this zone (Robinson and Traill 1996). In the Northern Plains region of Victoria, south-eastern Australia, extensive clearing of the temperate eucalypt woodlands for agriculture commenced in the late 1860s (LCC 1983). By the 1880s, most land had been surveyed and was either privately owned or leased for agriculture (LCC 1983). It is estimated that in 1869, prior to large-scale clearing, 76% of the Northern Plains contained woodland cover - the remaining 24% being native grasslands (Woodgate and Black 1988). In 1993, less than 6% of the Northern Plains contained tree cover, and almost all native grasslands had been eradicated (Bennett *et al.* 1998). Other than woodlands along the major river systems, most remnant vegetation in the Northern Plains occurs as small patches (<30 ha) or as linear strips along roads and streams (Bennett *et al.* 1994b). In addition to the extensive loss of habitat, all remnant vegetation has been disturbed and degraded to some extent since European settlement, either by mining, timber
harvesting, stock grazing, weed invasion, or soil degradation (Muir et al. 1995; NRE 1997; Raven 1997; Bennett et al. 1998).

The study area for this research (referred to hereafter as the Euroa floodplains) is located in the south-east corner of the Northern Plains, Victoria, near the town of Euroa (Fig. 2.1). It is bounded by the Strathbogie Mountain Range to the east and south-east, the Goulburn River to the west and south-west, and the Violet Town - Murchison Road to the north (Fig. 2.1). Covering an area of approximately 870 km², the study area is a gently sloping floodplain ranging in elevation from 120 m to 190 m above sea level (ASL). The major soil type is a fertile alluvial sedimentary deposit of Quartenary origin, with a small number of granitic outcrops of Silurian origin occurring in the south-east portion of the study area (LCC 1983; ECC 1997). The climate is temperate, with mean maximum temperatures exceeding 30°C in summer (December to February), and approximately 13°C in winter (June to August). The mean annual rainfall of 700 mm falls relatively evenly through the year, but with slightly higher monthly totals in winter (LCC 1983).

Prior to European settlement, the Euroa floodplains were mostly covered with Plains Grassy Woodland (ECC 1997) (Fig 2.2), a vegetation type dominated by an overstorey of Grey Box *Eucalyptus microcarpa*, Yellow Box *Eucalyptus melliodora*, Yellow Gum *Eucalyptus leucoxylon*, White Box *Eucalyptus albens* and River Red Gum *Eucalyptus camaldulensis*. *E. camaldulensis* is typically associated with watercourses, while the box species dominated the drier, less flood-prone areas (LCC 1983). The variable midstorey was comprised mostly of *Acacia* species with other shrubs and small trees (e.g. Drooping Cassinia, *Cassinia arcuata* and Buloke *Allocasuarina luehmannii*) and there was a grassy and herbaceous understorey. Clearing of the woodland for agriculture was extensive, leaving a landscape dominated by linear remnants and small patches set within an agricultural matrix of pasture and cropping farmland.
Figure 2.1. Location of the study area near Euroa, north-eastern Victoria. The inset shows the location of Euroa (solid square) within Victoria. The main diagram shows details of the Euroa floodplains study area (hatched area) and major roads and streams.

Study design and site selection

The dominant landscape features of the Euroa floodplains are the extensive network of linear woodland along roadsides and streams, and a scattering of small woodland patches within cleared agricultural land (Fig. 2.3). Large tracts of wooded vegetation are no longer present in the floodplains, but do occur outside the study area in the Strathbogie Mountain Range and along the Goulburn River, (Fig. 2.1). The Strathbogie Ranges are part of the mountainous Great Dividing Range and are a different physiographic region to the floodplains. The Goulburn
River forms the western boundary to the floodplain and contains an almost continuous tract of woodland along its length. Survey sites were selected to sample two main site types, namely linear and non-linear remnants.

![Plains grassy woodland](image)

**Figure 2.2.** Plains grassy woodland, with overstorey *Eucalyptus* trees, shrubby midstorey and a grassy and herbaceous understorey along a roadside strip near Euroa. Photo: R. van der Ree

Linear remnants occurred along streams (n = 14 sites) and roadsides (n = 15) within the Euroa floodplains and were typically 20 - 50 m in width. Survey sites in linear remnants were selected if they were a minimum of 1.0 ha in size, and where possible, contained continuous vegetation cover along their length.

Non-linear remnants (n = 13 sites) were patch or block-shaped habitats located within the Euroa floodplains or in the large tracts of wooded vegetation outside the study area. Non-linear remnants were comprised of four main site types - Creighton Hills, along the Goulburn River, in the Strathbogie Mountain Ranges and in floodplain patches (Fig. 2.1). The 'Creighton Hills' are the largest patch of woodland (~ 130 ha) within the Euroa floodplains (n = 3 sites). 'Floodplain
patches' were small (< 10 ha) patches of woodland occurring within the Euroa floodplains that were often associated with swamps or low-lying areas prone to inundation (n = 3). Large tracts of continuous or near-continuous woodland or forest only occurred outside the study area along the 'Goulburn River' (n = 3) and in the 'Strathbogie Ranges' (n = 4). All survey sites were located at least 1000 m from other sites in an effort to ensure spatial independence.

Satellite imagery (Natural Resources Systems, NRE) and aerial photography (1:25,000 scale) were used to measure woodland habitat within the study area. The length of linear remnants was measured in 125 m units (0.5 cm at 1:25,000 scale) and the width of linear remnants in 10 m units. The number and size of all woodland patches greater than 1.0 ha in size was recorded.

**Mammal survey**

The diversity and abundance of arboreal marsupials at each site were determined by surveying a transect of 1.0 ha. Transects were either 500 m, 333 m or 250 m in length depending on the width of the available habitat (for linear remnants) but the maximum width of survey transects was 50 m. In non-linear remnants, transects were 250 m long and 50 m wide. Arboreal marsupials were censused by spotlighting at night on foot using a 75-watt hand-held spotlight with a red filter. Spotlighting surveys commenced approximately one hour after dusk, and lasted for 30 - 35 minutes at each site. Based on the results of a pilot-study, each site was sampled twice within a 2-month period in 1996. All individuals detected visually or aurally within each 1.0 ha transect were identified and recorded. On occasions, the Sugar Glider *Petaurus breviceps* and *P. norfolcensis* could not be distinguished and were recorded as *Petaurus* species, a difficulty common to other studies (Traill 1998; Millis 2000).
Measurement of habitat features at survey sites

Floristic and structural attributes of the habitat were measured at all survey sites. All overstorey stems within each 1.0 ha plot were identified to species and placed in one of the following size-class categories; < 10 cm diameter at breast height (dbh), 11 - 30 cm, 31 - 70 cm, 71 - 100 cm, and > 100 cm dbh. Basal area (m$^2$ ha$^{-1}$) for each overstorey species was calculated from the mid-point of these size-class categories < 100 cm dbh. For stems > 100 cm dbh, basal area was calculated using a fixed value of 100 cm.

Statistical analysis

Analyses were undertaken at two levels: first, to compare the abundance and richness of arboreal marsupials between linear and non-linear remnants; and second, to compare the arboreal marsupial assemblage in linear remnants occurring along roadsides and streamides. At each survey site, the mean abundance of each species, total abundance of all species, and species richness, were calculated after two spotlighting censuses. The total abundance of arboreal marsupials was calculated as the sum of all detections of all species detected during two censuses. Species richness and mean abundance of each species between site types (linear vs. non-linear, and roadside vs. streamside vegetation) was compared using Mann-Whitney U-tests. Due to low sample sizes, the combined abundance of all *Petaurus* species (*P. breviceps, P. norfolcensis* and any *Petaurus* spp.) was calculated and compared using a Mann-Whitney U-test. The total abundance of arboreal marsupials was compared among site types by one-way analysis of variance (ANOVA). Data presented are means ± 1 standard error unless otherwise indicated.

Survey sites were located in wooded vegetation across a range of landscape positions, including streamsides, roadsides, swamps and in the Strathbogie Mountain Range. Hence, a large amount of variation in overstorey composition may be expected. Principal components analysis (PCA) was used to describe the
variation in overstorey floristic composition between survey sites in linear and non-linear remnants. PCA analysis was undertaken with SPSS (Release 6.0) and the axes were rotated with a varimax rotation to simplify the interpretation of factors.

RESULTS

Shape and arrangement of woodland habitat in the Euroa floodplains

The Euroa floodplains (Fig. 2.1) cover an area of 870 km$^2$ and contain approximately 3.6% tree cover (Fig 2.3). The majority (83%) of this tree cover is in the form of linear remnants associated with roads and streams. The total length of wooded linear habitat in the study area is 901.5 km; with 583.2 km occurring along road reserves and 318.3 km along streams. Wooded vegetation along roads and streams mainly varies in width from 20 to 50 m, but occasionally reaches 200 m in width along several streams. The remaining woodland vegetation in the Euroa floodplains comprises 50 patches greater than 1.0 ha in size (Fig. 2.4). Mean size of all patches (> 1 ha) is 13.6 ± 3.4 (s.e.) ha. The majority of patches are below 20 ha in size, and the two largest patches are 115 and 130 ha (Fig. 2.4). If the two largest patches are excluded, the mean size of the remaining 48 patches is 9.0 ± 1.2 ha. Isolated single trees and patches smaller than 1.0 ha are scattered throughout the cleared agricultural land and were not included in tree cover estimates because of their small size.
Figure 2.3. Aerial view of the agricultural landscape in the Euroa floodplains. Photo: A. Bennett.

Figure 2.4. Size-class distribution of woodland habitat patches (> 1 ha in size) within the Euroa floodplains study area. Note the discontinuous scale on the horizontal axis for patches > 36 ha.
Attributes of overstorey vegetation

Fourteen species of overstorey trees were present within the 42 survey sites (Table 2.1). Eight species, Victorian Blue Gum *Eucalyptus bicostata*, Red Box *Eucalyptus polyanthemos*, Red Stringybark *Eucalyptus macrorhyncha*, Narrow-leaved Peppermint *Eucalyptus radiata*, Broad-leaved Peppermint *Eucalyptus dives*, Long-leaved Box *Eucalyptus goniocalyx*, Mountain Gum *Eucalyptus dalrympleana* and Messmate *Eucalyptus obliqua* were recorded only within the Strathbogie Ranges and Creighton Hills. The remaining six species, namely *E. microcarpa*, *E. camaldulensis*, *E. melliodora*, *E. leucoxylon*, Blakely's Red Gum *Eucalyptus blakelyi*, and *A. luehmannii*, occurred in linear remnants, in the Creighton Hills, along the Goulburn River and in small patches on the floodplains (Table 2.1). Linear remnants along roadsides were dominated by *E. microcarpa* and woodland along streams was dominated by *E. camaldulensis* (Table 2.1).

An ordination of survey sites based on the basal area of overstorey tree species grouped the survey sites geographically. The position of sites in relation to the first two axes of the principal components analysis (Table 2.2) is shown in Fig. 2.5. Both axes appear to separate sites based on factors associated with moisture levels. The first factor separates sites dominated by *E. microcarpa* along roadsides within the floodplains from sites within the Strathbogie Ranges and along streams. The second factor appears to distinguish sites dominated by *E. camaldulensis* from those occurring on better draining soils.

The principal components analysis and consideration of Table 2.1 demonstrates three important points. First, survey sites within the Euroa floodplains are floristically different to those in the Strathbogie Ranges, and the sites in the Creighton Hills appear to be floristically intermediate. This reflects an elevational and rainfall gradient from the Euroa floodplains (120 - 190 m ASL, and mean annual rainfall of 700 mm) to sites in the Strathbogie Mountain Range (~ 600 m ASL, mean annual rainfall of 1000 mm, LCC 1984). The Creighton Hills are an outlier at the base of the Strathbogie Ranges with survey sites at an elevation of 220 m ASL. Second, there is overlap in floristic composition between sites in linear remnants along streams, floodplain patches and sites along the Goulburn
Table 2.1. Basal area (m$^2$ ha$^{-1}$) of overstorey tree species at survey sites in linear and non-linear remnants.

<table>
<thead>
<tr>
<th>Remnant type</th>
<th>Site location</th>
<th>E. pol (± 1 s.e.)</th>
<th>E. mac (± 1 s.e.)</th>
<th>E. rad (± 1 s.e.)</th>
<th>E. div (± 1 s.e.)</th>
<th>E. gon (± 1 s.e.)</th>
<th>E. dal (± 1 s.e.)</th>
<th>E. obl (± 1 s.e.)</th>
<th>E. bic (± 1 s.e.)</th>
<th>E. mic (± 1 s.e.)</th>
<th>E. cam (± 1 s.e.)</th>
<th>E. bla (± 1 s.e.)</th>
<th>E. mel (± 1 s.e.)</th>
<th>E. leu (± 1 s.e.)</th>
<th>A. lue (± 1 s.e.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-linear</td>
<td>Strathbogie Ranges (n = 4)</td>
<td>1.85 (1.85)</td>
<td>7.45 (4.30)</td>
<td>10.27 (6.15)</td>
<td>5.04 (2.69)</td>
<td>1.12 (1.12)</td>
<td>2.28 (2.28)</td>
<td>14.55 (8.74)</td>
<td>0.49 (0.49)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Non-linear</td>
<td>Creighton Hills (n = 3)</td>
<td>13.60 (7.25)</td>
<td>3.65 (1.16)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3.61 (0.69)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.001 (0.001)</td>
</tr>
<tr>
<td>Non-linear</td>
<td>Goulburn River (n = 3)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>29.57 (3.21)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Non-linear</td>
<td>Floodplain patches (n = 3)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1.70 (0.95)</td>
<td>11.53 (5.89)</td>
<td>0</td>
<td>2.70 (1.48)</td>
<td>1.83 (1.83)</td>
<td>4.22 (4.22)</td>
</tr>
<tr>
<td>Linear</td>
<td>Roadside strip (n = 15)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>26.37 (2.73)</td>
<td>2.07 (1.88)</td>
<td>0.002 (0.002)</td>
<td>0.61</td>
<td>0.04</td>
<td>0.18 (0.15)</td>
</tr>
<tr>
<td>Linear</td>
<td>Streamside strip (n = 14)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1.46 (0.66)</td>
<td>23.88 (2.67)</td>
<td>0</td>
<td>0.83 (0.53)</td>
<td>0</td>
<td>0.25 (0.17)</td>
</tr>
</tbody>
</table>
River. *E. camaldulensis* is the dominant overstorey species at these sites because they are periodically inundated. Finally, the survey sites in roadsides were floristically different to sites along streams because roadsides are less prone to flooding, and hence support different species of trees.

Table 2.2. Vector loadings on the first five axes of a principal components analysis of basal area for thirteen overstorey species in linear and non-linear remnants. The most highly correlated variables are given in bold.

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Loading for overstorey tree species</th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
<th>PC4</th>
<th>PC5</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>E. dives</em></td>
<td></td>
<td>0.84</td>
<td>0.10</td>
<td>-0.27</td>
<td>-0.24</td>
<td>0.19</td>
</tr>
<tr>
<td><em>E. dalrympleana</em></td>
<td></td>
<td>0.87</td>
<td>0.12</td>
<td>-0.10</td>
<td>-0.09</td>
<td>-0.43</td>
</tr>
<tr>
<td><em>E. radiata</em></td>
<td></td>
<td>0.86</td>
<td>0.11</td>
<td>-0.18</td>
<td>-0.16</td>
<td>-0.18</td>
</tr>
<tr>
<td><em>E. macrorhyncha</em></td>
<td></td>
<td>0.79</td>
<td>0.01</td>
<td>0.43</td>
<td>0.37</td>
<td>-0.12</td>
</tr>
<tr>
<td>Allocasuarina luehmannii</td>
<td></td>
<td>-0.15</td>
<td>0.96</td>
<td>0.05</td>
<td>0.08</td>
<td>0.03</td>
</tr>
<tr>
<td><em>E. leucoxylon</em></td>
<td></td>
<td>-0.13</td>
<td>0.94</td>
<td>0.09</td>
<td>0.04</td>
<td>0.03</td>
</tr>
<tr>
<td><em>E. melliodora</em></td>
<td></td>
<td>-0.16</td>
<td>0.41</td>
<td>-0.07</td>
<td>0.06</td>
<td>-0.09</td>
</tr>
<tr>
<td><em>E microcarpa</em></td>
<td></td>
<td>-0.22</td>
<td>-0.11</td>
<td>0.52</td>
<td>-0.72</td>
<td>-0.15</td>
</tr>
<tr>
<td><em>E. goniocalyx</em></td>
<td></td>
<td>0.25</td>
<td>-0.07</td>
<td>0.58</td>
<td>0.52</td>
<td>0.16</td>
</tr>
<tr>
<td><em>E. polyanthemos</em></td>
<td></td>
<td>0.13</td>
<td>-0.11</td>
<td>0.49</td>
<td>0.37</td>
<td>0.31</td>
</tr>
<tr>
<td><em>E. camaldulensis</em></td>
<td></td>
<td>-0.27</td>
<td>-0.17</td>
<td>-0.64</td>
<td>0.51</td>
<td>-0.26</td>
</tr>
<tr>
<td><em>E. blakelyi</em></td>
<td></td>
<td>-0.08</td>
<td>-0.01</td>
<td>0.31</td>
<td>-0.45</td>
<td>-0.19</td>
</tr>
<tr>
<td><em>E. obliqua</em></td>
<td></td>
<td>0.32</td>
<td>0.02</td>
<td>-0.32</td>
<td>-0.29</td>
<td>0.80</td>
</tr>
<tr>
<td>Variance (%)</td>
<td></td>
<td>24.7</td>
<td>16.0</td>
<td>13.6</td>
<td>13.2</td>
<td>9.1</td>
</tr>
<tr>
<td>Cumulative variance (%)</td>
<td></td>
<td>24.7</td>
<td>40.7</td>
<td>54.2</td>
<td>67.5</td>
<td>76.5</td>
</tr>
</tbody>
</table>
Figure 2.5. Location of 42 survey sites in relation to the first two principal components from an ordination based on the basal area of tree species in linear and non-linear remnants near Euroa, north-eastern Victoria. Solid symbols represent non-linear remnants (circles - Creighton Hills sites, n = 3; diamonds Goulburn River sites, n = 3; triangles floodplain patches, n = 3; squares Strathbogie Ranges, n = 4) and open symbols represent linear remnants (squares roadside sites, n = 15; circles streamside sites, n = 14). Some sites are not shown because of a high degree of overlap (e.g. Goulburn River sites are overlapped by streamside sites).

Comparison of the arboreal marsupial assemblage between linear and non-linear remnants

Seven species of arboreal marsupial were detected during the spotlighting surveys. The Common Ringtail Possum *Pseudocheirus peregrinus* was the most abundant species (n = 188 individuals), followed by *T. vulpecula* (n = 62), Koala *Phascolarctos cinereus* (n = 13), *P. norfolcensis* (n = 7), *P. breviceps* (n = 7), unidentified *Petaurus* species (n = 2), *P. tapoatafa* (n = 1) and Greater Glider *Petauroides volans* (n = 1) (Table 2.3). Of the 42 sites surveyed, *P. peregrinus* was detected at 30 sites, *T. vulpecula* at 24, *P. cinereus* at 11, *P. norfolcensis* at 7, *P. breviceps* at 5, and *P. tapoatafa* and *P. volans* at 1 site each (Table 2.3).
All species except *P. volans* and *P. tapoatafa* were detected in both linear and non-linear remnants. For species found in sufficient numbers for analysis (> 10 individuals), median abundances did not differ significantly between linear and non-linear remnants (Fig. 2.6) (Mann-Whitney U-test: *T. vulpecula* U = 1.27, p = 0.26; *P. peregrinus* U = 2.02, p = 0.15; *Petaurus* species U = 0.08, p = 0.78). The percentage of survey sites within each site type (linear vs. non-linear) where each species was observed was also similar (Table 2.3). When all species were combined, arboreal marsupials were significantly more abundant in linear remnants (mean 7.76 ± 0.86) than in non-linear remnants (4.77 ± 0.96) (one-way ANOVA, F = 4.34, p = 0.04) (Fig. 2.7).

Species richness at most sites varied between one and three, with a single site in the Strathbogie Mountain Ranges having no arboreal marsupials detected. Approximately 30% of sites in both linear and non-linear remnants had a species richness of one. Forty-eight percent of linear remnants and 23% of non-linear remnants had a species richness of two. Thirty-eight percent of non-linear remnants, and 20% of linear remnants, contained a species richness of three. The mean species richness of arboreal marsupials in linear remnants (1.92 ± 0.29) did not differ significantly from that in non-linear remnants (1.90 ± 0.29) (U = 0.05, p = 0.83) (Fig. 2.7).

In summary, it appears that linear woodland remnants within the Euroa floodplains support a similar assemblage of arboreal marsupials to the largest woodland patches that occur within the Euroa floodplains (i.e. Creighton Hills) and in continuous tracts of forest adjacent to the floodplains (Strathbogie Ranges and Goulburn River). There was no significant difference in species richness per site between linear and non-linear remnants. Similarly, there was no significant difference in the mean abundance of any species of arboreal marsupial between linear and non-linear remnants. However, arboreal marsupials as a group were significantly more abundant in linear remnants.
Table 2.3. Numbers of arboreal marsupials detected within 1.0 ha survey plots during spotlighting censuses, 1996.
Values in parentheses equal the percentage of sites where the species was detected.

<table>
<thead>
<tr>
<th>Species</th>
<th>Linear remnants (n = 29)</th>
<th>Non-linear remnants (n = 13)</th>
<th>Total individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Trichosurus vulpecula</em></td>
<td>50 (62)</td>
<td>12 (46)</td>
<td>62</td>
</tr>
<tr>
<td><em>Pseudocheirus peregrinus</em></td>
<td>153 (72)</td>
<td>35 (69)</td>
<td>188</td>
</tr>
<tr>
<td><em>Petaurus breviceps</em></td>
<td>5 (10)</td>
<td>2 (15)</td>
<td>7</td>
</tr>
<tr>
<td><em>Petaurus norfolcensis</em></td>
<td>4 (14)</td>
<td>3 (23)</td>
<td>7</td>
</tr>
<tr>
<td>unidentified <em>Petaurus</em></td>
<td>1 (3)</td>
<td>1 (8)</td>
<td>2</td>
</tr>
<tr>
<td><em>Petaurus</em> species combined</td>
<td>10 (28)</td>
<td>6 (31)</td>
<td>16</td>
</tr>
<tr>
<td><em>Phascolarctos cinereus</em></td>
<td>8 (24)</td>
<td>5 (31)</td>
<td>13</td>
</tr>
<tr>
<td><em>Petauroides volans</em></td>
<td>0 (0)</td>
<td>1 (8)</td>
<td>1</td>
</tr>
<tr>
<td><em>Phascogale tapoatafa</em></td>
<td>1 (3)</td>
<td>0 (0)</td>
<td>1</td>
</tr>
</tbody>
</table>
Figure 2.6. Mean abundance (+ 1 s.e.) of arboreal marsupials in linear and non-linear woodland remnants near Euroa. Solid columns are linear remnants (n = 29) and open columns are non-linear remnants (n = 13). Each two letter code on the horizontal axis refers to a species: (Pp) *Pseudocheirus peregrinus*; (Tv) *Trichosurus vulpecula*; (Pc) *Phascolarctos cinereus*; (Pb) *Petaurus breviceps*; (Pn) *Petaurus norfolcensis*; (Pet. spp.) all *Petaurus* species combined. *P. tapoatafa* and *P. volans* were detected at one site only and are not shown.

Figure 2.7. Mean species richness and total number of arboreal marsupials (+ 1 s.e.) observed at each site in linear and non-linear remnants. Solid columns represent linear remnants (n = 29), open columns non-linear remnants (n = 13).
Comparison of the arboreal marsupial assemblage between different types of linear remnant

Six species of arboreal marsupial were detected within linear remnants (Table 2.3, Fig. 2.8). The species most often encountered was *P. peregrinus* (n = 153 detections), followed by *T. vulpecula* (n = 50), *P. cinereus* (n = 10), *P. breviceps* (n = 5), and *P. norfolcensis* (n = 4). *P. peregrinus* and *T. vulpecula* were widespread within the linear remnants, occurring at 72% and 62% of sites, respectively (Table 2.3). *P. cinereus* was detected at approximately 25% of sites in linear remnants, *P. norfolcensis* at 14% of sites, *P. breviceps* at 10% of sites, and *P. tapoatafa* at 3% of sites.

There was a significantly greater abundance of *P. peregrinus* in roadside vegetation than streamside vegetation (Mann-Whitney U-test, U = 6.57, p < 0.01) (Fig 2.8). *T. vulpecula* showed an opposite trend and was more abundant in streamside than roadside vegetation (Fig 2.8) (U = 3.80, p = 0.051). The detection rates for *P. norfolcensis* and *P. breviceps* were insufficient to analyse the abundance for each species separately. When the abundance of all individuals of *Petaurus* species were combined, there was a significantly greater abundance of *Petaurus* species in sites along roadsides than streamsides (U = 5.54, p < 0.05). The mean abundance of all arboreal marsupials was greater in roadside (9.07 ± 1.11) than streamside sites (6.36 ± 1.25), but not significantly so (one-way ANOVA, p = 0.12) (Fig 2.9).

Species richness of arboreal marsupials at survey sites varied between one and three, and mean richness was significantly greater in sites along roadsides (2.20 ± 0.20) than streams (1.57 ± 0.14) (Mann-Whitney U-test, U = 5.12, p < 0.05) (Fig. 2.6).

Sightings of *P. cinereus* and *P. tapoatafa* were too few (eight sites and one site respectively) to permit an analysis of habitat preferences.
Figure 2.8. Mean abundance (+ 1 s.e.) of arboreal marsupials per site in linear remnants.
Solid columns are sites in roadside vegetation (n = 15) and open columns are sites in streamside vegetation (n = 14). Each two-letter code on the horizontal axis refers to a species: (Pp) *P. peregrinus*; (Tv) *T. vulpecula*; (Pc) *P. cinereus*; (Pb) *P. breviceps*; (Pn) *P. norfolcensis*; (Pet. spp.) all *Petaurus* species combined. *P. tapoatafa* is not shown because it was only observed once at a roadside site.

Figure 2.9. Mean species richness and total number of arboreal marsupials (+ 1 s.e.) per site in linear remnants.
Solid columns represent sites in roadside vegetation (n = 15), open columns sites in streamside vegetation (n = 14).
DISCUSSION

Shape and arrangement of woodland habitat in the Euroa floodplains

The Euroa floodplains are dominated by an agricultural matrix (96.4% of the study area) with remnant woodland vegetation occurring predominantly as an interconnected network of narrow linear remnants (83% of remnant vegetation), with a few relatively small patches (17%). There are no published examples of agricultural landscapes in Australia that possess a similar pattern in the spatial configuration of habitat. Rather, the other landscapes contained a mosaic of patches of varying size and shape (e.g. Suckling 1984; Bennett 1987, 1990; Saunders et al. 1993; Bentley and Catterall 1997; Downes et al. 1997; Fisher and Goldney 1997). Linear strips of vegetation occurred in these study areas, however they did not provide the bulk of remnant habitat in the landscape as was the case in the Euroa floodplains. Moreover, only Bennett (1987, 1990) and Saunders et al. (1993) undertook studies in landscapes with less than 10% suitable habitat remaining. Therefore, this study area provides an excellent opportunity to investigate the response of fauna to extensive loss of habitat and the arrangement of most habitat in a network of linear strips.

Internationally, the hedgerow and fencerow networks of Europe and North America provide analogous landscape patterns (Forman and Baudry 1984; Osborne 1984; Burel and Baudry 1990; Simpson et al. 1994; Burel and Baudry 1995). In these landscapes, hedgerows and fencerows typically occur at field margins where the intensity of cultivation is lower and often represent the boundary between properties (Burel and Baudry 1995; Forman 1997). In some highly cleared landscapes, the hedgerow and fencerow networks provide a large proportion of the natural vegetation in the landscape (Osborne 1984; Burel and Baudry 1990; Firbank 1997). For example, there is less than 1% tree cover in the agricultural landscape studied by Haas (1995) in the Great Plains of North Dakota, USA, and most occurs naturally along streams or as linear plantations.

Occurring outside the Euroa floodplains are several large tracts of wooded vegetation in the Strathbogie Ranges and along the Goulburn River. The extent of
wooded vegetation in these areas is more widespread than on the floodplains because they were less suitable for agriculture and the extent of clearing was lower. The Goulburn River was prone to flooding and the Strathbogie Ranges were too steep or rocky to cultivate. Conversely, the Euroa floodplains have fertile alluvial soils (ECC 1997) preferred for agricultural development, resulting in extensive clearing. Areas within the floodplains that remained uncleared were either less suitable for agriculture (e.g. subject to inundation - floodplain patches and streamsides; or too rocky for successful cultivation - Creighton Hills), or were protected from clearing due to legislation (roadsides).

Survey sites clustered into three major groups based on the composition of overstorey species. A rainfall, elevational and geological gradient explained the major difference in overstorey species composition between survey sites in the Strathbogie Ranges and those on the Euroa floodplains (Fig. 2.5 and Table 2.1). Sites in the Strathbogie Ranges contained Eucalyptus species characteristic of wet sclerophyll forest, while the Euroa floodplains were dominated by Eucalyptus species more typical of drier open woodland (Costermans 1992). The geographically and floristically intermediate sites - the Creighton Hills, were also intermediate in ordination space (Fig. 2.5). Sites within the Euroa floodplains that are associated with periodic inundation (i.e. along the Goulburn River, in floodplain patches and linear remnants along streams) were dominated by E. camaldulensis. Sites in linear remnants along roadsides were drier and were primarily dominated by E. microcarpa.

Therefore, linear woodland remnants in the Euroa floodplains are likely to be an important component for the conservation of biodiversity for two reasons. First, they represent the majority of wooded vegetation in the landscape. Second, the remnant woodland vegetation within the floodplains is floristically different to the large tracts occurring outside the study area, and thus provides the remaining examples of the most severely depleted woodland types.
The assemblage of arboreal marsupials in linear and non-linear remnants

At the landscape scale, the assemblage of arboreal marsupials recorded from sites in the floodplains and in adjacent large tracts of forest and woodland is largely intact, as six out of seven species expected to occur were detected (Bennett et al. 1998). The species not observed (Feathertail Glider *Acrobates pygmaeus*) is small in size and difficult to spotlight (Henry 1995), and hence may be present but undetected.

The composition of the arboreal marsupial assemblage was relatively similar in linear and non-linear remnants. This clearly indicates that both the linear and non-linear remnants provide habitat for arboreal marsupials. The only difference in species composition between linear and non-linear remnants was the detection of a single *P. tapoatafa* and *P. volans*, observed at single sites in linear and non-linear remnants, respectively. This difference in composition is best explained by habitat preferences rather than habitat fragmentation *per se*. *P. volans* is more typical of wetter forests at higher elevation and is common in the Strathbogie Ranges (Bennett et al. 1991; Downes et al. 1997a), while *P. tapoatafa* usually inhabits dry forest and woodlands (Menkhorst 1995a), more typical of the open woodlands of the floodplains.

Comparisons of the abundance of each species of arboreal marsupial, and of all species combined, clearly indicates that linear strips of wooded vegetation are capable of providing habitat for arboreal marsupials. First, there was no significant difference in the abundance of *P. peregrinus*, *T. vulpecula* or the petaurid gliders between linear and non-linear remnants. Further, the total abundance of arboreal marsupials detected at sites during two censuses was significantly higher in linear than non-linear remnants.

This study provides no evidence that linear remnants support a degraded or impoverished arboreal marsupial fauna in comparison with non-linear remnants. Therefore, it appears that linear remnants are important landscape features for arboreal marsupial conservation in this landscape. If linear remnants were suboptimal habitat where mortality exceeded reproduction (ie. a ‘sink’ habitat), one
might generally expect a lower abundance than within non-linear remnants (source habitats), although this may not always be the case (Pulliam 1988; Howe et al. 1991). To further test the hypothesis that linear remnants provide sub-optimal habitat, rates of reproduction, movement parameters and demographics within and between the potential 'source and sink habitat' need to be compared (Donovan et al. 1995; Diffendorfer 1998).

The arboreal marsupial assemblage within linear remnants

The linear remnants within the Euroa floodplains did not display uniform composition of tree species but rather varied according to their location along streams (dominated by *E. camaldulensis*) or roads (dominated by *E. microcarpa*). The variation in the abundance of arboreal marsupials between sites in roadside and streamside vegetation is most likely influenced by factors associated with the floristic composition of the overstorey. For example, *T. vulpecula* was more abundant within the *E. camaldulensis*-dominated woodlands while *P. peregrinus* was significantly more abundant in the *E. microcarpa*-dominated habitat along roadsides. Similar distribution patterns were identified during a large-scale survey of arboreal marsupials across northern Victoria (Bennett et al. 1991). A similar trend for *T. vulpecula* was also found in north-western Queensland, where it was more abundant in *E. camaldulensis* woodlands than in adjacent habitats (Munks et al. 1996).

The two larger possum species (*P. peregrinus* and *T. vulpecula*) were widespread across the linear remnants and detected in 72% and 62% of survey sites, respectively. However, the petaurids were detected at only 24% of survey sites in the linear remnants and therefore appeared to be uncommon across the entire study area. Similarly, *P. tapoatafa* was detected at just a single roadside site and appeared to be rare.
CONCLUSIONS

Habitat loss and fragmentation have been extensive in the Euroa floodplains and currently less than 5% tree cover remains. The majority of tree cover in the study area occurs as linear strips and relatively small patches set within cleared agricultural land. Linear woodland remnants are important for conservation because they provide the majority of the wooded habitat for arboreal marsupials in the landscape. Moreover, the linear remnants contain the majority of woodland types formerly widespread across the floodplains study area.

This study clearly demonstrates that the woodland mosaic in the Euroa floodplains is capable of supporting a diverse assemblage of arboreal marsupials. The assemblage of arboreal marsupials is largely intact, and includes six out of seven species expected to occur. The linear remnants appear to be important for the conservation of arboreal marsupials because there were no significant differences in mean species richness, or mean abundance of each species between the linear and non-linear remnants. Moreover, the total number of arboreal marsupials was significantly greater in linear than in non-linear remnants. These results reinforce other studies that have recognised the importance of the Euroa floodplains for the conservation of fauna (Davidson 1996; Raven 1997; Robinson et al. in press). This study also highlights the potential conservation value of linear landscape elements in highly fragmented landscapes.
CHAPTER 3
HABITAT USE BY ARBOREAL MARSUPIALS IN A HIGHLY-FRAGMENTED LINEAR LANDSCAPE

INTRODUCTION

Within the continuous forests and woodlands of eastern mainland Australia, broad patterns of distribution and habitat selection by arboreal marsupial species are relatively well-documented (e.g. Davey 1984; Kavanagh 1984; Lindenmayer et al. 1991; Milledge et al. 1991; Kavanagh and Bamkin 1995). Factors found to be important in influencing the distribution and abundance of arboreal marsupial species include forest type (Davey 1984; Kavanagh 1984; Bennett et al. 1991; Eyre and Smith 1997), foliage nutrient levels (Braithwaite et al. 1984; Kavanagh and Lambert 1990; Pausas et al. 1995), composition of surrounding habitat (Incoll 1995; Lindenmayer et al. 1999), topographic position (Lunney 1987; Lindenmayer et al. 1990b; Soderquist and Mac Nally 2000), slope (Lindenmayer et al. 1991) and the number of hollow-bearing trees (Smith and Lindenmayer 1988; Eyre and Smith 1997). Less well-documented and understood is the additional influence of habitat loss and fragmentation on the distribution and abundance of arboreal marsupials in highly modified environments (but see Pahl et al. 1988; Laurance and Laurance 1999).

Habitat fragmentation involves the subdivision of continuous habitat into smaller patches of varying size and shape, ultimately reducing the area of suitable habitat available (Andren 1994). Clearing of habitat is not a random process: in agricultural regions, vegetation occurring on fertile soils is generally cleared first in preference to vegetation on less fertile or rocky soils, on steeper terrain or in areas prone to flooding. Consequently, vegetation communities occurring on preferred agricultural soils are often poorly represented in the landscape and may only occur as remnants (Hobbs and Saunders 1993; Prober and Thiele 1993). Following habitat loss and fragmentation, the level of connectivity between
isolated patches decreases. This reduction in connectivity is being increasingly recognised as an important variable determining metapopulation persistence in patchy mosaic landscapes (Merriam 1991; Taylor et al. 1993; Bennett 1999). In addition, the collapse and modification of ecosystem functioning, the effects of which are still largely unknown, may have further impacts on the biota (Saunders et al. 1991). A prerequisite to the conservation of biota in highly fragmented landscapes is a thorough knowledge and understanding of their patterns of distribution and habitat requirements, as well as their response to the consequences of habitat alteration.

Since European settlement, the Northern Plains region of Victoria has experienced a massive decline in woodland cover (Woodgate and Black 1988; Bennett and Ford 1997). The Euroa floodplains in north-east Victoria (Fig. 2.1) currently supports less than 5% tree cover, and much of what remains is arranged linearly along roads and streams (Chapter 2). An initial landscape-scale survey in this area (Chapter 2) showed that despite this high level of habitat loss and fragmentation, at least six species of arboreal and scansorial marsupial occur in the area and utilise linear woodland remnants as habitat. This survey showed that the composition and richness of the assemblage of arboreal marsupials in linear habitats was similar to that in survey sites in nearby larger patches and continuous habitat (Chapter 2). Moreover, this study showed that the abundance of all species of arboreal marsupial combined was significantly greater in linear habitats than in larger patches. The study concluded that the linear remnants surveyed were of high quality for arboreal marsupials.

This chapter forms the first part of a detailed study of the ecology of arboreal marsupials in a linear network of roadside vegetation based on an intensive trapping and radiotelemetry program. Specifically, the objectives of this chapter were:

1) to describe the structure and floristic composition of woodland vegetation of a network of linear roadside habitat used for intensive trapping and radiotelemetry studies;

2) to determine the relative abundance and distribution of arboreal marsupial species in the linear network; and
3) to investigate habitat use and identify particular habitat components that influence the abundance of arboreal marsupials.

METHODS

Study area

The study was undertaken within the Euroa floodplain in an area of 30 km², approximately 10 km west of the township of Euroa (36°45' S, 145°30' E). The study area and its context within the Northern Plains of Victoria is described in Chapter 2. Typical of much of the Euroa floodplain, the study area has a continuous network of wooded habitat along roadsides and unused road reserves, and numerous small patches of woodland. The natural vegetation is open grassy woodland with a dominant overstorey of *E. microcarpa*, and smaller proportions of *E. polyanthemos*, *E. melliodora*, *E. macrorhyncha*, *E. leucoxylon*, *E. camaldulensis* and *E. blakelyi*. The midstorey is dominated by shrubs, especially Golden Wattle *Acacia pycnantha* and Lightwood *Acacia implexa*, with a grassy and herbaceous understorey. Grazing by domestic stock is common in many of the woodland remnants.

Trapping and animal handling techniques

Trapping transects were established in a continuous system of linear woodland remnants along roadsides and unused road reserves (Fig 3.1, Table 3.1). A transect is defined as a continuous strip of woodland not extending beyond the junction with other linear habitats (after Osborne 1984). Permanent trap stations were established along transects at intervals of 150 m by nailing metal brackets in trees at a mean height of 4.7 m (range 3.0 - 6.0 m). Actual trap position varied slightly from the exact 150 m location (mean deviation from 150 m location = 14.5 m, s.e. = 1.2) in order to establish trap stations in the nearest large diameter.
tree to maximise trap success. Arboreal marsupials were live-trapped in wire-mesh cage-traps (17 cm x 20 cm x 50 cm) with a drop-down door to minimise injury. Traps were baited with a mixture of peanut butter, rolled oats and honey, and a diluted honey and water mixture was sprayed on the tree trunk leading to the trap as an attractant.

Figure 3.1. The location and details of the trapping grid study area near Euroa in north-eastern Victoria.
Woodland vegetation occurring along roads and road reserves is shown as solid straight lines and vegetation along stream sides is shown as solid wavy lines. The 14.55 km of linear remnants trapped for arboreal marsupials is indicated by dashed lines adjacent to solid lines. Numbers represent transects surveyed.
Regular census trapping commenced in February 1997 and took place every two to three months until June 1998, for a total of eight trapping censuses. Each transect was usually trapped for four consecutive nights during each census. Traps were checked at first light each morning, and captured animals were restrained in cloth bags and identified, sexed, weighed, measured, examined for reproductive condition and released at the point of capture. At first capture, individuals were marked in the ear with a tattoo, and a metal fingerling tag covered in reflective coloured tape (Scotchlite, 3M, Victoria) was inserted at the base of the ear. At the commencement of the study, each glider was individually fitted with colour-coded ear tags to allow identification at night with a spotlight. However, due to high capture rates and a limited number of colours, there were insufficient colour combinations for all individuals. Gliders were then fitted with a single ear tag to distinguish between new and previously captured animals.

Table 3.1. Trapping transects established to census arboreal marsupials along roadsides and unused road reserves near Euroa, 1997 to 1998. Intensity of grazing by domestic stock: 1 = nil to slight, 2 = moderate, 3 = heavy.

<table>
<thead>
<tr>
<th>Transect Number</th>
<th>Transect length (km)</th>
<th>Reserve width (m)</th>
<th>Transect area (ha)</th>
<th>Grazing intensity</th>
<th>Number of trap stations</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2.10</td>
<td>40</td>
<td>8.4</td>
<td>1</td>
<td>15</td>
</tr>
<tr>
<td>2</td>
<td>1.35</td>
<td>20</td>
<td>2.7</td>
<td>3</td>
<td>9</td>
</tr>
<tr>
<td>3</td>
<td>1.05</td>
<td>20</td>
<td>2.1</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>4</td>
<td>1.55</td>
<td>40</td>
<td>6.2</td>
<td>1</td>
<td>10</td>
</tr>
<tr>
<td>7</td>
<td>1.85</td>
<td>20</td>
<td>3.7</td>
<td>3</td>
<td>12</td>
</tr>
<tr>
<td>8</td>
<td>1.85</td>
<td>20</td>
<td>3.7</td>
<td>3</td>
<td>12</td>
</tr>
<tr>
<td>9</td>
<td>2.40</td>
<td>20</td>
<td>4.8</td>
<td>3</td>
<td>17</td>
</tr>
<tr>
<td>11</td>
<td>2.40</td>
<td>20</td>
<td>4.8</td>
<td>2</td>
<td>17</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>14.55</strong></td>
<td><strong>-</strong></td>
<td><strong>36.4</strong></td>
<td><strong>-</strong></td>
<td><strong>99</strong></td>
</tr>
</tbody>
</table>
Animal abundance

Capture frequency at each trap station was calculated for each species of arboreal marsupial, and for all species of arboreal marsupial combined, as the number of captures per 100 trap nights to standardise for slight differences in trapping intensities among trap stations. A second abundance index, reflecting mean catch density per trap station (hereafter referred to as 'catch density'), was used to compensate for the decreasing number of traps available for capturing animals as the night progressed and traps were filled (Caughley 1977). This correction factor is recommended when trap success is above 20%, because capture frequency and actual density diverge at an increasing rate and the untransformed frequency may no longer be an accurate density index (Caughley 1977). The formula to calculate catch density given by Caughley (1977) is:

\[ y = e^{-x} \]

where \( y \) = proportion of traps containing no captures, and
\( x \) = estimated density of catches per trap.

Habitat assessments

The trapping grid was divided into sampling units, each 50 m long by the width of the linear remnant at that site (Fig. 3.2). Two measures of habitat width (m) were made at the beginning of each 50 m sampling unit. First, the road reserve width was measured from the surveyed boundary between public and private land on each side of the linear remnant; and second, overstorey canopy width was measured from outer canopy edge to outer canopy edge (Table 3.1). Area (ha) of the linear remnant was calculated using reserve width and length.

Floristic and structural attributes of the vegetation were measured within each 50 m sampling unit and were converted to a ha\(^{-1}\) value. All overstorey stems were identified to species and placed in one of the following size-class categories; < 10 cm diameter at breast height over bark (dbh), 11 - 30 cm, 31 - 70 cm, 71 - 100 cm,
and > 100 cm dbh. The number of dead *Eucalyptus* trees (all species combined) in each size-class was also recorded. The basal area (m$^2$ ha$^{-1}$) for each overstorey species, dead trees, and for all living eucalypts combined, was calculated by using the midpoint in each size-class. For stems > 100 cm dbh, basal area was calculated using a fixed value of 100 cm. The size-class (dbh) and species of trees bearing visible canopy hollows, as observed from the ground without the aid of binoculars were recorded. Canopy hollows were defined as any hole in the trunk or major branches at or above 1.3 m (*sensu* Soderquist and Mac Nally 2000). The density of *A. pycnantha* and *A. implexa* shrubs was also measured (number of stems ha$^{-1}$). The intensity of grazing by domestic stock (sheep and cattle) was subjectively classified as 1) low - fenced, rarely if ever grazed; 2) moderate - fenced, but occasional grazing, or 3) high - not fenced and unrestricted access by stock (Table 3.1). The distance (m) to the nearest intersection with another linear remnant was measured from the exact trap station to the intersection with another linear remnant.

To describe the habitat at each trap station, data from the two adjacent 50 m sampling units were combined, with the trap station at their midpoint (Fig. 3.2). This ensured a 50 m buffer between each 100 m transect. Mean values for all habitat variables were calculated from the two sampling units that made each 100 m transect. To describe the habitat across the entire trapping grid, data from all 50 m sampling units were used.

![Figure 3.2. Diagram of a linear strip showing three trap stations (A, B and C), 50 m sampling units (area between two vertical lines) and pooled 100 m transects (diagonal hatching) for each trap station.](image)
**Statistical analysis**

The distribution and abundance of arboreal marsupials were examined at three spatial levels:
1) for data pooled over the entire trapping grid;
2) for defined vegetation groups (see below); and
3) for individual trap stations.

Habitat use by species of arboreal marsupial was analysed by comparison among vegetation groups, and by investigating relationships at the trap station level between numbers of captures and measured habitat variables.

**Identification of vegetation groups**

Floristic and structural attributes were used to classify the vegetation at each trap station into groups of sites having similar composition. All variables (except *E. microcarpa* basal area and the number of large eucalypts) were transformed ($\log_{10}(x + 1)$) prior to analysis to reduce skewness. A similarity matrix was calculated between all habitat variables by using the Bray-Curtis measure of association after standardising all variables to between zero and one. Hierarchical clustering using the unweighted pair group mean averaging strategy (UPGMA) identified major vegetation groups. The analysis was run using PATN software (Belbin 1993). A comparison of the mean values of structural and floristic attributes for trap stations assigned to each vegetation group was undertaken by one-way analysis of variance (one-way ANOVA).
Determining habitat preferences

The influence of trap density (number of traps per unit area) on capture rates in linear strips that were 20 or 40 m in width was tested in the following manner. Capture frequency (number of times each individual was captured within a 4-day session) was calculated for each individual *P. norfolcensis*, *T. vulpecula* and *P. tapoatafa* in narrow (20 m) and wide (40 m) linear remnants within vegetation group 1 (see below). The Mann-Whitney U-test was then used to compare capture frequency in narrow and wide remnants for *P. norfolcensis* (per trapping session), and for *T. vulpecula* and *P. tapoatafa* (pooled across all trapping sessions due to insufficient sample sizes for each trapping sessions).

One-way ANOVA was used to compare mean abundance indices (i.e. captures per 100 trap nights and catch density) for arboreal marsupials (each species separately and all species combined) among vegetation groups. Initially, the effect of width (20 m vs. 40 m) on marsupial abundance indices was tested using one-way ANOVA, and subsequently, results from trap stations in 40 m wide remnants were excluded. Tukey's honestly significant difference tests were used to determine means that differed significantly among vegetation groups. Catch density measures were transformed to the 4th root to increase normality and homoscedasticity. ANOVA tests were conducted by using SPSS (Release 6.0).

The relationship between arboreal marsupial abundance and habitat variables measured at each trap station was investigated by using stepwise multiple regression. Highly intercorrelated habitat variables (r > 0.60) at trap stations were identified using Pearson correlations and either excluded from further analyses or reduced to a smaller number of orthogonal variables using principal components analysis (PCA).
RESULTS

Attributes of remnant vegetation

Linear network

A total of 295 habitat-sampling units were used to assess the overstorey and midstorey vegetation within a 14.55 km network of linear woodland. Seven species of *Eucalyptus* were detected, with *E. microcarpa* the most common species, occurring in 96% of the sampling units (Fig. 3.3). The six other species listed in decreasing frequency of occurrence were *E. blakelyi*, *E. leucoxylon*, *E. melliodora*, *E. camaldulensis*, *E. macrorhyncha*, and *E. polyanthemos* (Fig. 3.3). *E. polyanthemos* was detected at only one site and is excluded from further statistical analyses. Dead *Eucalyptus* trees were relatively common, occurring in 146 sampling units. The most common midstorey species were *A. pycnantha* and *A. implexa*, occurring at 157 and 28 habitat sampling units, respectively. *A. luehmannii* and Drooping Sheoak *Allocasuarina verticillata* were present at 22 and 8 sampling units, respectively.

The mean basal area of *Eucalyptus* trees within 14.55 km of linear network was 34.13 (± 0.77) m² ha⁻¹. The size-class distribution of overstorey trees varied across the linear network (Table 3.2). *Eucalyptus* saplings were present in approximately half of the sampling units, while small, medium and large trees were present in all or almost all sampling units (Table 3.2). The mean density of hollow-bearing trees across the entire linear network was 20.6 (± 0.9) ha⁻¹. There was a wide range in the number of stems in each size-class and in the density of stems containing hollows within each sampling unit (Table 3.2).
Figure 3.3. Mean basal area (± 1 s.e.) of overstorey *Eucalyptus* species and dead trees within 14.55 km of linear habitat trapped for arboreal marsupials. The tree species are *E. microcarpa* (E. mic), *E. blakelyi* (E. bla), *E. leucoxylon* (E. leu), *E. melliodora* (E. mel), *E. camaldulensis* (E. cam), *E. macrorhyncha* (E. mac) and *E. polyanthemos* (E. pol). Dead trees are dead *Eucalyptus* trees. Values above each column represent the number of 50 m sampling units in which the species was detected (n = 295).

Table 3.2. Summary of the size-class distribution of *Eucalyptus* stems and the number of hollow-bearing trees in the linear network near Euroa, northeastern Victoria.

<table>
<thead>
<tr>
<th>Habitat feature</th>
<th>Number of sampling units where present (% of total)</th>
<th>Mean density ha⁻¹ (± s.e.)</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Saplings</td>
<td>167 (56.6%)</td>
<td>20.5 (2.4)</td>
<td>0 - 554</td>
</tr>
<tr>
<td>Small trees</td>
<td>290 (98.3%)</td>
<td>100.5 (4.4)</td>
<td>0 - 450</td>
</tr>
<tr>
<td>Medium trees</td>
<td>295 (100%)</td>
<td>87.1 (2.9)</td>
<td>10 - 270</td>
</tr>
<tr>
<td>Large trees</td>
<td>283 (95.9%)</td>
<td>23.3 (0.8)</td>
<td>0 - 70</td>
</tr>
<tr>
<td>Hollow-bearing trees</td>
<td>261 (88.5%)</td>
<td>20.6 (0.9)</td>
<td>0 - 120</td>
</tr>
</tbody>
</table>


Description of vegetation groups

The 99 trap stations were clustered into three groups based on the floristic and structural composition of the habitat within 100 m transects of each station. Floristic and structural variation among these vegetation groups is displayed in Table 3.3.

The characteristic feature of vegetation group one (46 trap stations) was an overstorey dominated by *E. microcarpa*, with small but relatively similar amounts of *E. camaldulensis*, *E. blakelyi* and *E. macrorhyncha* (Table 3.3). Mean basal area of all *Eucalyptus* species and mean number of medium-sized *Eucalyptus* stems were significantly lower in this group than in other groups (*p* < 0.001 for both variables). *A. pycnantha* stems were significantly more abundant (*p* < 0.001) in this group, with an almost 10-fold difference with the next vegetation group. Grazing intensity by domestic stock was typically low, and there was a rich and diverse understorey vegetation.

The overstorey of vegetation group two (40 trap stations) was also dominated by *E. microcarpa* but other overstorey species were more common. In this group, the basal area of *E. blakelyi*, *E. leucoxylon*, *E. melliodora* and dead *Eucalyptus* trees was intermediate between vegetation groups one and three (Table 3.3). Structurally, the mean basal area of all *Eucalyptus* species, the number of hollow-bearing trees, and the number of large and medium-sized *Eucalyptus* trees were also intermediate between groups one and three. *A. pycnantha* was at its lowest abundance in this group. Sites in this group were unfenced, which allowed unrestricted access by domestic stock. Consequently, the understorey was very disturbed, consisting primarily of introduced pasture grasses with some native grass species.

The third vegetation group (13 trap stations) contained the most floristically diverse overstorey with a significantly greater basal area of *E. blakelyi*, *E. leucoxylon*, *E. melliodora*, *A. luehmannii*, *A. verticillata* and *A. implexa* than any other group (all *p* < 0.001). The basal area of *E. microcarpa* was significantly lower (*p* < 0.001) in this group than other groups. Vegetation group 3 also
contained more large *Eucalyptus* stems, more hollow-bearing trees, and a greater basal area of dead trees than other vegetation groups (all *p* < 0.001). Grazing intensity by domestic stock was very high, resulting in a disturbed understorey comprised primarily of introduced pasture grasses with some native grass species.

**Table 3.3. Comparison of structural and floristic habitat variables between vegetation groups.**

Values are means for sites in each group. Letters in superscript next to means (a, b, c, ordered from highest to lowest) show results of Tukey's honestly significant difference test where one-way ANOVA detected a significant difference between group means. Means with the same letter are not significantly different.

ns not significant, ** p < 0.01, *** p < 0.001

<table>
<thead>
<tr>
<th>Habitat variable</th>
<th>Vegetation group</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1 (n = 46)</td>
</tr>
<tr>
<td>Basal area (m² ha⁻¹) of:</td>
<td></td>
</tr>
<tr>
<td><em>E. microcarpa</em></td>
<td>27.6ᵇ</td>
</tr>
<tr>
<td><em>E. camaldulensis</em></td>
<td>0.5</td>
</tr>
<tr>
<td><em>E. blakelyi</em></td>
<td>0.2ᵇ</td>
</tr>
<tr>
<td><em>E. leucoxylon</em></td>
<td>0</td>
</tr>
<tr>
<td><em>E. melliodora</em></td>
<td>0ᵇ</td>
</tr>
<tr>
<td><em>E. macrorhyncha</em></td>
<td>0.2</td>
</tr>
<tr>
<td><em>A. luehmannii</em></td>
<td>0.01ᵇ</td>
</tr>
<tr>
<td><em>A. verticillata</em></td>
<td>0ᵇ</td>
</tr>
<tr>
<td>Dead trees</td>
<td>0.4ᵇ</td>
</tr>
<tr>
<td>All <em>Eucalyptus</em> stems</td>
<td>28.5ˢ</td>
</tr>
<tr>
<td>Density (indivs. ha⁻¹) of:</td>
<td></td>
</tr>
<tr>
<td>Hollow-bearing trees</td>
<td>17.4ᵇ</td>
</tr>
<tr>
<td>Large <em>Eucalyptus</em> trees</td>
<td>20.0ᵇ</td>
</tr>
<tr>
<td>Medium <em>Eucalyptus</em> trees</td>
<td>66.1ᵇ</td>
</tr>
<tr>
<td>Small <em>Eucalyptus</em> trees</td>
<td>107.9</td>
</tr>
<tr>
<td><em>Eucalyptus</em> saplings</td>
<td>28.8ᵃ</td>
</tr>
<tr>
<td><em>A. pycnantha</em> stems</td>
<td>326.0ᵃ</td>
</tr>
<tr>
<td><em>A. implexa</em> stems</td>
<td>3.4ᵃ</td>
</tr>
</tbody>
</table>

There was a high level of intercorrelation between basal area of the four most abundant species of eucalypt at each trap station (Table 3.4). A principal components analysis identified three factors that together accounted for 83.0% of
the variation (Table 3.5). The first component (49.1% of the variation in the data) differentiated between trap stations dominated by *E. blakelyi*, *E. melliodora* and *E. leucoxylon*, and those dominated by *E. microcarpa*. The second component (17.4% of the variation) was positively associated with *E. macrorhyncha* basal area. The third component (16.5% of the variation) was associated with *E. camaldulensis* basal area, and occurred where small drainage lines crossed the linear roadside network.

A further two habitat variables, namely grazing intensity and the abundance of *A. pycnantha* stems, were highly correlated (\( r = -0.90, p < 0.001 \)). Consequently, grazing intensity was excluded from further analyses. The remaining habitat variables displayed differing levels of intercorrelation, but correlation coefficients were all below 0.60 and 74% of correlations were less than 0.40.

### Table 3.4. Correlation coefficients for the relationship between basal area (m² ha⁻¹) of six *Eucalyptus* species at 99 trap stations in the linear network near Euroa.

Tree species are *E. microcarpa* (E. mic), *E. blakelyi* (E. bla), *E. leucoxylon* (E. leu), *E. melliodora* (E. mel), *E. camaldulensis* (E. cam), and *E. macrorhyncha* (E. mac). Basal area measurements were log transformed prior to analyses. *** p < 0.001.

<table>
<thead>
<tr>
<th>Tree species</th>
<th>E. bla</th>
<th>E. mic</th>
<th>E. cam</th>
<th>E. mac</th>
<th>E. leu</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. mic</td>
<td>-0.65  ***</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>E. cam</td>
<td></td>
<td>-0.08 ns</td>
<td>0.07 ns</td>
<td></td>
<td></td>
</tr>
<tr>
<td>E. mac</td>
<td></td>
<td>-0.03 ns</td>
<td>-0.05 ns</td>
<td>-0.05 ns</td>
<td></td>
</tr>
<tr>
<td>E. leu</td>
<td>0.54  ***</td>
<td>-0.60  ***</td>
<td>-0.10 ns</td>
<td>-0.04 ns</td>
<td></td>
</tr>
<tr>
<td>E. mel</td>
<td>0.68  ***</td>
<td>-0.81  ***</td>
<td>0.01 ns</td>
<td>0.14 ns</td>
<td>0.57  ***</td>
</tr>
</tbody>
</table>
Table 3.5. Vector loadings on the first three axes of a principal components analysis of basal area for six *Eucalyptus* species. The most highly correlated variables are in bold.

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Loading for overstorey tree species</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>PC1</td>
<td>PC2</td>
<td>PC3</td>
</tr>
<tr>
<td><em>E. microcarpa</em></td>
<td>-0.90</td>
<td>-0.07</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td><em>E. blakelyi</em></td>
<td>0.84</td>
<td>-0.06</td>
<td>-0.05</td>
<td></td>
</tr>
<tr>
<td><em>E. melliodora</em></td>
<td>0.90</td>
<td>0.17</td>
<td>0.08</td>
<td></td>
</tr>
<tr>
<td><em>E. leucoxylon</em></td>
<td>0.78</td>
<td>-0.11</td>
<td>-0.12</td>
<td></td>
</tr>
<tr>
<td><em>E. macrorhyncha</em></td>
<td>0.01</td>
<td>0.99</td>
<td>-0.03</td>
<td></td>
</tr>
<tr>
<td><em>E. camaldulensis</em></td>
<td>-0.04</td>
<td>-0.03</td>
<td>0.99</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Variance (%)</th>
<th>Cumulative variance (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>49.1</td>
<td>49.1</td>
</tr>
<tr>
<td></td>
<td>17.4</td>
<td>66.5</td>
</tr>
<tr>
<td></td>
<td>16.5</td>
<td>83.0</td>
</tr>
</tbody>
</table>

*Spatial arrangement of vegetation groups*

Vegetation groups were spatially clumped across the landscape, forming almost continuous strips of similar vegetation (Fig. 3.4). Vegetation group 1 occurred in the eastern portion of the trapping grid, where the reserve width was either 20 m or 40 m. Vegetation groups 2 and 3 occurred mainly in the western portion of the trapping grid, and reserve width was 20 m.
Figure 3.4. Spatial arrangement of vegetation groups in a linear roadside network near Euroa, north-eastern Victoria.
Remnant woodland vegetation is shown along roads and unused road reserves (solid straight lines) and along streamsides (solid wavy lines). Each number represents the location of a trap station (n = 99) and corresponds to the vegetation group (1, 2 or 3) at that trap station.

Arboreal marsupials

Abundance in the linear network

Six species of arboreal marsupial were trapped during 3189 trap nights between February 1997 and June 1998. (Fig. 3.5, Tables 3.6, 3.7). There was a total of 1356 captures of arboreal marsupials - an overall trap success rate of 42.5% (Fig. 3.5, Table 3.6). Within 14.55 km of linear habitat, 211 individual $P. norfolcensis$, 1 $P. breviceps$, 75 $T. vulpecula$, 14 $P. peregrinus$, 10 Yellow-footed Antechinus $Antechinus flavipes$, and 42 $P. tapoatafa$ were captured (Fig. 3.5).

Arboreal marsupials were widely distributed throughout the linear network, with captures at all 99 trap stations. $P. norfolcensis$ was the most widespread species, being trapped at every trap station (n = 99). $T. vulpecula$ was the next most widespread (n = 76), followed by $P. tapoatafa$ (n = 55), $P. peregrinus$ (n = 10), $A. flavipes$ (n = 7) and $P. breviceps$ (n = 1).
Figure 3.5. The number of arboreal marsupials trapped along 14.55 km of linear remnants near Euroa between February 1997 and June 1998. Open columns represent females, shaded columns represents males. Values above columns represent the total number of captures of each species (males and females combined).
Table 3.6. Trapping results for arboreal marsupials in 14.55 km of remnant linear woodland near Euroa, north-eastern Victoria. Species are: (Pn) *P. norfolcensis*; (Tv) *T. vulpecula*; (Pt) *P. tapoatafa*; (Pp) *P. peregrinus*; (Af) *A. flavipes* and (Pb) *P. breviceps*. Arboreal marsupials refers to all species combined.

<table>
<thead>
<tr>
<th>Census date</th>
<th>No. of trap nights</th>
<th>Number of captures</th>
<th>Number of captures per 100 trap nights</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Pn</td>
<td>Tv</td>
<td>Pt</td>
</tr>
<tr>
<td>February 1997</td>
<td>473</td>
<td>82</td>
<td>13</td>
</tr>
<tr>
<td>March 1997</td>
<td>358</td>
<td>55</td>
<td>26</td>
</tr>
<tr>
<td>May / June 1997</td>
<td>319</td>
<td>61</td>
<td>35</td>
</tr>
<tr>
<td>August 1997</td>
<td>401</td>
<td>128</td>
<td>51</td>
</tr>
<tr>
<td>October 1997</td>
<td>436</td>
<td>124</td>
<td>67</td>
</tr>
<tr>
<td>December 1997</td>
<td>405</td>
<td>105</td>
<td>52</td>
</tr>
<tr>
<td>February / March 1998</td>
<td>395</td>
<td>141</td>
<td>61</td>
</tr>
<tr>
<td>May / June 1997</td>
<td>402</td>
<td>136</td>
<td>75</td>
</tr>
<tr>
<td>TOTAL</td>
<td>3189</td>
<td>832</td>
<td>380</td>
</tr>
</tbody>
</table>
Effect of width of linear remnants

In vegetation group 1, *P. norfolcensis*, *T. vulpecula* and *P. tapoatafa* were captured at higher rates in 40 m than in 20 m wide linear remnants (Table 3.7). The number of *P. norfolcensis* captures per 100 trap nights and *P. norfolcensis* catch density were significantly greater in 40 than 20 m wide strips (One-way ANOVA, $p < 0.05$ and $p < 0.001$, respectively) (Table 3.7). *T. vulpecula*, was captured eight times more often and catch density was 19.5 times greater in 40 than 20 m wide strips ($p < 0.001$ for both abundance indices). *P. tapoatafa* was slightly more abundant in wider habitat, but not significantly so ($p > 0.05$) (Table 3.7).

This result can be attributed to 40 m wide linear remnants having a greater amount of habitat and therefore supporting more animals, rather than trap density significantly influencing the trappability of animals. This interpretation is supported by the lack of a significant difference in capture frequency per individual animal for *P. norfolcensis* (Mann Whitney, $U = 17487.0$, $p > 0.05$), *P. tapoatafa* ($U = 123.0$, $p > 0.05$) or *T. vulpecula* ($U = 251.0$, $p > 0.05$) between 20 and 40-m wide strips within vegetation group 1. This suggests that individual animals are equally likely to be captured in 20 and 40 m wide linear remnants despite different trap densities.

Therefore, when comparing the abundance of arboreal marsupials between vegetation groups, only data from trap stations located within 20 m wide remnants are used. When developing multiple regression models of arboreal marsupial abundance at each trap station, width (measured as canopy edge to canopy edge) was used as a potential explanatory variable.
Table 3.7. Effect of linear remnant width within vegetation group one on abundance indices of arboreal marsupials.
Captures are per 100 trap nights. Values are means ± 1 s.e. ns not significant, * p < 0.05, *** p < 0.001.

<table>
<thead>
<tr>
<th>Abundance index</th>
<th>Width of linear remnant</th>
<th>F-ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>20 m (n = 20)</td>
<td>40 m (n = 26)</td>
</tr>
<tr>
<td>Arboreal marsupials:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>- captures</td>
<td>31.79 ± 2.53</td>
<td>52.20 ± 3.41</td>
</tr>
<tr>
<td>- catch density</td>
<td>0.42 ± 0.04</td>
<td>1.05 ± 0.11</td>
</tr>
<tr>
<td><em>P. norfolcensis:</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>- captures</td>
<td>27.22 ± 2.31</td>
<td>35.81 ± 2.42</td>
</tr>
<tr>
<td>- catch density</td>
<td>0.37 ± 0.04</td>
<td>0.82 ± 0.09</td>
</tr>
<tr>
<td><em>T. vulpecula:</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>- captures</td>
<td>1.42 ± 0.48</td>
<td>11.93 ± 1.97</td>
</tr>
<tr>
<td>- catch density</td>
<td>0.02 ± 0.01</td>
<td>0.39 ± 0.08</td>
</tr>
<tr>
<td><em>P. tapoatafa:</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>- captures</td>
<td>2.04 ± 0.76</td>
<td>2.90 ± 0.77</td>
</tr>
<tr>
<td>- catch density</td>
<td>0.04 ± 0.01</td>
<td>0.11 ± 0.03</td>
</tr>
</tbody>
</table>

Dispersion of captures

*a) All arboreal marsupials*

The mean number of captures per 100 trap nights at each trap station for all arboreal marsupials in the linear network was 42.3 (s.e. ± 1.6, range 6.3 - 81.3). The mean capture rate and catch density per trap station were significantly greater in vegetation group 3 than in groups 1 or 2 (p < 0.001 for both, Table 3.8). Both correlation and stepwise multiple regression analyses between arboreal marsupial abundance (number of captures and catch density) and habitat variables identified canopy width, overstorey composition and the number of *A. pycnantha* stems as significant explanatory variables (Tables 3.9 and 3.10). In the regression models, canopy width explained the most variance (15% and 20% of the variance, respectively), with the second significant step being a positive relationship with *Eucalyptus* species composition (overstorey PC1). The number of *A. pycnantha* stems was the third and final significant habitat variable identified. The regression model explaining arboreal marsupial captures accounted for 28.9% of
the variance and the catch-density regression model accounted for 33.0% (Table 3.10).

b) *Petaurus norfolcensis*

*Petaurus norfolcensis* was the most abundantly trapped and widespread arboreal marsupial in the linear network, with a mean success of 25.8 (± 1.3, range 3.1 - 59.4) captures per 100 trap nights. The mean capture rate of *P. norfolcensis* in vegetation group 1 was greater than in groups 2 or 3, but this difference was only marginally significant (*p* = 0.051, Table 3.8). The catch density of *P. norfolcensis* did not differ between vegetation groups (Table 3.8).

The relative abundance of *P. norfolcensis* was significantly positively correlated with the abundance of *A. pycnantha* stems and canopy width, and negatively correlated with *Eucalyptus* basal area (Table 3.9). A negative correlation between the capture rate of *P. norfolcensis* and distance to the nearest intersection was also detected (Table 3.9). *A. pycnantha* abundance was the first significant step in multiple regression analyses between *P. norfolcensis* abundance and habitat variables (Table 3.10). The next two significant steps were a positive relationship with canopy width and a negative relationship with distance to the nearest intersection (Table 3.10). Overstorey species composition was not a significant explanatory variable in the models.

c) *Trichosurus vulpecula*

*Trichosurus vulpecula* had a mean capture rate of 11.86 (s.e. 1.31, range 0 - 54.5) captures per 100 trap nights throughout the linear network. This species displayed clear habitat preferences in relation to overstorey composition (Tables 3.8 and 3.9). Both the mean number of captures per 100 trap nights and mean catch density were significantly greater in vegetation group 3 than 2, and greater in vegetation group 2 than 1 (*p* < 0.001 for both) (Table 3.8). Vegetation group 3 has the most diverse *Eucalyptus* overstorey, including *E. leucoxylon*, *E. melliodora*, *E. blakelyi*, *E. microcarpa* and *E. macrorhyncha*, while Groups 1 and 2 are primarily dominated by *E. microcarpa.*
The importance of overstorey species composition in explaining the abundance of *T. vulpecula* was also identified by correlation (Table 3.9) and stepwise multiple regression (Table 3.10) analyses. Abundance of *T. vulpecula* was significantly positively correlated with *Eucalyptus* species composition (overstorey PC1), the number of *A. implexa* stems, and the density of hollow-bearing trees (Table 3.9). For the capture rate of *T. vulpecula*, overstorey species composition (PC1) was the first and only significant variable in the stepwise multiple regression model explaining 37% of the variance (Table 3.10). For *T. vulpecula* catch density, PC1 explained 19% of the variance, and the number of *A. pycnantha* stems accounted for a further 14% (Table 3.10).

d) *Phascogale tapoatafa*

*Phascogale tapoatafa* was widely distributed in low abundance throughout the linear network, with a mean of 3.1 (s.e. 0.4, range 0 - 15.6) captures per 100 trap nights. Neither the number of captures nor catch density of *P. tapoatafa* differed significantly between vegetation groups (Table 3.8). Correlation and stepwise multiple regression analyses also failed to elucidate those factors influencing *P. tapoatafa* abundance (Tables 3.9 and 3.10). Clearly, the floristic and structural descriptions of the habitat do not adequately explain the dispersion of *P. tapoatafa* as revealed by trapping.

e) *Pseudocheirus peregrinus*

The capture rate for *P. peregrinus* was low, with a mean of 0.9 (s.e. 0.4, range 0 - 31.2) captures per 100 trap nights. There were insufficient captures to test for habitat preferences.

f) *Antechinus flavipes*

*Antechinus flavipes* was uncommon in the linear network, with a mean of 0.5 (s.e. 0.2, range 0 - 12.5) captures per 100 trap nights. Although small sample sizes preclude statistical testing, captures appeared to be spatially clumped, with 14 of
16 captures originating from a 900 m length of linear remnant (Transect 7 - see Fig. 3.1). Within this particular area, individuals were consistently captured throughout the duration of the study. This section occurred in vegetation group 2, characterised by an overstorey of *E. microcarpa* with small proportions of *E. melliodora, E. leucoxylon,* and *E. blakelyi*. The understorey in this 900 m section was highly disturbed due to grazing by domestic stock and lacked native shrubs and herbs.

*g* *Petaurus breviceps*

*Petaurus breviceps* was captured once at a trap station in vegetation group 1.

**Table 3.8. Abundance indices for each species of arboreal marsupial and all arboreal marsupials combined, in 20 m wide linear strips in three vegetation groups.**

Values are means ± s.e. Letters in superscript next to means (a, b, c, ordered from highest to lowest) show results of Tukey's honestly significant difference test where one-way ANOVA detected a significant difference between group means. Means with the same letter are not significantly different. *n* refers to the number of trap stations occurring in each habitat group. Captures are per 100 trap nights. *ns* not significant, *p* < 0.05, ***p* < 0.001

<table>
<thead>
<tr>
<th>Abundance index</th>
<th>Vegetation group</th>
<th>F-ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1 (n = 20)</td>
<td>2 (n = 40)</td>
</tr>
<tr>
<td>Arboreal marsupials:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>- captures</td>
<td>31.79b</td>
<td>37.75b</td>
</tr>
<tr>
<td>- catch density</td>
<td>0.42b</td>
<td>0.57b</td>
</tr>
<tr>
<td><em>P. norfolcensis</em>:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>- captures</td>
<td>27.22</td>
<td>20.76</td>
</tr>
<tr>
<td>- catch density</td>
<td>0.37</td>
<td>0.35</td>
</tr>
<tr>
<td><em>T. vulpecula</em>:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>- captures</td>
<td>1.42c</td>
<td>11.45b</td>
</tr>
<tr>
<td>- catch density</td>
<td>0.02c</td>
<td>0.21b</td>
</tr>
<tr>
<td><em>P. tapoatafa</em>:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>- captures</td>
<td>2.04</td>
<td>3.71</td>
</tr>
<tr>
<td>- catch density</td>
<td>0.04</td>
<td>0.07</td>
</tr>
</tbody>
</table>
Table 3.9. Correlation coefficients between indices of arboreal marsupial abundance and habitat variables.
Captures are the number of captures per 100 trap nights, and catch density (after Caughley 1977) is explained in the text. 
^t denotes variables that have been log_{10}(variable + 1) transformed. Significant correlations (p < 0.01) given in bold.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Petaurus norfolcensis</th>
<th>Trichosurus vulpecula</th>
<th>Phascogale tapoatafa</th>
<th>Arboreal marsupials</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Captures</td>
<td>Catch density^t</td>
<td>Captures</td>
<td>Catch density</td>
</tr>
<tr>
<td>No. of hollow-bearing trees^t</td>
<td>-0.18</td>
<td>-0.10</td>
<td>0.34</td>
<td>0.23</td>
</tr>
<tr>
<td>Intersection distance</td>
<td>-0.27</td>
<td>-0.15</td>
<td>0.17</td>
<td>0.14</td>
</tr>
<tr>
<td>A. pycnantha stems^t</td>
<td>0.41</td>
<td>0.51</td>
<td>-0.01</td>
<td>0.20</td>
</tr>
<tr>
<td>A. implexa stems^t</td>
<td>-0.06</td>
<td>0.03</td>
<td>0.28</td>
<td>0.25</td>
</tr>
<tr>
<td>A. luehmannii basal area^t</td>
<td>-0.24</td>
<td>-0.11</td>
<td>0.42</td>
<td>0.32</td>
</tr>
<tr>
<td>Canopy width (m)</td>
<td>0.43</td>
<td>0.52</td>
<td>0.11</td>
<td>0.27</td>
</tr>
<tr>
<td>Eucalyptus basal area^t</td>
<td>-0.27</td>
<td>-0.26</td>
<td>0.15</td>
<td>0.04</td>
</tr>
<tr>
<td>Overstorey PCA1</td>
<td>-0.24</td>
<td>-0.09</td>
<td>0.58</td>
<td>0.44</td>
</tr>
<tr>
<td>Overstorey PCA2</td>
<td>-0.01</td>
<td>-0.02</td>
<td>0.04</td>
<td>0.02</td>
</tr>
<tr>
<td>Overstorey PCA3</td>
<td>0.02</td>
<td>0.01</td>
<td>-0.03</td>
<td>-0.01</td>
</tr>
</tbody>
</table>
Table 3.10. Significant structural and floristic habitat variables influencing arboreal marsupial abundance indices identified through multiple stepwise regression modeling.

\[ \text{\textsuperscript{t}} \text{ denotes variables that have been } \log_{10}(\text{variable} + 1) \text{ transformed.} \]

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Variables contributing significantly to regressions. (**, \ P &lt; 0.001)</th>
<th>Regression coefficients</th>
<th>(r^2) (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arboreal marsupials:</td>
<td>Canopy width***</td>
<td>0.44</td>
<td></td>
</tr>
<tr>
<td>- captures</td>
<td>Overstorey species composition (PC1)**</td>
<td>5.45</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Number of <em>A. pycnantha</em> stems***</td>
<td>0.02</td>
<td>28.9</td>
</tr>
<tr>
<td>- catch density[t]</td>
<td>Canopy width***</td>
<td>0.003</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Overstorey species composition (PC1)**</td>
<td>0.03</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Number of <em>A. pycnantha</em> stems***</td>
<td>0.0001</td>
<td>33.0</td>
</tr>
<tr>
<td><em>P. norfolcensis:</em></td>
<td>Number of <em>A. pycnantha</em> stems***</td>
<td>0.015</td>
<td></td>
</tr>
<tr>
<td>- captures</td>
<td>Distance to the nearest intersection***</td>
<td>-0.012</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Canopy width***</td>
<td>0.376</td>
<td>35.1</td>
</tr>
<tr>
<td>- catch density</td>
<td>Number of <em>A. pycnantha</em> stems***</td>
<td>0.000504</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Canopy width***</td>
<td>0.012</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Distance to the nearest intersection***</td>
<td>-0.000194</td>
<td>42.9</td>
</tr>
<tr>
<td><em>T. vulpecula:</em></td>
<td>Overstorey species composition (PC1)**</td>
<td>7.69</td>
<td>37.1</td>
</tr>
<tr>
<td>- captures</td>
<td>Number of <em>A. pycnantha</em> stems***</td>
<td>0.17</td>
<td></td>
</tr>
<tr>
<td>- catch density</td>
<td>Overstorey species composition (PC1)**</td>
<td>0.000472</td>
<td>33.1</td>
</tr>
<tr>
<td><em>P. tapoatafa:</em></td>
<td>Number of <em>A. pycnantha</em> stems***</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>- captures</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>- catch density</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>

DISCUSSION

Linear habitat network

In the Euroa floodplains, approximately 85% of the remaining woodland occurs along roadsides, unused road-reserves and streams as relatively narrow strips of woodland (see Chapter 2). In the trapping grid area, these are continuous and form an interconnected network (Fig. 3.1). The linear strips of woodland are typically oriented along north-south and east-west axes to coincide with property boundaries, as well as a northwest-southeast axis to parallel the major
watercourses in the area. The resulting landscape is largely anthropogenic, forming a rectilinear corridor network (Forman 1991), that dissect different vegetation groups.

Three vegetation groups were defined based on structural and floristic variables. The major differences among groups included the species composition of the overstorey and the presence or absence of an A. pycnantha midstorey. The distribution of the six Eucalyptus species can best be explained by subtle variation in edaphic factors. E. microcarpa is widespread and common on the slopes and plains on the inland side of the Great Dividing Range (Costermans 1992) and occurred in all three vegetation groups. Its decreasing dominance in vegetation groups 2 and 3 may be related to soil conditions because it prefers heavier alluvial soils (Costermans 1992). Two of the three dominant eucalypt species in vegetation group 3 (E. melliodora and E. blakelyi) are often associated with each other and prefer slightly moister soils on the drier plains (Boland et al. 1984; Costermans 1992). E. leucoxylon, most abundant in vegetation group 3, also favours heavier soils but can tolerate wider environmental conditions and is more widespread into drier climes than E. melliodora or E. blakelyi (Boland et al. 1984). E. polyanthemos and E. macrorhyncha are typically found on dry foothills and gentle slopes, with E. polyanthemos more common on dry stony or gravelly soils and E. macrorhyncha occurring on a variety of soil types but mainly well-drained and moderately fertile soils (Boland et al. 1984; Costermans 1992). E. camaldulensis is usually associated with watercourses (Costermans 1992) and occurred along roads and road reserves at stream crossings.

The presence and abundance of A. pycnantha is largely a reflection of management practices as indicated by the high correlation with grazing intensity. Domestic stock (e.g. sheep and cattle) are implicated in woodland decline because they damage vegetation by grazing and trampling, limit recruitment by grazing seedlings (Wilson 1990; Prober and Thiele 1993; Scougall et al. 1993; Bennett et al. 1994b; Yates et al. 1994, 2000) and alter soil structure, thus preventing or limiting seed germination or seedling survival (Scougall et al. 1993; Yates et al. 2000).
The size-class distribution of the *Eucalyptus* trees across the linear network was relatively even, with trees in the small, medium and large size-classes occurring in > 95% of sampling units. Of particular concern, however, was the lack of overstorey regeneration, as saplings only occurred in approximately half of the sampling units. As for *A. pycnantha*, the lack of overstorey regeneration is most likely due to grazing by domestic stock. Nonetheless, the woodland occurring in the linear network is high quality habitat for arboreal marsupials because of the abundance of large and hollow-bearing trees, occurring at a mean density of 23 and 20 stems ha\(^{-1}\), respectively. Historically, up to 30 trees greater than 80 cm dbh ha\(^{-1}\) occurred in the box-ironbark forests of central and northern Victoria (Newman 1961). Large trees are important ecosystem components because the number and size of hollows they provide increases with tree diameter (Mackowski 1984; Bennett et al. 1994b; Soderquist 1999). Large trees also have large surface areas for foraging (Dickman 1991), provide fallen logs in a range of sizes for ground-dwelling species (Scotts 1991), and probably provide larger quantities of nectar because they flower more regularly than small trees (Wilson and Bennett 1999).

### Habitat preferences of arboreal marsupials

The width of linear habitats has been shown to positively influence the composition of bird assemblages in highly modified agricultural landscapes (Arnold and Weeldenburg 1990; Cale 1990; Keller et al. 1993; Parish et al. 1994). While data investigating the relationship between habitat width and arboreal marsupial abundance in agricultural landscapes are scant, results from a study in tropical Queensland concluded that forested corridors of moderate width (20-80 m) supported five of the six species known to occur in the area (Laurance and Laurance 1999). However, the sixth species (*Lemuroid Ringtail Possum Hemibelideus lemuroides*) occurred only in very wide corridors of at least 200 m width that comprised primary rainforest (Laurance and Laurance 1999). In the present study, the abundance indices of *P. norfolcensis* and *T. vulpecula* (in vegetation group 1) were significantly greater in 40 m than 20 m wide strips.
Trap density did not significantly influence the trappability of animals, suggesting that the greater capture rates in the wider habitat is because the larger total area supports more animals than narrow habitats. Furthermore, direct comparison of the relative abundance of each species of arboreal marsupial can not be made because variation in their trappability, may influence abundance estimates (Laurance 1992).

*Petaurus norfolcensis* was the most widespread species, being trapped at all trap stations along the network of roadside vegetation. Clearly, woodland vegetation along the linear network is suitable for supporting a resident population of *P. norfolcensis*. Previous studies have indicated that areas supporting winter flowering or mixed-species stands of *Eucalyptus* trees were the preferred habitat of *P. norfolcensis* because they provide a winter nectar source - an apparently critical resource (Menkhorst *et al.* 1988). In the Euroa study area, *P. norfolcensis* was resident in all three vegetation groups, including stands of pure *E. microcarpa* (late summer - autumn flowering) or mixed-species stands (including some winter flowering species).

A study of the foraging ecology of *P. norfolcensis* at this site (Holland 1998) found that during winter, individuals spent 98% of their foraging time searching in eucalypts for honeydew and manna, which offer similar energy rewards to nectar (Paton 1980). Moreover, concurrent radiotracking studies (Chapter 5) and additional trapping results (R. van der Ree, unpub. data) demonstrated that *P. norfolcensis* were resident and foraged in the same general location within and between years. This indicates that even when eucalypts were not flowering abundantly, sufficient food resources could be obtained within each home range. It appears that in this study area, *P. norfolcensis* can thrive in the absence of winter flowering species, but when eucalypts are in flower they will utilise these nectar sources to supplement other more reliable, year-round energy sources.

The abundance of *A. pycnantha* was identified as the most important habitat variable in multiple regression models of the abundance of *P. norfolcensis* (Table 3.10). The gum of *A. pycnantha* may provide an important alternative source of carbohydrate during winter, particularly in vegetation group 1 where winter
flowering eucalypts were absent. Elsewhere in eastern Australia, gum-producing *Acacia* species provide important dietary components for *P. breviceps* (Smith 1982; Howard 1989), *P. norfolcensis* (Menkhorst and Collier 1987), Yellow-bellied Glider *Petaurus australis* (Carthew et al. 1999) and Leadbeater’s Possum *Gymnobelideus leadbeateri* (Smith 1984a). However, in this area, foraging in *A. pycnantha* shrubs during three consecutive seasons (summer, autumn and winter) accounted for less than 2% of total foraging time (Holland 1998), which increased markedly during spring (Holland, unpub. data). It was noted, however, that the importance of *A. pycnantha* as a food source may have been underestimated because *P. norfolcensis* were easily disturbed when in such trees (Holland 1998). Alternatively, the abundance of *A. pycnantha* may be a surrogate for other factors, such as the level of disturbance by domestic stock.

Canopy width and distance to the nearest intersection were also identified as significant explanatory variables for both the capture rate and catch density of *P. norfolcensis*. Canopy width is a measure of the total area of habitat, and as habitat area increases, the overall population size increases and more individuals are available to be trapped. The negative relationship between the abundance of *P. norfolcensis* and distance to the nearest intersection with another linear habitat is explained by the potential role of intersections as focal points between adjacent social groups (see Chapter 5). Home range overlap of adjacent social groups is greater at intersections than in straight linear strips (Chapter 5). Therefore, potentially more individuals occupy linear remnants in close proximity to intersections than at increasing distances away.

*Trichosurus vulpecula* has the widest distribution of any Australian marsupial (Kerle 1984) and in Victoria is only absent from Mallee scrub, treeless heaths and tall wet forests (Menkhorst 1995b). It was widespread in the Euroa study area, but was most abundant in mixed stands of eucalypt species. The abundance indices for *T. vulpecula* were significantly greater in vegetation group 3 which contained the greatest diversity of *Eucalyptus* species, including the largest proportions of *E. leucoxylon*, *E. melliodora*, and *E. blakelyi*. These species tend to occur on soils of higher nutrient status and thus may have high foliar nutrient levels (Braithwaite et al. 1984), which are favoured by *T. vulpecula* (Landsberg
1987). At the landscape level, *T. vulpecula* showed a strong habitat preference for woodlands dominated by *E. camalduensis* (Chapter 2), which may have been due to the availability of preferred foliage and trees with larger hollows in this woodland type. In this study at the local level, abundance of *T. vulpecula* was significantly positively correlated with the density of hollow-bearing trees (Table 3.9), possibly reflecting a similar trend.

*Phascogale tapoatafa* is a small, carnivorous arboreal marsupial whose range includes south-western, south-eastern and northern Australia (Cuttle 1983). Within Victoria, *P. tapoatafa* occupies a broad geographic band across central Victoria, mostly restricted to dry forests and woodlands (Menkhorst 1995a). These forests and woodlands have undergone considerable loss and fragmentation since European settlement (Woodgate and Black 1988; Robinson and Traill 1996). Further modification through mining, grazing, logging and firewood collection is widespread (Robinson and Traill 1996) and is believed to have contributed to the species' decline (Menkhorst 1995a). *P. tapoatafa* is classified as 'vulnerable' in Victoria (NRE 1999) and an Action Statement has been prepared under the *Flora and Fauna Guarantee Act* (1988) (Humphries and Seebeck 1997).

*Phascogale tapoatafa* was relatively widespread across the linear network and was trapped at 55% of trap stations. There was no significant difference in the mean abundance of *P. tapoatafa* between vegetation groups nor did any habitat variables explain their pattern of occurrence. In addition, their abundance indices were not related to reserve width (20 vs. 40 m). The lack of a clear, detectable response to vegetation group or width by *P. tapoatafa* may be because they occur at low densities (Soderquist 1995), and include small woodland patches in adjacent farmland in their home range (van der Ree and Bennett 1999). Alternatively, the habitat in the Euroa study area, though highly fragmented, may be of uniformly high quality (van der Ree and Bennett 1999) so that minor variation in overstorey composition or structure does not influence abundance indices in a statistically significant way.

*Pseudocheirus peregrinus* is widely distributed in Victoria and occupies rainforest, forest, woodland and scrub habitats (Henry 1996). Trapping results in
this study indicate that *P. peregrinus* occurs at low abundance in the linear habitat network. These results may not reflect true abundance because this species and the closely related Western Ringtail Possum *Pseudocheirus occidentalis* are notoriously difficult to capture by cage-trapping with the type of bait used in this study (Jones *et al.* 1994, Simon Ward, pers. comm.). Incidental observations collected during spotlighting and radiotracking fieldwork (R. van der Ree, unpub. data) indicate that the species is abundant and widely distributed throughout the linear network of the trapping grid. Spotlighting surveys reported in Chapter 2 and other studies in north-eastern Victoria (Bennett *et al.* 1991) also clearly indicate that this species is more abundant than the trapping results suggest. Indeed, the highest detection rates for *P. peregrinus* recorded by Bennett *et al.* (1991) were in mixed-box forests similar to those in the Euroa area.

*Antechinus flavipes* is a small (20 - 50 g in the Euroa area, R. van der Ree, unpub. data) insectivorous dasyurid, widely distributed in a band across central Victoria from the north-east to the south-west (Menkhorst 1995d). Because of its small body size, it was able to escape from some of the wire cage traps used in this study. It is unlikely, given the high intensity of trapping and that most traps used prevented their escape, that additional *A. flavipes* populations in other areas of the trapping grid would have remained undetected. Indeed, a subsequent study using Elliott traps modified with door-locking mechanisms failed to detect any new *A. flavipes* populations within the same linear network (van der Ree and Bennett 1999). The population identified here appears to be localised, as 88% of captures came from within a 900 m length of a 20 m-wide heavily-grazed linear strip. Further work is required to ascertain the status and ecology of the species in these linear remnants.

*Petaurus breviceps* is widespread throughout eastern Australia occurring in a variety of woodland and forest types (Henry and Suckling 1984). During this study, *P. breviceps* was detected once at one trap station, but it does occur in an adjacent patch (~130 ha) of regenerating woodland (Creighton Hills - refer Chapter 2) (R. van der Ree, unpub. data). Its absence in the linear network is surprising because in other areas *P. breviceps* typically occurs in sympatry with *P.*
norfolcensis (Quin 1995; Traill and Lill 1997). In this area, *P. norfolcensis* may exclude *P. breviceps* from linear remnants.

This hypothesis of competitive exclusion of *P. breviceps* is most likely due to the increased efficiency of territory defense associated with habitat geometry, rather than resource availability *per se*. In contiguous woodland habitats, *P. norfolcensis* may be less efficient in defending territory against invasion from all directions; whereas in linear habitats, potential invasion points by other species are at the end of each linear habitat. Changing the density of potential nest sites by varying the diameter of entrance holes has been shown to influence the relative abundance of *P. norfolcensis* and *P. breviceps* within an area (Traill and Lill 1997). However, the availability of suitable tree-hollows does not adequately explain the absence of *P. breviceps* from the linear network. In the Euroa area, hollow-bearing trees do not appear to be limiting because there are on average 20 hollow-bearing trees ha$^{-1}$, considerably more than in the box and ironbark forest where Traill and Lill (1997) undertook their study.

**CONCLUSIONS**

The remnant woodland vegetation occurring as a network of linear strips along roads and road reserves at Euroa in north-eastern Victoria provides high quality habitat for a diverse assemblage of co-occurring species of arboreal marsupial. The density of large trees probably reflects pre-fragmentation levels, and is most likely the major factor influencing overall habitat quality because of the range of resources such trees provide. The richness of arboreal marsupials is high, with six species present, including two of state-wide conservation concern. Importantly, these two species, *P. tapoatafa* and *P. norfolcensis*, had high capture rates. Other species, such as *A. flavipes*, were detected infrequently, and their persistence in the landscape does not appear secure. Important habitat components influencing the abundance of arboreal marsupials included the composition of the *Eucalyptus* overstorey, the abundance of an *Acacia* midstorey, and habitat width.
CHAPTER 4
POPULATION ECOLOGY OF THE SQUIRREL GLIDER
Petaurus norfolcensis, WITHIN A NETWORK OF REMNANT LINEAR HABITATS

INTRODUCTION

Petaurus norfolcensis is distributed in a broad geographic band from the base of Cape York through Queensland and eastern New South Wales to western Victoria (Menkhorst et al. 1988; Quin et al. 1996b; Sharpe and Goldingay 1998). Within Victoria, it now has a patchy distribution on the inland side of the Great Dividing Range with a small population occurring near Stawell, and a larger more-widespread population in north-east Victoria (Menkhorst et al. 1988). It is listed as 'endangered' in Victoria (NRE 1999), because of the extent of decline in geographic range and the vulnerability of surviving populations to further loss. Its preferred habitat coincides with fertile soils that have been extensively cleared of their natural vegetation for agriculture (Menkhorst et al. 1988). In New South Wales, it is classified as 'vulnerable' under the Threatened Species Conservation Act 1995, and its persistence in Queensland is threatened by habitat loss (Rowston 1998).

Studies of the ecology of P. norfolcensis have been undertaken in Victoria (Alexander 1981; Menkhorst and Collier 1987; Menkhorst et al. 1988; Traill 1995; Traill and Lill 1997; Holland 1998), New South Wales (Quin 1995; Sharpe and Goldingay 1998) and Queensland (Rowston 1998; Millis 2000). All of these studies, with the exception of that by Holland (1998), have been undertaken in areas of continuous forest or in a combination of continuous forest and forest patches of varying size. In Victoria, however, many populations of P. norfolcensis occur in small, and often isolated, woodland remnants along roads and streams (Menkhorst et al. 1988). Indeed, the long-term persistence of P. norfolcensis in Victoria outside formal conservation reserves is likely to be
dependent upon its ability to survive in narrow linear habitats and small patches of remnant woodland set within a cleared agricultural matrix. The risk of extinction is enhanced for small isolated populations because of their vulnerability to the vagaries of demographic, genetic and environmental stochasticity (Caughley 1994), further exacerbated by natural catastrophes. Reduced levels of landscape connectivity in fragmented landscapes may also limit dispersal, thus preventing the recolonisation of habitat patches following extinction (Bennett 1999). It is therefore crucial that investigations are undertaken into the biology and ecology of vulnerable species living in fragmented habitats to assess their conservation status and to provide information to aid recovery efforts (Redpath 1995a).

Small patches and linear strips of vegetation are particularly vulnerable to various biotic and abiotic edge effects that may reduce habitat quality (Janzen 1986; Laurance and Yensen 1991; Saunders et al. 1991; Collinge 1996; Gascon et al. 1999). For example, alterations to the microclimate (solar radiation, wind regimes) may affect the structure or floristics of the vegetation that in turn may impact on the fauna. Therefore, linear strips may provide sub-optimal habitat for many species because they are usually narrow and the amount of 'core' area remaining unaffected from edge effects is very small or non-existent (Collinge 1996). The shape may also have direct effects, such as influencing the spatial organisation of animals by determining the distribution of resources (see Chapter 5). If linear habitats were sub-optimal for a particular species, one might expect demographic parameters such as reproductive success, survival, or territoriality to be affected (Yahner and Mahan 1997).

In this study, I investigated the population ecology of *P. norfolcensis* in an interconnected network of remnant linear woodland in north-eastern Victoria. The landscape mosaic in the Euroa floodplains comprises linear strips of remnant woodland and cleared agricultural land with numerous isolated trees and small woodland patches and was found to support a resident population of *P. norfolcensis* (Chapter 3). The aim of this study was to investigate the population dynamics and life history of this population. Specific objectives were:

1) to estimate the size and density of the population;

2) to investigate the reproductive biology;
3) to assess survival rates and longevity; and
4) to compare the population ecology of *P. norfolcensis* in the linear network with populations of *P. norfolcensis* and other petaurids in areas of continuous habitat.

**METHODS**

**Study area**

A population of *P. norfolcensis* was studied by trapping in a 30 km$^2$ area approximately 10 km west of the township of Euroa in the Northern Plains region of Victoria (36°45’S, 145°30’E). The composition of woodland vegetation and the spatial arrangement of habitats are described in Chapter 3.

**Trapping and animal handling techniques**

The procedures for trapping arboreal marsupials are detailed in Chapter 3, and only modifications to those methods are given here. Additional trapping was undertaken before and after the census-trapping period (February 1997 to June 1998) and along additional transects during the census trapping period to fit and remove radiocollars for two concurrent studies (Chapter 5 and Holland 1998) (Fig. 4.1). Census trapping consistently sampled the same area over an 18-month period, while additional trapping sampled a smaller area with a varying trapping intensity to catch specific animals for radiotracking purposes. Hence, results from census trapping were used to calculate parameters requiring consistent sampling protocols, namely abundance and density estimates, survival and longevity, while the additional trapping data were also used to describe reproductive parameters, body weight and social organisation.
Figure 4.1. The location and details of the trapping grid near Euroa in north-eastern Victoria.
Woodland vegetation occurring along roads and road reserves is shown as solid straight lines and vegetation along streamsides is shown as solid wavy lines. The 14.55 km of linear habitat sampled during census trapping is indicated by dashed lines adjacent to solid lines. Transects trapped additionally to census trapping are shown by dotted lines.

Age estimation

A combination of characters was used to estimate the age of gliders (Table 4.1) (Suckling 1984; Quin 1995; Jackson 2000b). Body weight and incisor wear were the best parameters to estimate age. Age estimates for young animals (< 18 months of age) could be reliably made using these parameters, as found in other studies (Suckling 1984; Quin 1995; Jackson 2000b). After 18 months of age,
estimates were less reliable due to overlap between different characters. The colour of the patagium, which was found in other studies to be useful in estimating age (Suckling 1984; Quin 1995; Jackson 2000b), was only suitable in this study for young (< 18 months) animals. After this age, the variation in colour-change was not consistent with increasing age.

Animals were weighed to the nearest gram using Salter spring balances. If pouch young were present, their crown-rump length was estimated and the stage of development recorded. Approximate month of birth was estimated by comparing crown-rump length and stage of development with those described by Smith (1979) and Quin (unpub. data). Weight of pouch young was then derived from age-weight regressions calculated by Smith (1979) and subtracted from the adult female weight. In all calculations, the weight of a glider refers to body weight at first capture in each trapping session - thereby minimizing the effect of any weight loss that may have occurred as a result of successive captures within the same trapping session.

### Female reproductive condition

Female *P. norfolcensis* were allocated to one of six reproductive categories (after Quin (1995): 1) juvenile virgin females (pouch small, tight and undeveloped; hairs white; teats < 1 mm); (2) pregnant females (pouch lining thickening; pouch wall glandular, muscular and richly vascularised; may or may not have previously bred); 3) females carrying pouch young; 4) lactating females (females with loose pouch and one or two large lactating teats); 5) females recently bred (pouch and teats large but not lactating); 6) adult females non-breeding (pouch larger and deeper than in virgin females, but reproductive activity not apparent, hairs brown/yellow, often black scale in pouch; teats > 1 mm).
Table 4.1. Parameters used to estimate ages of *P. norfolcensis* (modified from Suckling 1984; Quin 1995; Jackson 2000).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimated age (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>&lt;1</td>
</tr>
<tr>
<td>Male weight (g)</td>
<td>&lt;200</td>
</tr>
<tr>
<td>Female weight (g)</td>
<td>&lt;180</td>
</tr>
<tr>
<td>Wear of upper incisors</td>
<td>none to slight</td>
</tr>
<tr>
<td>Wear of lower incisors</td>
<td>white, no cracks</td>
</tr>
<tr>
<td>Pouch condition (females)</td>
<td>small and shallow with fine white hairs, teats &lt;1 mm long</td>
</tr>
<tr>
<td>Frontal gland condition</td>
<td>not developed</td>
</tr>
<tr>
<td>Patagium colour</td>
<td>white</td>
</tr>
</tbody>
</table>

**Survival and longevity**

Animals that successfully entered the trappable population (i.e. recruits) were defined as those animals that after first capture were again captured in at least one subsequent trapping session (after Quin 1995). Hence, recruitment differentiates between new animals that are trapped only once, such as transients, dispersing animals or animals living at the edge of the trapping grid, and new animals that are recruited into the population and are resident at least until the next trapping session. Residents were considered to have disappeared from the trapping grid when not captured for two or more consecutive trapping sessions. Survival in each age class was determined by estimating the age of gliders at the time of their disappearance from the trappable population (after Quin 1995). The cause of
disappearance, such as dispersal or death, and the possibility of survival after leaving the grid, could not be confirmed for most animals.

Population size and density estimates

The population size during each trapping census was determined by calculating the minimum number known to be alive (MNKTBA). The MNKTBA method assumes that an individual not captured during a census, but known to be present before and after that census, is present in the area despite not actually being caught (Krebs 1999). This method will therefore include trap-shy individuals that are rarely captured. As in other investigations of petaurid population dynamics (Quin 1995; Jackson 2000b), transients were included in MNKTBA estimates. This is because many individuals trapped once were often caught on the ends of transects, or were juveniles or subadults born on the grid that dispersed before they could be captured a second time. The MNKTBA technique was selected to compute population size because it is the only method of population estimation that has been used consistently in other studies of *Petaurus* species (Suckling 1984; Quin 1995; Sharpe 1996; Jackson 2000b; Millis 2000), thus allowing comparable results. The MNKTBA estimate is unreliable during the first and last trapping sessions because it requires trapping before and after the session in question.

Density (number of individuals ha\(^{-1}\)) was calculated using the MNKTBA population size estimates divided by the size of the study area. Density can be problematic to calculate as the effective size of the study area is often larger than the actual area trapped because of individuals whose home ranges occur on the edge of the trapping grid (Krebs 1999). A commonly used technique to compensate for this sampling effect is to add a boundary strip equal to one half the width of the home range area to the size of the trapping grid (Krebs 1999). The spatial arrangement of woodland habitat in this study area (linear, and with numerous small patches within the cleared agricultural matrix) complicates this
technique. Knowledge of the movement patterns of the study organism is required in order to calculate an appropriately-sized boundary strip (Krebs 1999).

Therefore, the effective size of the trapping grid was calculated by summing the area of linear habitats (canopy width multiplied by transect length) actually trapped and the area included within a boundary strip. I used the results of a detailed radiotelemetry study of movement patterns of *P. norfolcensis* (Chapter 5) to estimate the size of the boundary strip. The mean maximum distance from linear habitats that each glider (n = 46) moved out to clumps of trees in farmland was 66.0 m (Chapter 5). Therefore, the area of woodland habitat occurring in cleared agricultural land within 65 m from the nearest linear habitat (measured from reserve boundary to tree trunk) was included in calculation of density estimates. The boundary strip also included the area of linear wooded habitats that abutted the trapping grid to a length of 400 m (equal to half the greatest home range length). The greatest mean range length during any season was 797 m (recorded for 30 adult and juvenile gliders in autumn, 1998, R. van der Ree, unpub. data). Maximum values were used to calculate the size of the boundary strip to ensure density was not overestimated.

The trappability of *P. norfolcensis* for each trap session (excluding the first and last trapping session) was determined as the proportion of animals known to be alive that were actually captured during that trapping session.

**Social organisation and group composition**

Den trees that were occupied by radio-collared *P. norfolcensis* (Chapter 6) were observed at dusk by stagwatching (see Lindenmayer *et al.* 1990) to determine the composition and size of social groups. Social groups were defined as comprising those animals that shared the same den tree for two or more nights (*sensu* Smith 1980) (see Chapter 5 for more details). The identity of radio-collared gliders was known and, where possible, the identity of non-collared gliders was determined by the colour combination of their reflective ear tags as they emerged from tree
hollows. The sex or identity of gliders without ear tags or radio-collars could not be determined. Due to the high density of hollow-bearing trees in the study area (Chapter 3), it was not logistically feasible to watch all potential den trees. Hence, most stagwatching was undertaken during the main radiotracking sessions (summer and autumn, 1998) when den trees occupied by radio-tagged individuals could be identified and the largest number of volunteer observers were available.

RESULTS

Trappability of gliders

The percentage of gliders known to be alive that were actually trapped during each trapping session varied between 60% and 90% (Fig. 4.2). The trend was similar for both sexes, and trappability of males was always higher than for females, except for December 1997, when female trappability slightly exceeded male trappability.

Figure 4.2. Trappability of *P. norfolcensis* during censuses in linear remnants near Euroa, north-eastern Victoria. Estimates are considered reliable from March 1997 to February 1998. Males are shown by solid squares, females by open diamonds.
Population size and density estimates

Between December 1996 and November 1998 (census and additional trapping combined) 1343 captures (628 captures of males, 715 of females) of 251 *P. norfolcensis* (107 males, 144 females) were made. During census trapping between February 1997 and May 1998, 211 *P. norfolcensis* (91 males, 120 females) were captured 832 times (401 males, 431 females). The MNKTBA population estimate based on census trapping results ranged from a minimum of 69 individuals in March 1997 to a peak of 112 in February 1998 (Fig 4.3). Estimates during the first and last trapping sessions are unreliable and should be regarded cautiously because trapping is required before and after the session in question.

The effective size of the census-trapping grid was estimated to be 72.6 ha. This comprised 59.2 ha of linear habitat (41.1 ha actually trapped and 18.1 ha at the ends of each transect) and 13.4 ha of woodland occurring in farmland within 65 m of census trapping transects. There was an increase in estimated overall density from 0.95 individuals ha\(^{-1}\) in March 1997 to 1.54 individuals ha\(^{-1}\) in February 1998 (Fig. 4.4).

![Census date vs. Number of individuals](image)

**Figure 4.3.** Population size estimates (MNKTBA) for *P. norfolcensis* during each census in linear habitats.

Squares represent males, diamonds represent females, and triangles the total population (males and females combined). Estimates for February 1997 and May 1998 are likely to be underestimates.
Figure 4.4. Estimated density of *P. norfolcensis* in linear habitats using the MNKTBA estimates of population size.
Squares represent males, diamonds represent females, and triangles the total population (males and females combined). Estimates for February 1997 and May 1998 are likely to be underestimates.

Population structure and sex ratio

The age structure of the population of *P. norfolcensis* comprised four age-classes that were present during each census (Fig. 4.5). The proportion of individuals in each > 1 yr age-class was relatively even over time, suggesting that the population had a stable age-structure. The age-class that fluctuated the most was the < 1 yr age-class, in response to variation in the number of recently independent juveniles entering the trappable population. The number of juveniles (< 1 yr) peaked between March and May in both years, but particularly so in 1998, when a large influx of new juveniles entered the trappable population.
Figure 4.5. Age-structure of the population of *P. norfolcensis* living in the network of linear habitats at Euroa. Data are based on numbers known to be alive in each trapping census.

The population of *P. norfolcensis* (adults and juveniles combined) occupying linear habitats near Euroa was always female dominated (Table 4.2). The overall sex ratio ranged from 0.70 : 1 (male : female) in October and December 1997 to almost parity (0.98 : 1) in May 1998. Sex ratios did not differ significantly from parity in any trapping census (Chi-square tests with Yates correction, 1 df, p > 0.05). Overall sex ratios tended towards parity in February 1998 and May 1998 (0.90 : 1 and 0.98 : 1, respectively) with the recruitment of a male-biased cohort of juveniles into the trappable population in February 1998 (Table 4.2). The only instance of a male-biased sex ratio occurred during the final trapping session in May 1998, when population estimates are least reliable. The sex ratio of the total number of gliders trapped during the study was also female biased, but not significantly so (Chi-square tests with Yates correction, 1 df, p > 0.05) (Table 4.2).
Table 4.2. Sex ratio (males : females) of juveniles (< 1 yr), adults (> 1 yr) and all gliders in a population of *P. norfolcensis* in a network of linear habitats near Euroa, north-eastern Victoria.

Sex ratios were calculated from MNKTBA estimates for each trapping session, except for the sex ratio of all gliders during the study period, which was based on the total number of gliders captured. The number of gliders is given in parentheses.

<table>
<thead>
<tr>
<th>Month / Year</th>
<th>Juvenile</th>
<th>Adult</th>
<th>Overall</th>
</tr>
</thead>
<tbody>
<tr>
<td>February 1997</td>
<td>0.67 : 1</td>
<td>0.76 : 1</td>
<td>0.74 : 1</td>
</tr>
<tr>
<td></td>
<td>(4 : 6)</td>
<td>(22 : 29)</td>
<td>(26 : 35)</td>
</tr>
<tr>
<td>March 1997</td>
<td>0.67 : 1</td>
<td>0.74 : 1</td>
<td>0.73 : 1</td>
</tr>
<tr>
<td></td>
<td>(6 : 9)</td>
<td>(23 : 31)</td>
<td>(29 : 40)</td>
</tr>
<tr>
<td>May 1997</td>
<td>0.60 : 1</td>
<td>0.89 : 1</td>
<td>0.82 : 1</td>
</tr>
<tr>
<td></td>
<td>(6 : 10)</td>
<td>(31 : 35)</td>
<td>(37 : 45)</td>
</tr>
<tr>
<td>August 1997</td>
<td>0.40 : 1</td>
<td>0.77 : 1</td>
<td>0.74 : 1</td>
</tr>
<tr>
<td></td>
<td>(2 : 5)</td>
<td>(41 : 53)</td>
<td>(43 : 58)</td>
</tr>
<tr>
<td>October 1997</td>
<td>–</td>
<td>0.67 : 1</td>
<td>0.70 : 1</td>
</tr>
<tr>
<td></td>
<td>(2 : 0)</td>
<td>(41 : 61)</td>
<td>(43 : 61)</td>
</tr>
<tr>
<td>December 1997</td>
<td>0.75 : 1</td>
<td>0.70 : 1</td>
<td>0.70 : 1</td>
</tr>
<tr>
<td></td>
<td>(6 : 8)</td>
<td>(39 : 56)</td>
<td>(45 : 64)</td>
</tr>
<tr>
<td>February 1998</td>
<td>1.33 : 1</td>
<td>0.75 : 1</td>
<td>0.90 : 1</td>
</tr>
<tr>
<td></td>
<td>(20 : 15)</td>
<td>(33 : 44)</td>
<td>(53 : 59)</td>
</tr>
<tr>
<td>May 1998</td>
<td>0.89 : 1</td>
<td>1.04 : 1</td>
<td>0.98 : 1</td>
</tr>
<tr>
<td></td>
<td>(16 : 18)</td>
<td>(28 : 27)</td>
<td>(44 : 45)</td>
</tr>
<tr>
<td>All gliders captured during study period</td>
<td>0.78 : 1</td>
<td>0.63 : 1</td>
<td>0.76 : 1</td>
</tr>
<tr>
<td></td>
<td>(39 : 50)</td>
<td>(59 : 79)</td>
<td>(91 : 120)</td>
</tr>
</tbody>
</table>

**Recruitment, persistence and transients**

New gliders were detected in the trappable population during every trapping census (Fig. 4.6). Excepting the first trapping session in February 1997, the largest influx of new animals into the trappable population occurred in February 1998 with 33 new captures, the majority (85 %) of which were juveniles (< 1 yr). These juveniles were born during winter or spring of 1997 (Fig. 4.9).
Animals were recruited into the population during each trapping census and recruits originated from all age groups (Table 4.3). Most recruits were in the < 1 yr and 1 - 2 yr age groups (Table 4.3), representing either juveniles born on the trapping grid (probably mostly those in the < 1 yr age group) or gliders born outside the study area and dispersing into the trappable population (probably mostly those in the 1 - 2 yr age class). Males and females were recruited into the population in approximately equal proportions in the < 1 and 1 - 2 yr age groups, while in the 2 - 3 and > 3 yr age groups, females made up the majority of recruits (Table 4.3).

Animals trapped only during a single census (termed single captures) originated from all age groups and all times of the year. The largest number of single captures were of animals in the 0 - 1 yr age-class, probably mostly animals born
on-site that then dispersed or died (refer longevity section below). Animals in the
1 - 2 yr age-class were also probably dispersing through the study area searching
for suitable territories to occupy. A smaller number of older animals in the 2 - 3
yr (n = 8) and > 3 yr (n = 3) age classes were either trapped at the ends of transects, were first trapped at the start of the study and presumably perished shortly after their first capture, or were transients that did not occupy a stable home-range.

Table 4.3. Recruitment of *P. norfolcensis* by age and sex into a population inhabiting a network of linear habitats near Euroa, north-eastern Victoria. Recruitment is defined as entry into the trappable population by animals that are resident for at least one subsequent trapping census. Values in parentheses are the number of new animals that were not trapped during a subsequent census (i.e. single captures).

<table>
<thead>
<tr>
<th>Trapping census</th>
<th>Gender</th>
<th>Age class (years)</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>&lt; 1</td>
<td>1 - 2</td>
</tr>
<tr>
<td>March 1997</td>
<td>M</td>
<td>2 (1)</td>
<td>2 (-)</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>2 (4)</td>
<td>- (-)</td>
</tr>
<tr>
<td>May 1997</td>
<td>M</td>
<td>1 (1)</td>
<td>4 (-)</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>4 (2)</td>
<td>3 (-)</td>
</tr>
<tr>
<td>August 1997</td>
<td>M</td>
<td>- (-)</td>
<td>3 (1)</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>1 (-)</td>
<td>5 (1)</td>
</tr>
<tr>
<td>October 1997</td>
<td>M</td>
<td>- (2)</td>
<td>1 (1)</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>- (-)</td>
<td>3 (1)</td>
</tr>
<tr>
<td>December 1997</td>
<td>M</td>
<td>4 (2)</td>
<td>- (2)</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>3 (5)</td>
<td>2 (1)</td>
</tr>
<tr>
<td>February 1998</td>
<td>M</td>
<td>10 (6)</td>
<td>1 (1)</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>6 (6)</td>
<td>- (-)</td>
</tr>
<tr>
<td>May 1998*</td>
<td>M</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>10</td>
<td>-</td>
</tr>
<tr>
<td>Total*</td>
<td>M</td>
<td>17 (12)</td>
<td>11 (5)</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>16 (17)</td>
<td>13 (3)</td>
</tr>
</tbody>
</table>

Results for February 1997 are excluded because it was the first trapping census, and residents could not be distinguished from recruits.

* In May 1998, recruits and transients could not be separated because it was the final trapping census, and hence just a single figure is given. Therefore, the grand total row does not include the May 1998 data.
The majority of residents that disappeared from the trapping grid during the study period were in the > 1 yr age-classes (i.e. 1 - 2, 2 - 3 and > 3 yr age-classes) (Fig. 4.7). The number of resident gliders disappearing from the < 1 yr age class was low (Fig. 4.7) because many were trapped only once, and hence did not qualify as residents (Table 4.3). The number of animals disappearing from each > 1 yr age-class is approximately similar. Residents in the 1 - 2 year age class probably dispersed, whereas older animals (> 2 yrs) may have disappeared due to a combination of age-related mortality or predation.

Predation accounted for the known loss of 11 gliders from the tagged population - most of which were detected through radiotelemetry (Chapter 5). Nine individuals (six juveniles and three adults) were detected with injuries consistent with owl predation (Fleay 1968; Kavanagh 1988), usually consisting of the tail neatly severed at the base, and sometimes including skin from the animal's back. Both the Powerful Owl *Ninox strenua* and Barking Owl *Ninox connivens* are known to prey upon *P. norfolcensis* (Fleay 1947; Traill 1993; Schulz 1997) and have been heard calling in the study area (R. van der Ree pers obs, M. Venosta, pers. comm.). One juvenile was probably killed by a feral cat *Felis catus* (front limbs chewed) and the predator for the remaining adult was not known.

It was not possible to accurately determine longevity because of the relatively short duration of the study. A small number of animals estimated to be > 3 yrs of age at the commencement of the study were present for two years of the study, suggesting ages of at least 5 years.
Reproduction

*Petaurus norfolcensis* successfully reproduced within the linear habitat network. Female reproductive condition varied throughout the year (Fig 4.8) and followed the categories and sequence described by Quin (1995). There was a distinct breeding season, with pouch young present in all months between May and January (Fig 4.8). There appeared to be some variation between years, with pouch young appearing later in 1998 (August) than in 1997 (May) (Fig. 4.8). The estimated month of birth followed a similar pattern. Young were estimated as being born between May and December, with a peak in births in 1997 occurring in late autumn to winter (June to October) (Fig 4.9). The peak in births was less evident in 1998, probably because fewer individuals were examined (Fig 4.8, Table 4.4). The age of sexual maturity is estimated to be 12 - 18 months, as animals typically first carried pouch young when in the 1 - 2 yr age class. One animal estimated to be a juvenile of 10 - 11 months of age gave birth to twins, but this litter was presumed to have been lost because she was observed carrying a second litter of twins two months later.
A total of 82 litters was observed, the majority of which were twins (65%) or single young (34%) (Fig 4.9) - one litter in August 1998 comprised triplets. When females were observed with large pouches containing lactating or enlarged teats, it was assumed they had recently bred and given birth to a number of young equal to the number of enlarged or lactating teats. An estimated 41 additional litters were recorded under these criteria, accounting for a total of 123 litters (Table 4.4). Mean size of all litters (n = 123) across the study period was 1.7. Eleven females gave birth to two litters during the 1997-breeding season (May - December 1997). It is not known whether the first litters were lost before weaning or were successfully reared. During the study, all adult females bred and the mean natality rate was 1.9 young per female per year for the whole study (Table 4.4). A summary of the reproduction of *P. norfolcensis* in the linear habitat network is given in Table 4.4.

![Graph](image)

**Figure 4.8. Reproductive condition of female *P. norfolcensis* captured between December 1996 and November 1998.**
The number of individuals examined is given at the top of each column, and includes gliders trapped during both census and additional trapping.
Figure 4.9. Estimated month of birth for litters of one (solid bars), two (open bars), or three young (diagonal hatching) between October 1996 and November 1998, near Euroa. Only observed pouch young are included.

Table 4.4. Summary of reproductive data for adult *P. norfolcensis* occupying linear habitats near Euroa, between 1996 and 1998.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>1996</th>
<th>1997</th>
<th>1998</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of adult females</td>
<td>22</td>
<td>78</td>
<td>12</td>
<td>87</td>
</tr>
<tr>
<td>Females breeding (%)</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>100(^A)</td>
</tr>
<tr>
<td>Litter size - 1</td>
<td>7</td>
<td>24</td>
<td>2</td>
<td>33</td>
</tr>
<tr>
<td>Litter size - 2</td>
<td>15</td>
<td>64</td>
<td>9</td>
<td>88</td>
</tr>
<tr>
<td>Litter size - 3</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Total no. of litters</td>
<td>22</td>
<td>89</td>
<td>12</td>
<td>123</td>
</tr>
<tr>
<td>Total no. of young born</td>
<td>37</td>
<td>155</td>
<td>23</td>
<td>215</td>
</tr>
<tr>
<td>Mean litter size</td>
<td>1.7</td>
<td>1.7</td>
<td>1.9</td>
<td>1.7</td>
</tr>
<tr>
<td>Natality rate(^B)</td>
<td>1.7</td>
<td>2.0</td>
<td>1.9</td>
<td>1.9(^A)</td>
</tr>
</tbody>
</table>

\(^A\) These values are means calculated over three breeding seasons
\(^B\) Number of young per adult female per year
Body weight

The mean (± s.e.) body weight of adult male and female *P. norfolcensis* between December 1996 and November 1998 was 258.4 ± 1.6 g and 235.9 ± 1.3 g, respectively. Mean body weight of males and females fluctuated relatively consistently throughout the year, with peaks in weight discernible in autumn of 1997 and 1998 (Fig 4.10). The major peak, in May 1998, represented the maximum body weights attained throughout the study period (males 299.3 ± 5.0 g, females 271.3 ± 4.7 g). This coincided with maximum flowering of *E. microcarpa* (R. van der Ree, unpub. data), the dominant tree species in the area. Minimum adult male and female body weights were recorded in November 1998 with 227.4 ± 8.3 g and 214.7 ± 5.27 g, respectively. The lightest male and female juveniles recorded from the trappable population were 133 g and 119 g, respectively. Based on weight and age regressions calculated by Smith (1979), the time from birth until capture for these two individuals was approximately 140 to 160 days.

![Figure 4.10](image_url)  
*Figure 4.10. Variation in mean body weight (± s.e.) of adult (> 1 yr of age) *P. norfolcensis* between December 1997 and November 1998.*  
Males are shown by solid squares, females by open diamonds.
Social organisation

*Petaurus norfolcensis* occupied hollows in large old trees for diurnal shelter with groups of from one to six individuals occupying the same hollow simultaneously. The mean number of individuals observed emerging from an occupied tree was 2.53 (Chapter 6). The size and composition of groups of gliders occupying a particular hollow varied from day to day because gliders regularly swapped nest trees (Chapter 6). Social groups were identified based on the identity of individuals that regularly shared the same den tree on two or more occasions (after Smith 1980). In addition, members of the same social group regularly occupied different combinations of trees from a suite of those available (e.g. during summer 1997-1998, one social group collectively occupied 16 den trees, Table 6.4). Consequently, members of some social groups may have gone undetected because it was not possible to radiotrack all members of the same group simultaneously, nor could all known nest trees of a social group be stagwatched simultaneously.

Social groups were of mixed-sex, and their composition varied from at least one adult male and adult female (Transect 1, Upper Group) to at least two adult males, two adult females, and juvenile offspring (Transect 1, Middle Group) (Table 4.5). While the relationship between males in multiple male groups was not determined, the overall group structure suggests a polygynous mating strategy. This assessment of social group composition (Table 4.5) was made in summer 1998, and coincided with the entry of recently independent juveniles into the trappable population (i.e. those born in winter 1997). Consequently, group sizes may have been at their maximum before dispersal of young occurred.
Table 4.5. Composition of social groups of *P. norfolcensis* in summer, 1997-1998.

M = male, F = female. Age-class in years is given in superscript text. Gliders of unknown identity are denoted by question mark and are probably juveniles, although this was not confirmed. All identified females raised litters in mid to late 1997.

<table>
<thead>
<tr>
<th>Group name</th>
<th>Identity of gliders</th>
</tr>
</thead>
<tbody>
<tr>
<td>Transect 7</td>
<td>M^{8}_{3}</td>
</tr>
<tr>
<td>Transect 11 (Middle)</td>
<td>M^{15}_{4}</td>
</tr>
<tr>
<td>Transect 1 (Lower)</td>
<td>M^{10}_{&gt;3}</td>
</tr>
<tr>
<td>Transect 1 (Middle)</td>
<td>M^{9}_{1-2}</td>
</tr>
<tr>
<td>Transect 1 (Upper)</td>
<td>M^{2}_{1-3}</td>
</tr>
</tbody>
</table>
Table 4.6. Comparison of the population dynamics of *P. norfolcensis* populations at Euroa and elsewhere in Australia.
Data sources are: (Quin 1995; Traill 1995; Sharpe 1996; Millis 2000). Means are presented.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>North-east Victoria</th>
<th>Coastal northern New South Wales</th>
<th>South-east Queensland</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Euroa (this study)</td>
<td>Chiltern Box-Ironbark National Park</td>
<td>Limeburners Creek</td>
</tr>
<tr>
<td></td>
<td>258</td>
<td>249</td>
<td>213</td>
</tr>
<tr>
<td>Body mass (g) Male</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>235</td>
<td>220</td>
<td>192</td>
</tr>
<tr>
<td>Body mass (g) Female</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.95 - 1.54</td>
<td>0.49</td>
<td>0.89 - 1.54</td>
</tr>
<tr>
<td>Density (range, No. ha⁻¹)</td>
<td>0.49</td>
<td>0.49</td>
<td>0.42</td>
</tr>
<tr>
<td>Sex ratio</td>
<td>Parity</td>
<td>Male biased</td>
<td></td>
</tr>
<tr>
<td>Birth season</td>
<td></td>
<td></td>
<td>Apr. - Nov.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Jul. - Dec.</td>
</tr>
<tr>
<td>Litter size</td>
<td>1.7</td>
<td>1.7</td>
<td>1.8</td>
</tr>
<tr>
<td>Natality rate</td>
<td>1.9</td>
<td></td>
<td>1.7</td>
</tr>
<tr>
<td>Dispersal age (months)</td>
<td>8 - 15</td>
<td>M: 13.2, F: 11.8</td>
<td></td>
</tr>
<tr>
<td>Social organisation</td>
<td>Polygamous/polygynous</td>
<td>Polygynous</td>
<td>Polygynous</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Monogamous</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Random/polyandry</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Random/polyandry</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Random/polyandry</td>
</tr>
<tr>
<td>Size of social group - mean (range)</td>
<td>2.53 (1 - 9)</td>
<td>(1 - 10)</td>
<td>(2 - 3)</td>
</tr>
</tbody>
</table>
DISCUSSION

Abundance and density

A large number of *P. norfolcensis* were resident within the linear habitat network at Euroa. Density estimates (0.95 - 1.54 ha\(^{-1}\)) were similar to those recorded for *P. norfolcensis* in continuous forest at Limeburners Creek on the northern coast of New South Wales (0.89 - 1.54 ha\(^{-1}\))(Quin 1995). However, the density at Euroa was up to three times that recorded from a study based on data collected from nest-boxes at Chiltern, north-east Victoria (0.40 - 0.49 ha\(^{-1}\)) (Traill and Coates 1993; Traill 1995) and from a trapping study at Bungawalbin Nature Reserve in north-eastern New South Wales (0.42 ha\(^{-1}\)) (Sharpe 1996). On the south coast of New South Wales, the population density of *P. norfolcensis* based on spotlighting was estimated to be 0.01 - 0.2 ha\(^{-1}\) (Davey 1989, cited in Gibbons and Lindenmayer 1997).

Thus, the density of *P. norfolcensis* in the linear network of narrow, wooded habitats at Euroa is at least equal to the maximum densities recorded for this species elsewhere in Australia, and in comparison with a number of other studies, it is up to seven times greater. This implies that the habitat at Euroa is of high quality for *P. norfolcensis*. Different sampling methods employed in the various studies may yield varying density estimates. However, the density estimates reported in this study are likely to be conservative because the size of the boundary strip added to the area of the trapping grid was calculated from the mean maximum distances that gliders moved into paddock trees to feed.

The density of other petaurids living in fragmented habitats varies widely. At Willung in south-east Victoria, the density of *P. breviceps* in roadside habitat ranged between 4.8 and 12.8 ha\(^{-1}\) and in the largest forest patch studied (a 10 ha section of a 49 ha patch, density ranged between 2.0 and 3.6 ha\(^{-1}\) (Suckling 1984). In fragmented habitat surrounded by plantations of the introduced Caribbean Pine *Pinus caribaea* in north Queensland, the density of *P. breviceps* and the Mahogany Glider *Petaurus gracilis* was 0.43 - 0.48 ha\(^{-1}\) and 0.15 - 0.16 ha\(^{-1}\) respectively (Jackson 2000b).
Population structure and sex ratio

The population age structure was relatively even-aged, with four similar sized age-cohorts dominating the population. A similar distribution of individuals within each age class was found in the population of *P. norfolcensis* at Limeburners Creek (Quin 1995). At Euroa, fluctuations in age-class distribution over the study period were moderate, with the greatest fluctuations occurring in the 0 - 1 yr age class because of the entry of recently independent juveniles into the trappable population. Gradual changes in age-class distribution over time were also evident at Limeburners Creek (Quin 1995). Similar numbers in each age-class, and the presence of gradual changes rather than abrupt irruptions or decline, indicate that rates of reproduction and mortality were relatively consistent over time. This suggests that the population within the linear network is stable.

Despite capturing more females than males, the sex ratio for the overall population never differed significantly from parity. As the study progressed however, the sex ratios came closer to parity. This appears to be caused by a relatively large number of juvenile males entering the trappable population from December 1997 onwards.

Longevity, survival and dispersal

Accurate aging of *P. norfolcensis* beyond two or more years of age was difficult, a problem common with other studies of Petaurids (e.g. Quin 1995; Jackson 2000), and is exacerbated by the relatively short nature of many field studies (two to three years). The maximum age estimate of at least five years indicated for *P. norfolcensis* in this study is similar to age estimates of five to six years reported for this species by Quin (1995). Maximum ages for *P. breviceps* in wild conditions are up to seven to nine years (Suckling 1984; Klettenheimer *et al.* 1997), however typical longevity of individuals is estimated to be around five to six years (Suckling 1984; Quin 1995). Maximum longevity was estimated to be at
least five years for *P. gracilis* (Jackson 2000b) and at least six years for *P. australis* (Goldingay and Kavanagh 1990). In summary, longevity in this population of *P. norfolcensis* at Euroa appears to be similar to that observed elsewhere for this species and genus.

Causes of mortality of *P. norfolcensis* in the study area include predation by native and introduced predators, as well as anthropogenic causes. Owl predation was the most common cause of natural mortality observed, with one instance of predation by *F. catus*. Other predators occurring in the area that are known to prey upon petaurids include the Red Fox *Vulpes vulpes* (Brunner et al. 1976; Triggs et al. 1984; Brown and Triggs 1990; Lunney et al. 1990), Tree Goanna *Varanus varius*, Laughing Kookaburra *Dacelo novaeguineae*, and Southern Boobook *Ninox novaeseelandiae*. Predation by owls within the study area is also believed to account for two instances of predation on *P. tapoatafa*, as two tails of this species were severed at their base and found on the ground. Other observations of predation on arboreal marsupials in the study area include *V. varius* eating a *P. peregrinus*, and on two different occasions, a Wedge-tailed Eagle *Aquila audax* was observed consuming a *P. peregrinus* and a *T. vulpecula*. The major anthropogenic cause of death for *P. norfolcensis* was dehydration or starvation after individuals became entangled with barbed wire fencing adjacent to roadside vegetation (van der Ree 1999). No road-kills were observed along the unsealed, low-volume roads within the study area, but two carcasses of *P. norfolcensis* were found nearby along the Hume Highway, the major arterial highway between the cities of Sydney, Canberra and Melbourne.

Rates of predation were not explicitly quantified in the studies of the ecology of *P. norfolcensis* in continuous habitat and hence conclusions are tentative. However, Quin (1995) reported that between July 1986 and November 1998 he found one carcass of *P. norfolcensis* that he believed was killed by an owl and he did not observe direct predation on either *P. norfolcensis* or *P. breviceps*. Between March and September 1996, Sharpe (1996) observed two instances of predation of *P. norfolcensis* by *V. varius* at Bungawalbin Nature Reserve. Over a two and a half year period at Chiltern National Park, a breeding pair of *N. strenua* consumed at least 40 *P. norfolcensis* and 18 *P. breviceps* (Traill 1993). The
spatial arrangement of the habitat may be of less importance for relatively 'specialised' predators (e.g. large owls) than the amount of habitat in the landscape that supports populations of prey (Redpath 1995b).

A number of studies in fragmented landscapes have suggested that rates of predation within small remnants or on the edges of larger remnants may be greater than within the 'interior' of large patches (Andren and Angelstam 1988; Yahner 1988; Paton 1994). These studies have been mainly based on measures of predation on bird's nests. In a study in New South Wales with a similar woodland type to that at Euroa, predation on eggs in artificial nests by avian predators was significantly higher in linear than in large remnants (Major et al. 1999b). The higher levels of predation may occur because certain predators (typically more generalist species) are advantaged by the presence of the edge or ecotone (Soulé and Gilpin 1991), are species that prefer the cleared matrix (Andren et al. 1985; Andren 1992; Major et al. 1999b), or use linear landscape elements as travel corridors (May and Norton 1996; Bergin et al. 2000). Furthermore, the extirpation of large predators may allow smaller generalist predators to dominate, altering relative predation rates between different sized prey species (Laurance 1997b). An alternative hypothesis is that predators, such as owls, are able to concentrate their foraging within clearly-defined areas (e.g. remnant woodland) (Meunier et al. 2000), and thus may forage more efficiently because woodland-dependent prey are not widely dispersed. Clearly, additional research is required to quantify the level of predation on arboreal marsupials in relation to remnant shape (linear vs. block shaped) and within the context of the surrounding landscape mosaic (Bergin et al. 2000).

Reproduction

Reproduction by *P. norfolcensis* in linear wooded habitats at Euroa followed a similar pattern to that recorded at Chiltern, Limeburners Creek and in south-east Queensland (Quin 1995; Traill 1995; Millis 2000). Breeding was seasonal, as in the other populations, and there was a major peak in births during winter months,
especially between June and August. Mean litter size at Euroa (1.7) was similar to that recorded at Chiltern, Limeburners Creek and south-east Queensland (1.7, 1.8 and 1.7 - 1.9, respectively) (Quin 1995; Traill 1995; Millis 2000). The lactation period of approximately 140 to 160 days for *P. norfolcensis* is sufficiently short to allow the production of a second litter within a single breeding season, which occurred at Chiltern and Limeburners Creek (Quin 1995; Traill 1995). Polyoestry has also been observed in *P. breviceps* (Smith 1979; Quin 1995; Traill 1995; Jackson 2000b), and *P. gracilis* if the first litter is lost (Jackson 2000b), however the larger *P. australis* is limited to one litter per year (Henry and Craig 1984; Goldingay 1992).

Mean natality rate of *P. norfolcensis* in linear habitats at Euroa (1.9) was lower than that recorded at Limeburners Creek (2.53) (Quin 1995). The higher mean natality rate at Limeburners Creek can be attributed to approximately 60% of females raising a second litter during 1987 and 1988, while just 14% of females at Euroa raised a second litter during 1997. There may be a more constant supply of food resources in the aseasonal environment in north-eastern New South Wales, resulting in higher natality rates there than in the more temperate climate at Euroa (Quin et al. 1996b). Comparable data are not given by Traill (1995) or Millis (2000) for other study areas. The natality rate at Euroa is identical to that recorded for *P. gracilis* in north Queensland (Jackson 2000b). This is most likely due to a size-related constraint resulting in longer times for gestation, lactation and weaning because of larger body size for *P. gracilis* than *P. norfolcensis*, despite *P. gracilis* occupying a more productive tropical climate.

**Social organisation**

At Euroa, *P. norfolcensis* nested communally and typically formed mixed-sex social groups. While it appeared that some animals did not belong to a social group (Chapter 6), most formed social groups that consisted of up to two adult males and two or more adult females as well as a number of offspring (Table 4.5). The presence of multiple adults of both sexes within a social group suggests
polygamy or polygyny, however as the level of dominance by male group members is unknown, interpretation of the social system as either would be tentative. There appears to be some flexibility in social organisation by *P. norfolcensis* at different sites; the populations at Chiltern and Limeburners Creek were interpreted to be polygynous (Quin 1995; Traill 1995) and at Bungawalbin it was considered a monogamous system (Sharpe 1996). In south-east Queensland, Millis (2000) concluded that groups formed as a result of access to food resources (female resource polygyny) and that mating occurred randomly and opportunistically.

Variation in the social organisation of other petaurids is widespread (see review by Quin 1995), and interpretations range from polygyny to monogamy for populations of both *P. breviceps* and *P. australis*, depending on their geographic location and availability of food resources. Typifying this variation is the identification of a population of *P. australis* in north Queensland where the social organisation included groups that were monogamous, polygynous, polyandrous and a bachelor group (D. Quin, pers. comm.). It has become evident that there are limitations to interpreting social systems based solely on the composition of nesting groups because of the potential for mating to occur with individuals from outside the social group (Millis 2000). A study of paternity in populations of *P. norfolcensis* in south-east Queensland using genetic techniques showed that mating outside of the social group was common and that the overall pattern of mating appeared to be random (Millis 2000).

Different social systems are typically characterised by variation in sex ratios, extent of sexual dimorphism and sex-biased dispersal rates (Greenwood 1980; Dobson 1982; Smith and Lee 1984; Sadler and Ward 1999). Populations with polygynous mating systems typically have female-biased sex ratios, greater male body sizes, male-biased dispersal and greater rates of male juvenile mortality (Greenwood 1980; Dobson 1982; Smith and Lee 1984; Sadler and Ward 1999). At Euroa, sex-ratios were typically female biased (though never significantly different from parity), and adult males were slightly heavier than females (by approximately 20 g). However, male-biased dispersal and higher rates of male vs. female juvenile mortality were not evident from the available data. In contrast,
more resident and single capture females from all > 1 yr age-classes disappeared from the trapping grid than males. In addition, equal numbers of males and females in the 1 - 2 yr age class were recruited into the trappable population, suggesting that both sexes dispersed. Clearly, further detailed investigation of social group composition over a longer time-period, as studied for _P. breviceps_ by Sadler and Ward (1999) and _P. norfolcensis_ by Millis (2000) is required to elucidate the formation, composition and functioning of social groups.

**CONCLUSIONS**

It is clear that the network of linear remnants near Euroa provides sufficient resources to support a stable, self-sustaining population of _P. norfolcensis_. Gliders were resident within the linear strips and density estimates were almost identical to those at Limeburners Creek and up to three times that recorded at Chiltern and Bungawalbin Nature Reserve. All adult females residing within the linear strips reproduced, and young were recruited into the trappable population each year. Moreover, the reproductive parameters of natality rate, litter size, and timing of reproduction were identical, or very similar, to those reported in other studies that examined the biology of _P. norfolcensis_. Estimates of maximum longevity at Euroa suggest that life-span is also comparable to those estimated from continuous forest.

At present, the habitat at Euroa is of sufficient size, quality and spatial arrangement that the population of _P. norfolcensis_ can persist without requiring recruits from a 'source' population. However, the persistence of the population into the future is not assured due to ongoing habitat loss and degradation. The fragmented woodland habitat faces numerous threats including loss of habitat due to incremental tree removal for road widening or pasture improvement, and the degradation of habitat quality due to increased nutrient levels, salinisation, die-back, firewood collection, grazing, and lack of regeneration. This study clearly demonstrates that the present-day conservation value of remnant woodland habitat for _P. norfolcensis_ is high. It also recognises that the Euroa area is significant for
the conservation of *P. norfolcensis* within Victoria. Appropriate management of potentially threatening processes is required to ensure the conservation potential of all remnant woodland into the future.
CHAPTER 5

SPATIAL ARRANGEMENT OF THE SQUIRREL GLIDER
*PETARUS NORFOLCENSIS*, IN A NETWORK OF
REMNANT LINEAR HABITATS

INTRODUCTION

The spatial organisation of the arboreal marsupials of the Family Petauridae (*P. gracilis, P. australis, P. breviceps, P. norfolcensis*) and Family Pseudocheiridae (*P. volans*) within large tracts of forest and woodland has been well-documented (Henry 1984; Henry and Craig 1984; Kehl and Borsboom 1984; Suckling 1984; Goldingay 1992; Quin *et al.* 1992; Quin 1995; Comport *et al.* 1996; Sharpe 1996; Jackson 2000a). However, the conversion of continuous tracts of habitat into mosaics with small patches of more-or-less suitable habitat following clearing and fragmentation may present significant challenges for population survival (Merriam 1995). Our understanding of the spatial organisation of populations in continuous habitats is unlikely to accurately represent the situation in highly fragmented landscapes. Consequently, the need to investigate parameters such as home range size and shape, territoriality, and dispersal in fragmented landscapes has been highlighted (Saunders and de Rebeira 1991; Merriam 1995; McIntyre and Wiens 1999).

To survive and reproduce, individuals must have access to an area that contains sufficient resources to fulfill their dietary, breeding and shelter requirements. Because resources are distributed over both spatial and temporal scales, animals in heterogeneous landscapes may need to include different areas of habitat into their range to satisfy these needs. Furthermore, foraging theory suggests that the optimum size and shape of this area will be a habitat configuration that minimises energy expenditure and predation risk while maximising energy gain (Schoener 1971). In fragmented landscapes, these resources may be distributed among multiple habitat patches (e.g. Redpath 1995). The ability of animals to move
within and among landscape elements will be influenced by their level of mobility and the spatial arrangement of the habitat (Wiens et al. 1997; Bennett 1999). Therefore, the spatial organisation of animals in relation to the pattern of habitat available is one of the most important responses at the individual level that will influence a species' persistence in fragmented landscapes (Ims et al. 1993).

Linear strips of vegetation are common components of many fragmented landscapes and the management or establishment of such corridors is often recommended as a potential strategy to alleviate the deleterious effects of increasing isolation between fragments (e.g. Mwalyosi 1991; Saunders and Hobbs 1991; Newmark 1993; Claridge and Lindenmayer 1994; Wheeler 1996; Fleury and Brown 1997; Bennett 1999). However, the potential detrimental consequences associated with residing in a linear habitat may be great. It has been suggested that colonial species that feed on widely dispersed food items from a central place may be especially disadvantaged in linear habitats (Recher et al. 1987). Home ranges are likely to be long and narrow, and if the distance that animals must travel to fulfill their essential requirements exceeds that which is energetically feasible, local extinction may result. Therefore, species with large area requirements or low levels of dispersal or mobility may be more prone to extinction within small, linear fragments (Laurance 1991a). Consequently, it is imperative that species- and landscape-specific studies on habitat use and movement patterns be undertaken within fragmented landscapes (Saunders and de Rebeira 1991; Soulé and Gilpin 1991; Wilson and Lindenmayer 1995).

In south-eastern Australia, a large proportion of the wooded habitat within the range of *P. norfolcensis* has been converted into cleared farmland (Menkhorst et al. 1988). Much of the remaining habitat is highly fragmented, occurring as numerous small patches (< 30 ha) and many linear strips along roads and streams (Bennett et al. 1994b). The aim of this study was to examine the spatial organisation of *P. norfolcensis* in a network of linear woodland remnants near Euroa, north-eastern Victoria. Specifically, the objectives of this study were:

1) to measure and describe the size and shape of *P. norfolcensis* home ranges in a network of linear habitats;
2) to investigate the influence of habitat geometry on home range parameters; and
3) to investigate the dispersal and fate of juveniles.

METHODS

Study area

A population of *P. norfolcensis* was studied by trapping and radiotelemetry in a 30 km$^2$ area approximately 10 km west of the township of Euroa in the Northern Plains region of Victoria (36°45'S, 145°30'E). The composition of woodland vegetation and the spatial arrangement of habitats are described in Chapter 3.

Handling and radio-tracking techniques

The procedures for trapping *P. norfolcensis* are detailed in Chapter 3. Animals to be fitted with radiocollars were usually captured during census trapping sessions (see Chapter 3), or if census-trapping sessions did not coincide with the radiotracking studies, additional trapping was undertaken.

Adult gliders were selected for radiotracking from widely dispersed areas of the trapping grid (Fig. 5.1) to sample animals from as large an area as possible. The first animals captured in each target area that satisfied the following criteria were fitted with radiocollars. First, individuals had to be resident (captured in at least two previous trapping sessions) and second, females were to be non-lactating (to minimise risk to dependent young remaining in a nest). Target areas were geographically distributed across the trapping grid, and included simple linear habitats (straight sections of linear remnants) and the intersections of multiple linear remnants. Juveniles chosen for radiotracking were selected according to their estimated age (< 1 yr) (see Chapter 4 for aging techniques). All transmitters
were single stage (Sirtrack, New Zealand) and mounted on neck collars. Radiotransmitters for adults were either tuned loop or cable-tie with whip antenna, weighing approximately 6.5 g and 5 g, respectively. Radiotransmitters for juveniles were mounted on expanding, break-away collars (after Soderquist 1993) and weighed approximately 7 g. In all cases, collars weighed less than 5% of body weight. Radiocollars were fitted and removed at the commencement and completion of each tracking session.

Radiotracking was undertaken on foot using a receiver operating in the 150 MHz range with a collapsible 3-element Yagi antenna (Titley Electronics, Ballina, New South Wales). Reflective markers mounted to trees were spaced 100 m apart along the network of linear remnants to enable determination of the observer's location. The location of animals was determined by pacing on foot to the nearest reflective marker. The accuracy of locations was high because the actual tree in which the animal was located could usually be identified. The error associated with each location was estimated to be ± 10 m. One diurnal location or "fix" per animal was collected each day to identify den trees, and up to four nocturnal fixes spaced > 2 hrs apart were obtained per animal each night. *P. norfolcensis* can move distances in excess of 300 m in 15 min (Holland 1998), indicating that they are capable of traversing the entire length of their home range within a 2 hour period. Consequently, it is assumed that nocturnal fixes were independent and that each fix made an equal contribution to the home range estimate (White and Garrott 1990). Nocturnal fixes were collected almost every night during each tracking period, usually commencing at least one hour after dusk. Den trees were identified every day during tracking periods.
Figure 5.1. The location and details of the linear woodland remnants near Euroa in north-eastern Victoria where *P. norfolcensis* were radiotracked. Woodland vegetation occurring along roads and road reserves is shown as solid straight lines and vegetation along stream sides is shown as solid wavy lines. The linear remnants in which gliders were radiotracked are indicated by dashed lines adjacent to solid lines.

Monitoring of *P. norfolcensis* was conducted during four radiotracking sessions, each of three to six weeks duration, in 1998. Summer (21/1/98 - 4/3/98) and autumn (17/4/98 - 2/6/98) were the major tracking periods, with 20 and 30 individuals, respectively, tracked in each season. The winter (23/7/98 - 19/8/98) and spring (5/11/98 - 27/11/98) tracking periods formed part of a study on the time budget and foraging behavior of *P. norfolcensis* (Holland 1998), with nine
and six individuals, respectively, tracked in each season. As commonly occurs in radiotelemetry studies, this design was a trade-off between the number of individuals tracked and the intensity with which they are monitored (White and Garrott 1990). In this study, a large number of animals were intensively monitored in summer and autumn, and then intensive monitoring continued with a subset of animals in winter and spring.

**Analysis of home range**

Home range is defined as 'that area traversed by the individual in its normal activities of food gathering, mating and caring for young' (Burt 1943, p351). Therefore, in this study, home range estimates are derived from diurnal fixes (one diurnal location per animal per day) and nocturnal fixes (up to four nocturnal locations > 2 hr apart per animal per night). A range of techniques are available to describe and analyse home range characteristics, each with their own assumptions and limitations (Kenward 1987; Harris et al. 1990; White and Garrott 1990; Kenward and Hodder 1996). However, the linear arrangement of woodland habitat in this area surrounded by cleared agricultural land, greatly limited the number of suitable analysis techniques. Commonly used techniques that assume an underlying probability distribution were unsuitable because they produced "ballooning isopleths" that invariably included areas of cleared agricultural land within the estimate (Harris et al. 1990; Kenward and Hodder 1996; Andreassen et al. 1998). Minimum area polygons, with fewer assumptions than the probabilistic methods, were also unsuitable because they too included areas of the unused agricultural matrix in estimates. Consequently, two non-parametric estimates incorporating fewer statistical assumptions were used to describe spatial organisation; namely, observed range length and grid cell estimator (White and Garrott 1990). Both estimates were calculated manually because of the inability of computer packages to deal with the linear nature and geometric arrangement of the habitat (Kenward and Hodder 1996).
Range length is a measure of the overall length of an animal's home range (m) (Fig. 5.2a) and has been used in studies of other species that occupy linear habitats (e.g. Platypus *Ornithorhynchus anatinus* in streams Serena 1994; Gust and Handasyde 1995; Serena *et al.* 1998). Range length may also provide a reliable index of home range size for comparisons among individuals (Desy *et al.* 1989; Slade and Russell 1998). The grid cell method estimates home range area (ha) by overlaying a grid over a map of the area on which locations of fixes have been plotted (Fig. 5.2b) (Voigt and Tinline 1980; Harris *et al.* 1990). A value for home range area is then derived by summing the area of each grid cell in which fixes occur (White and Garrott 1990). The choice of grid cell size is arbitrary, and can have a major influence on both over- or under-estimation of home range size (Macdonald *et al.* 1980), potentially limiting the biological relevance of the estimate (White and Garrott 1990). In this study, grid cell size was set at 20 x 20 m, which corresponded to the level of accuracy of fixes (± 10 m) (as recommended by Kenward 1987; Kenward and Hodder 1996) as well as to the width of the narrowest linear habitats. In addition, various "rules" determine the treatment of unoccupied cells adjacent to, or in between, occupied cells (Voigt and Tinline 1980). In this study, I assumed that within linear remnants, any unoccupied cells between occupied cells were included in the estimate, and that the entire width of the linear remnant (20 or 40 m) was utilised by gliders. When animals were located in small patches of woodland within the cleared agricultural matrix (hereafter referred to as 'paddock clumps'), I assumed gliders traveled there via the most direct route from the nearest linear habitat (Fig. 5.2b).

For both estimates, the influence of outlying fixes, or forays outside the normal home range, were reduced by manually deleting the 5% of fixes that were located at the ends of each range and that contributed most to the estimate (after Gust and Handasyde 1995). The *a priori* choice to exclude 5% of fixes was made because it provides an objective, repeatable method for comparison of the 'normal' home range between studies (White and Garrott 1990). The resulting measures were termed the '95%' estimate (incorporating 95% of fixes) and the 100% estimate (incorporating 100% of fixes). Unless otherwise stated, all home range estimates reported in this chapter refer to the 95% measure.
A comparison of home range parameters obtained in summer and autumn (when the majority of radiotracking was done) was undertaken for individuals that were tracked in both seasons. I matched the number of summer fixes per individual with that obtained in autumn, by commencing with the first fix and including all subsequent fixes until an equal number of data points had been reached.

The dependence of home range size on the number of fixes was determined by plotting cumulative home range length against the number of consecutive independent fixes for randomly selected adult male (n = 5) and adult female (n = 5) *P. norfolcensis* tracked in summer or autumn.

![Figure 5.2 A) Calculation of range length as the sum of the two solid lines and B) calculation of home range area using the grid cell method as the sum of all grid cells. Solid squares denote telemetry fixes, shaded areas denote remnant woodland habitat and white denotes cleared agricultural land.](image)

**Home range overlap**

The extent of home range overlap between gliders was calculated by determining the proportion of overlap between individuals (White and Garrott 1990), using their 95% home range estimate. Overlap was only computed for summer and autumn data between adults whose ranges overlapped or were adjacent to each other during the same season. Overlap values were then pooled across the two seasons to increase sample size. Data from juveniles, individuals and groups that
were spatially separated by one or more home ranges, and data collected during different seasons, were excluded. Home range overlap was determined by calculating the proportion of animal A's home range overlapped by animal B, and the proportion of animal B's home range overlapped by animal A. To compute inter- and intra-social group overlap within each tracking session, gliders were regarded as belonging to the same social group if they co-occupied the same den tree for two or more nights (after Smith 1980).

Composition of habitat within home ranges
A detailed description of habitat survey procedures is given in Chapter 3.

RESULTS

Radiotracking effort

A total of 4942 independent locations or 'fixes' were obtained for 51 individual *P. norfolcensis* radiotracked in four seasons between December 1997 and November 1998. Of these 51 individuals, 40 were adults (estimated age > 1 yr at fitting of collar) and 11 were juveniles (estimated age < 1 yr). Sufficient data were collected for 90% of adults (n = 36) and 90% of juveniles (n = 10) to calculate reliable home range estimates (see next section). Predation or early removal of the radio-collar due to excessive fur loss limited the amount of data that could be collected for five individuals (four adults and 1 juvenile) and they are excluded from further analyses. Of the remaining 46 individuals (totaling 4879 fixes), 38 were tracked in one season, five in two seasons, one in three seasons, and three in four seasons. The tracking intensity and the number of adults monitored varied between the seasons (Table 5.1). A similar intensive effort was expended in summer and autumn, and a reduced but similar effort was undertaken in winter and spring (Table 5.1).
*Petaurus norfolcensis* were radiotracked in different parts of the linear habitat network, including straight sections and complex intersections of linear habitats (Fig 5.1).

Table 5.1. Summary of radiotracking effort for adult *P. norfolcensis* tracked in linear woodland remnants during each season in 1997-1998. n = number of individuals tracked. Days = mean number of days on which fixes were obtained. Fixes = number of fixes obtained. Values are means ± 1 s.e.

<table>
<thead>
<tr>
<th>Season</th>
<th>Gender</th>
<th>n</th>
<th>Days</th>
<th>Diurnal fixes</th>
<th>Nocturnal fixes</th>
<th>Total fixes</th>
</tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer</td>
<td>Male</td>
<td>10</td>
<td>40.1 ± 2.3</td>
<td>39.7 ± 2.2</td>
<td>51.9 ± 2.3</td>
<td>91.0 ± 4.5</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>10</td>
<td>39.1 ± 2.2</td>
<td>38.5 ± 2.3</td>
<td>51.3 ± 1.8</td>
<td>89.0 ± 3.7</td>
</tr>
<tr>
<td>Autumn</td>
<td>Male</td>
<td>8</td>
<td>33.9 ± 1.9</td>
<td>33.5 ± 2.1</td>
<td>58.6 ± 3.8</td>
<td>92.3 ± 4.9</td>
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<tr>
<td></td>
<td>Female</td>
<td>11</td>
<td>34.5 ± 1.7</td>
<td>34.5 ± 1.7</td>
<td>59.5 ± 3.4</td>
<td>94.1 ± 4.4</td>
</tr>
<tr>
<td>Winter</td>
<td>Male</td>
<td>3</td>
<td>19.3 ± 0.3</td>
<td>19.3 ± 0.3</td>
<td>36.0 ± 1.3</td>
<td>55.3 ± 1.5</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>3</td>
<td>19.7 ± 0.7</td>
<td>19.3 ± 0.3</td>
<td>35.7 ± 0.7</td>
<td>55.0 ± 0.6</td>
</tr>
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<td>Spring</td>
<td>Male</td>
<td>3</td>
<td>17.0 ± 0.0</td>
<td>15.3 ± 0.3</td>
<td>20.0 ± 1.0</td>
<td>35.3 ± 1.2</td>
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<td>Female</td>
<td>3</td>
<td>18.3 ± 0.3</td>
<td>16.3 ± 0.3</td>
<td>20.0 ± 0.6</td>
<td>36.3 ± 0.9</td>
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</table>

Influence of number of radiotracking locations on home range

As with many home range estimates (White and Garrott 1990), an estimate derived using the grid cell method will increase incrementally as more locations are obtained. For the 10 adult gliders randomly selected from the summer (n = 5) and autumn (n = 5) periods, range length rapidly increased with the first 10 to 20 fixes obtained (Fig 5.3). The rate of increase began to level off after approximately 30 fixes for eight of the 10 individuals, and began to asymptote after approximately 50 fixes. The range length for the remaining two individuals continued to increase until approximately 60 fixes for the male, and 70 fixes for
the female. These data suggest that to accurately estimate home range dimensions for adult *P. norfolcensis* during a season, at least 50 independent locations are required per individual. Only range length is plotted because range length and area are highly correlated (Spearman rank correlation between estimates of range length and area for each individual within each tracking period, \( n = 63, r_s = 0.91, p < 0.0001 \), for both 95% and 100% estimates).

**Figure 5.3.** Cumulative range length vs. number of consecutive fixes for (A) five randomly selected male *P. norfolcensis* and (B) five randomly selected female *P. norfolcensis* radiotracked during summer or autumn 1998 in linear remnants near Euroa, north-eastern Victoria.
Home range shape

All 4942 fixes obtained from tracking 51 *P. norfolcensis* were located within remnant woodland - no animals were detected in cleared grassy farmland (Figs. 5.5 - 5.8). Consequently, home ranges were narrow, linear and elongated - being largely determined by the shape and arrangement of woodland habitat in the study area. Linear remnants along roads and unused road reserves provided the majority of habitat for most gliders, as almost 85% of the total fixes collected (n = 4872) from 46 gliders were located within linear habitats. The remaining 15% of fixes were detected from within small woodland patches in the agricultural matrix. The highest use of these 'paddock clumps' by a single glider was 57 out of 71 fixes (80.3%), recorded for an adult male during summer. Paddock clumps were used by 37 gliders (19 male and 21 female) for foraging, denning, or as stepping stones between other paddock clumps and linear remnants. Nine (three male and six female) gliders were not observed to visit paddock clumps during radiotracking.

The maximum perpendicular distance to a paddock clump from a linear remnant was 240 m for a nocturnal fix and 195 m for a diurnal fix. The average maximum perpendicular distance for all 46 gliders was less, with a mean of 66.0 (± 9.5) m for males and females combined (Fig. 5.4). The mean distance of all fixes in paddock clumps from the nearest linear remnant for males and females combined was 39.6 (± 4.7) m for nocturnal fixes and 21.8 (± 5.9) m for diurnal fixes (Fig. 5.4). For the 37 gliders observed to utilise paddock clumps, the largest gap in overstorey canopy cover that was crossed was 70 m (mean maximum gap size 30.5 ± 2.9 m). On no occasions were gliders observed to run along the ground to reach isolated patches of trees. The paddock clumps that were visited ranged in size from single trees (both living and dead) to patches up to 6.3 ha, but most were less than 1 ha.
Figure 5.4. Mean perpendicular distance from the nearest wooded linear remnant to fixes of *P. norfolcensis* in small patches of woodland (paddock clumps) in the agricultural matrix. Solid bars are males (n = 22 individuals), clear bars are females (n = 24), hatched bars are males and females combined (n = 46). Data are pooled across all seasons. Error bars + 1 s.e.

**Home range size**

All adult gliders displayed spatially stable home ranges within the season that they were monitored. Home range area and length (95% estimates) ranged in size from 0.69 to 6.17 ha and from 225 to 1900 m, respectively (Table 5.2). Within each season, mean range area (95%) varied from 1.29 - 2.84 ha and mean range length (95%) varied from 322 to 839 m (Table 5.2).

Within each season, the mean home range estimates for male gliders were consistently larger than for females (Table 5.2), and these differences were statistically significant in all seasons except summer (Table 5.2).
Table 5.2. Comparison of home range estimates for adult *P. norfolcensis* radiotracked during each season within a network of linear habitats near Euroa, 1998.
Values are means ± 1 s.e. with range in parentheses. Significance levels for one-way ANOVA between sexes within each season on log-transformed data are shown as - ns not significant, * p < 0.1, ** p < 0.05, *** p < 0.01.

<table>
<thead>
<tr>
<th>Season</th>
<th>Gender</th>
<th>Home range area (ha)</th>
<th>100% of fixes</th>
<th>95% of fixes</th>
<th>Home range length (m)</th>
<th>100% of fixes</th>
<th>95% of fixes</th>
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<tr>
<td></td>
<td>Male</td>
<td>3.54 ± 0.37</td>
<td>2.76 ± 0.25</td>
<td>1001 ± 140</td>
<td>763 ± 74</td>
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<tr>
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<td>(n = 10)</td>
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<td>(510 - 1165)</td>
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<td>Female</td>
<td>3.40 ± 0.53</td>
<td>2.45 ± 0.43</td>
<td>1095 ± 193</td>
<td>765 ± 132</td>
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<td>(n = 10)</td>
<td>(1.02 - 6.56)</td>
<td>(0.69 - 4.79)</td>
<td>(510 - 2580)</td>
<td>(345 - 1735)</td>
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<td>F-ratio</td>
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<td>1.13 ns</td>
<td>0.06 ns</td>
<td>0.19 ns</td>
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<tr>
<td>Summer</td>
<td>Male</td>
<td>3.77 ± 0.59</td>
<td>2.74 ± 0.54</td>
<td>1169 ± 217</td>
<td>839 ± 184</td>
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<tr>
<td></td>
<td>(n = 8)</td>
<td>(2.26 - 6.80)</td>
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<td>(565 - 2215)</td>
<td>(380 - 1900)</td>
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<td>Female</td>
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<td>1.86 ± 0.19</td>
<td>736 ± 93</td>
<td>516 ± 49</td>
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<td>(n = 11)</td>
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<td>(330 - 895)</td>
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<tr>
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<td>F-ratio</td>
<td>4.26 **</td>
<td>3.76 *</td>
<td>4.13 *</td>
<td>3.88 *</td>
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<tr>
<td>Autumn</td>
<td>Male</td>
<td>3.43 ± 0.68</td>
<td>2.84 ± 0.38</td>
<td>993 ± 307</td>
<td>833 ± 211</td>
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<td>(555 - 1585)</td>
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<tr>
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<td>1.37 ± 0.13</td>
<td>608 ± 121</td>
<td>343 ± 32</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(n = 3)</td>
<td>(1.68 - 3.34)</td>
<td>(1.14 - 1.58)</td>
<td>(420 - 835)</td>
<td>(285 - 395)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>F-ratio</td>
<td>1.39 ns</td>
<td>16.83 ***</td>
<td>1.43 ns</td>
<td>9.62 **</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Winter</td>
<td>Male</td>
<td>2.49 ± 0.10</td>
<td>2.02 ± 0.33</td>
<td>647 ± 46</td>
<td>550 ± 25</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(n = 3)</td>
<td>(2.28 - 2.62)</td>
<td>(1.38 - 2.50)</td>
<td>(580 - 735)</td>
<td>(510 - 595)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>1.58 ± 0.28</td>
<td>1.29 ± 0.31</td>
<td>368 ± 57</td>
<td>322 ± 77</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(n = 3)</td>
<td>(1.12 - 2.10)</td>
<td>(0.9 - 1.9)</td>
<td>(280 - 475)</td>
<td>(225 - 475)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>F-ratio</td>
<td>6.75 *</td>
<td>2.69 ns</td>
<td>11.93 **</td>
<td>6.48 *</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*a Note that the number of fixes required before home range size begins to asymptote was not reached during spring, and estimates are likely to underestimate home range size.
Seasonal and long-term home range estimates

The majority of gliders were intensively tracked in one season (mostly summer or autumn), and so a comparison of home range size in different seasons for the same individual is limited to five animals (two males, three females) that were tracked in both summer and autumn. During the summer tracking period, range length (95%) was significantly longer (paired sample t-test, $t = -3.45$, df = 4, $p < 0.05$) and range area (95%) was significantly larger ($t = -3.71$, df = 4, $p < 0.05$) than during the autumn tracking period. On average, range area (95%) and range length (95%) were 19% smaller in autumn than in summer. Meaningful comparisons of home range estimates could not be made with winter and spring due to a reduced tracking effort relative to the summer and autumn seasons.

Long-term home range estimates were calculated for the four individuals tracked in three (individual M12) or four (individuals M1, F7, F4) seasons (Table 5.3). Long-term home range estimates (95%) for M1 and M12 were up to twice as large as any estimate derived within a single season. This probably represents a range shift rather than an enlargement of the home range because the region of the home range occupied during summer and autumn was not revisited after the presumed shift (winter and spring). It could not be determined whether M1 invaded the territory of M12, or whether M1 moved into the area vacated by M12, because both animals 'shifted' between the autumn and winter tracking periods. The long-term home range estimate for both females was either equal to (F7), or slightly larger (0.26 ha for F4) than, any estimate calculated for a single season.

Social organisation

Petaurus norfolcensis formed social groups that occupied up to 16 known den trees during one tracking season (summer 1998, Chapter 6). Members of a social group often occupied different den trees on the same night, but on occasions they would simultaneously occupy the same den tree (Chapter 6). These patterns of den tree use clearly satisfied the criterion used by Smith (1980), that gliders
belonged to the same social group if they shared the same nest for two or more
days during a tracking session. Further details about the composition of social
groups and analyses of patterns of den tree use are given in Chapters 4 and 6.

Table 5.3. Comparison of home range size (ha) of four adult *P. norfolcensis*
radiotracked in three or four seasons in linear habitats near Euroa, 1998.
Home range area was derived using the grid cell estimator with 95% of fixes.
The number of fixes from which the estimate was calculated is given in
parentheses. The combined estimate is derived from all data collected over 3 or 4
seasons.

<table>
<thead>
<tr>
<th>Identity</th>
<th>Summer</th>
<th>Autumn</th>
<th>Winter</th>
<th>Spring</th>
<th>Combined</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male 1</td>
<td>2.56 (103)</td>
<td>2.04 (83)</td>
<td>3.14 (55)</td>
<td>2.18 (33)</td>
<td>5.44 (274)</td>
</tr>
<tr>
<td>Male 12</td>
<td>3.14 (103)</td>
<td>not tracked</td>
<td>2.08 (58)</td>
<td>2.50 (36)</td>
<td>5.18 (197)</td>
</tr>
<tr>
<td>Female 4</td>
<td>1.74 (107)</td>
<td>1.44 (69)</td>
<td>1.58 (56)</td>
<td>1.90 (35)</td>
<td>2.16 (268)</td>
</tr>
<tr>
<td>Female 7</td>
<td>2.94 (105)</td>
<td>2.04 (71)</td>
<td>1.14 (55)</td>
<td>0.90 (36)</td>
<td>2.94 (266)</td>
</tr>
</tbody>
</table>

**Habitat geometry and spatial organisation**

Habitat geometry, or the spatial arrangement of linear remnants, appeared to have
a strong influence on home range shape, size and overlap. The autumn tracking
period was used to investigate the effect of habitat geometry on home range size
and shape by selecting for radiotracking, animals that either lived in a straight
section of linear remnant (n = 9) or that incorporated an intersection within their
home range (n = 10).

Animals living within straight sections of linear remnants occupied home ranges
that were typically narrow and oriented along the linear remnant (Figs. 5.5 and
5.6). As habitat geometry became more complicated (e.g. at the junction of two
or more linear habitats), home range shape became more complex. Gliders
usually incorporated two or three arms of an intersection into their home range,
but completely avoided other remaining arms (Figs. 5.7 and 5.8). Animals
occupying home ranges that incorporated complex junctions had significantly larger (one-way ANOVA on log-transformed data: 100% area, p < 0.05; 95% area, p = 0.0556) and significantly longer (100% length, p < 0.01; 95% length p < 0.01) home ranges than animals occupying simple linear habitats (Table 5.4).

As expected, the extent of overlap of home ranges (95% of fixes) of members of the same social group (mean 72.6% ± 2.7, n = 46) was significantly greater than between individuals of adjacent social groups (mean 14.0% ± 2.1, n = 108) (Mann-Whitney U-Test Z = 9.03, p < 0.0001). Overlap in home range between members of the same social group was high at both intersections (mean 69.7%, ± 3.4, n = 14) and within straight sections (mean 73.9% ± 3.6, n = 32) (Z = -1.05, p > 0.05) (Figs 5.9 and 5.10). The extent of overlap in home range size (95% of fixes) between individual gliders from adjacent colonies was significantly lower in straight sections (mean 6.3% ± 1.8, n = 74) than at complex junctions (mean 30.75% ± 4.3, n = 34) (Z = -6.55, p < 0.001) (Figs. 5.8 and 5.9).

Table 5.4. A comparison of home range estimates for adult *P. norfolcensis* occupying straight sections or junctions of linear habitats. All data are from animals radiotracked in autumn 1998.

<table>
<thead>
<tr>
<th>Landscape position</th>
<th>n</th>
<th>Number of fixes</th>
<th>Home range area (ha)</th>
<th>Home range length (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>100%</td>
<td>95%</td>
</tr>
<tr>
<td>Complex junction</td>
<td>10</td>
<td>98.5 ± 2.8</td>
<td>3.77 ± 0.50</td>
<td>2.67 ± 0.45</td>
</tr>
<tr>
<td>Straight section</td>
<td>9</td>
<td>87.4 ± 5.5</td>
<td>2.33 ± 0.20</td>
<td>1.75 ± 0.14</td>
</tr>
</tbody>
</table>

n = number of individuals tracked. Values are means ± 1 s.e. Refer to methods for description of each home range estimate.
Figure 5.5. Radiotracking locations (solid black squares) for *Petaurus norfolcensis* (Male 9) occupying a straight section of linear remnant. The plot shows 104 fixes (100%) collected in summer, 1998, with many overlapping. Remnant woodland is denoted by grey shading and cleared agricultural grasslands by white.
Figure 5.6. Radiotracking locations (solid black squares) for *Petaurus norfolcensis* (Female 70) occupying a straight section of linear remnant adjacent to an intersection. The plot shows 108 fixes (100%) collected in autumn, 1998, with many overlapping. Remnant woodland is denoted by grey shading and cleared agricultural grasslands by white.
Figure 5.7. Radiotracking locations (solid black squares) for *Petaurus norfolcensis* (Male 31) occupying an intersection of linear remnants. The plot shows 98 fixes (100%) collected in autumn, 1998, with many overlapping. Remnant woodland is denoted by grey shading and cleared agricultural grasslands by white.
Figure 5.8. Radiotracking locations (solid black squares) for *Petaurus norfolcensis* (Female 93) occupying an intersection of linear remnants. The plot shows 78 fixes (100%) collected in summer, 1998, with many overlapping. Remnant woodland is denoted by grey shading and cleared agricultural grasslands by white.
Figure 5.9. Home range overlap between individuals of *P. norfolcensis* occupying a straight section of linear remnant.
Solid black lines represent the size and location of the combined range of each social group, plotted from the 95% home range estimates of individual group members. Remnant woodland habitat is denoted by grey shading and cleared agricultural grasslands by white. Paddock clumps are not shown.
Figure 5.10. Overlap of home ranges between adjacent social groups of *Petaurus norfolcensis* occupying an intersection between five linear remnants. Solid black lines represent the size and location of the combined range of each social group, plotted from the 95% home range estimates of individual group members. Remnant woodland habitat is denoted by grey shading and cleared agricultural grasslands by white. Paddock clumps are not shown.
Spatial organisation and survival of juveniles

Eleven juvenile gliders (< 1 year of age when first collared) were fitted with expanding break-away collars and were radiotracked in Autumn 1998. The range in the number of fixes per individual was large (range 3 - 119, mean 70.5) because seven of the 11 juveniles fitted with collars were found dead during the tracking period. Consequently, the minimum number of fixes required to estimate home range size for adults (approximately 50 fixes, Fig. 5.3) was not attained for most juveniles. To maximise the value of the available data, a minimum of 25 fixes collected over at least 20 days was used to calculate home range estimates. Within these criteria, home range dimensions of ten juveniles (Table 5.5) were calculated, although they are likely to underestimate the actual area used.

Home ranges of juvenile gliders were similar in shape to those of adults, incorporating both linear habitats and paddock clumps into their home range. Juvenile home ranges were spatially stable during the tracking period and remained in the general vicinity of where the animals were initially trapped and fitted with collars. Home range dimensions for juvenile females were larger than for juvenile males (Table 5.6). In comparison with adults, juvenile male home ranges were similar in size to that of adult males while juvenile females occupied ranges that were larger than for adult females, despite fewer fixes being collected on average for most juveniles. Large exploratory excursions were undertaken by some juveniles; however, during the tracking period, no juveniles were observed to disperse.

Predation accounted for the mortality of 64% (7 out of 11) of the juvenile gliders tracked. In all seven cases, the carcass and radiocollar were retrieved from the ground shortly after death. Predation by owls, probably either *N. strenua* or *N. connivens*, both of which are occasionally observed in the study area (pers obs., Venosta, unpub. data) is believed to be responsible for six deaths. The carcasses were found with the tail neatly severed at the base, and on some the dorsal skin and fur was still attached. The seventh carcass was found with the chest and front legs mauled, revealing splintered bones, suggesting predation by *F. catus*. A cat
was observed within 50m from where the carcass was found on the night predation occurred.

Table 5.5. Summary of radiotracking effort for juvenile *Petaurus norfolcensis* radiotracked in linear habitats near Euroa, in autumn 1998. Includes all juveniles with more than 25 fixes collected over a minimum of 20 days. 'Days' is the number of days on which fixes were obtained. Values are means ± 1 s.e.

<table>
<thead>
<tr>
<th>Gender</th>
<th>n</th>
<th>Days</th>
<th>Diurnal fixes</th>
<th>Nocturnal fixes</th>
<th>Total fixes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>5</td>
<td>34.6 ± 5.50</td>
<td>34.0 ± 5.6</td>
<td>52.4 ± 11.4</td>
<td>86.4 ± 16.0</td>
</tr>
<tr>
<td>Female</td>
<td>5</td>
<td>28.0 ± 2.21</td>
<td>25.0 ± 3.6</td>
<td>29.6 ± 10.7</td>
<td>54.6 ± 13.0</td>
</tr>
</tbody>
</table>

Table 5.6. Characteristics of home ranges of juvenile *Petaurus norfolcensis* based on a minimum of 20 days of tracking and 25 independent fixes. Values are means ± 1 s.e. with range in parentheses. Refer to text for description of home range estimates.

<table>
<thead>
<tr>
<th>Gender</th>
<th>n</th>
<th>Home range area (ha)</th>
<th>Home range length (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>100%</td>
<td>95%</td>
</tr>
<tr>
<td>Male</td>
<td>5</td>
<td>3.67 ± 0.88</td>
<td>2.47 ± 0.69</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1.08 - 6.13)</td>
<td>(0.98 - 4.97)</td>
</tr>
<tr>
<td>Female</td>
<td>5</td>
<td>6.41 ± 2.28</td>
<td>4.34 ± 1.50</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(2.10 - 13.20)</td>
<td>(1.44 - 8.85)</td>
</tr>
<tr>
<td>Males and females</td>
<td>10</td>
<td>5.04 ± 1.24</td>
<td>3.41 ± 0.84</td>
</tr>
<tr>
<td>combined</td>
<td></td>
<td>(1.08 - 13.2)</td>
<td>(0.98 - 8.85)</td>
</tr>
</tbody>
</table>
Habitat characteristics

In the Euroa area, most linear habitats are associated with roads and road reserves (see Chapter 2) and hence the intersections of linear habitats were usually the intersection of two or more roads. At road intersections, a proportion of the roadside vegetation is affected by disturbance and clearing associated with road works. Consequently, the amount or quality of habitat for gliders that occupy these areas may be reduced. To test this, I compared selected habitat variables in all 50 m habitat sampling units (see Chapter 3 for habitat assessment details) that occurred within 100 m of an intersection (n = 46) with an equal number of randomly selected sampling units > 500 m from the nearest intersection (Table 5.7). The density of hollow-bearing trees and *Eucalyptus* basal area were significantly lower at intersections than further away, but there was no significant difference in the density of large eucalypts or *A. pycnantha* stems (Table 5.7).

Table 5.7. Comparison of floristic and structural habitat variables within linear habitats positioned near (< 100 m) and far (> 500 m) from the intersection of linear habitats.

Distance refers to distance from the nearest intersection, n = the number of 50 m habitat sampling units, values are means ± s.e. Significance levels for one-way ANOVA between distance categories shown as - ns = not significant, * p < 0.05, ** p < 0.01.

\[^t\] density of *Acacia pycnantha* stems transformed $\log_{10} (x + 1)$ prior to analysis.

<table>
<thead>
<tr>
<th>Distance</th>
<th>n</th>
<th>Density (stems ha$^{-1}$) of:</th>
<th></th>
<th>Eucalyptus basal area (m$^2$ ha$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Hollow-bearing trees</td>
<td>Large</td>
<td>Acacia pycnanth$^{t}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>eucalypts</td>
<td></td>
</tr>
<tr>
<td>&lt; 100 m</td>
<td>46</td>
<td>17.7 ± 2.2</td>
<td>18.7 ± 1.8</td>
<td>113.4 ± 18.4</td>
</tr>
<tr>
<td>&gt; 500 m</td>
<td>46</td>
<td>25.8 ± 2.7</td>
<td>23.5 ± 2.4</td>
<td>265.4 ± 83.0</td>
</tr>
<tr>
<td>F-ratio</td>
<td></td>
<td>5.42 *</td>
<td>2.65 ns</td>
<td>0.11 ns</td>
</tr>
</tbody>
</table>
DISCUSSION

Home range size and habitat quality

Consistent patterns in the spatial organisation of *P. norfolcensis* were observed throughout the interconnected network of linear woodland habitats. All home ranges, and indeed all radiotracking fixes, were of animals occupying woodland habitat. Gliders were never observed moving, or even suspected of moving, along the ground - movement was always observed to be via adjoining branches or by gliding from tree to tree. This is in contrast to *P. breviceps* which was regularly observed travelling 250 m across treeless pasture to reach *Acacia* food trees (Suckling 1984). Home ranges of *P. norfolcensis* at Euroa were consistently small, and shape was largely determined by the geometry of the available habitat. Importantly, this study clearly demonstrates that individuals of *P. norfolcensis* occupy permanent home ranges and are resident in linear woodland remnants in the Euroa area, thereby suggesting that the linear network provides sufficient resources that are energetically feasible to obtain.

Home ranges of *P. norfolcensis* in the linear network are markedly smaller than these recorded elsewhere for this species, despite potential methodological differences. The largest estimate of mean home range area (95%) for individuals of either gender in a single season of tracking was 2.84 ± 0.38 ha (adult males, n = 3, winter 1998), which is less than one-third of the mean home range size reported for *P. norfolcensis* at Chiltern, north-eastern Victoria in 1988-1990 (9.47 ha, 95% harmonic mean estimate, n = 9 individuals, calculated from Traill 1995). Home range estimates were also smaller than those recorded in continuous forest at Limeburners Creek (3.0 - 3.5 ha) and Bungawalbin Nature Reserve (4.5 ha), although the difference is less pronounced (Quin 1995; Sharpe 1996).

Range length was not formally measured by Quin (1995), Traill (1995) or Sharpe (1996), making direct comparisons between studies difficult. However, both Quin (1995) and Traill (1995) present data regarding maximum distances moved. At Limeburners Creek, the maximum nightly movements, assuming a straight line between captures, was 320 and 500 m for two adult males (Quin 1995). At
Chiltern, gliders typically foraged within 400 m of their nest hollow, and the maximum-recorded nightly movement, which was considered exceptional, was 950 m for a male (Traill 1995). At Euroa, the largest estimate of mean home range length (95%) for individuals of either gender in a single season of tracking was $839 \pm 184$ m (adult males, $n = 8$, autumn 1998). These data suggest that at Euroa, home range length is longer than that within the continuous forests at Limeburners Creek and Chiltern. This is not surprising given the linear nature of the habitat.

Habitat composition and structure and environmental productivity influence the amount and quality of available food, and are therefore believed to be major determinants of home range size (Lindstet et al. 1986). Experimental studies have shown that supplemental feeding, which is analogous to improving environmental productivity, usually increases population densities and decreases home range size for most of the mammals and birds studied (Boutin 1990). Indeed, differences in productivity (measured as the density of flowering trees) are believed to account for smaller home ranges and greater population density of another petaurid, *P. australis*, at Kioloa compared with Bombala in New South Wales (Goldingay 1992). In north Queensland, the home range size of pairs of *P. gracilis* were smaller when part of their range included riparian vegetation, which provided a greater diversity of food species than non-riparian habitats (Jackson 2000a).

The factors most likely to be influencing habitat quality for *P. norfolcensis* at Euroa are the abundance of large trees and soil nutrient levels. In the Euroa study area, there is a high density (approx. $23 \text{ ha}^{-1}$, Chapter 3) of large diameter trees ($> 70 \text{ cm DBH}$) in the remnant woodland vegetation along roads and road reserves. This is at least 10 times greater than that recorded in the box and ironbark forests at Chiltern where previous work in Victoria on the spatial organisation of *P. norfolcensis* was undertaken (Traill 1995). The Chiltern area is comprised largely of regrowth forest that dates back to the late 1800s when it was almost totally cleared of trees for gold mining. It has since been intensively managed for silviculture and many of the large trees removed for timber (Meredith 1984; Traill 1995). In contrast, the linear woodland remnants at Euroa
are largely pre-European in age and most have remained uncleared since settlement in the 1860s.

Large trees are an important component of woodland ecosystems for *P. norfolcensis* for several reasons. First, they provide hollows in a range of size and form that *P. norfolcensis* require for shelter and breeding sites. The high density of hollow-bearing trees at Euroa may also influence the size of the population, as studies of other hollow-dependent fauna have demonstrated (e.g. Smith and Lindenmayer 1988; Newton 1994). Observations on the use of den trees by *P. norfolcensis* (Chapter 6) showed that each individual used numerous tree hollows, generally in very large old trees. Consequently, the relatively high density of large hollow-bearing trees as potential den sites in this study area is a critical resource. Second, the trunk and branches of large trees provide a larger surface area on which gliders can forage for invertebrates, compared with smaller diameter trees. Hence, large trees represent a potentially less-costly foraging area because the number of trees which must be visited to harvest sufficient resources is reduced. Third, in comparison with smaller trees, large trees usually have rougher and more deeply-fissured bark at their base and extending up the tree (R. van der Ree, pers. obs.), a microhabitat which can support high densities of invertebrates (Baehr 1990). While foraging, individual *P. norfolcensis* preferentially selected trees with a diameter > 30 cm on which to peel bark and search for invertebrates (Holland 1998). Finally, in box and ironbark forests, a significantly greater proportion of large diameter trees flower than small trees, and, for the same flowering intensity, large trees produce more flowers per tree than small trees (Wilson and Bennett 1999). Thus, large trees appear to be a more reliable source of nectar than small trees.

The occurrence and density of possums and gliders in south-eastern Australia are positively associated with nutrient levels in the soil and foliage (Braithwaite *et al.* 1984; Kavanagh and Lambert 1990). In the Euroa floodplains, roadsides and unused road reserves occur on public land within productive farmland (Chapter 2). They were spared from clearing due to their public land status - not due to their unsuitability for agriculture. These woodland remnants are not located on poor or rocky soils, steep slopes or otherwise unproductive land, but occur on
fertile alluvial soils (ECC 1997), and presumably possess high levels of foliar nutrients. Conversely, at Chiltern, where home ranges of *P. norfolcensis* were approximately four-times larger than those recorded at Euroa, soils are shallow and rocky with low nutrient levels (ECC 1997). Species richness of canopy arthropods in *Eucalyptus* species is positively associated with foliar nutrient levels (Majer *et al.* 1990; 1992; Recher *et al.* 1996). Thus, woodlands on alluvial soils of high nutrient status potentially provide a rich food source of arthropods for *P. norfolcensis*.

**Influence of habitat geometry on spatial organisation of *P. norfolcensis***

Habitat geometry (shape and arrangement of habitat) appeared to exert an influence on home range size, shape and overlap between individuals. Central place foraging theory proposes that the optimum home range or territory is one in which the time and energy expended during foraging (or territory defense) is minimised for maximum gain (Covich 1976; Pyke *et al.* 1977; Dill 1978; Andersson 1981; Recher *et al.* 1987). In other words, home range size and shape will take the form that most efficiently satisfies nutritional and energy requirements. The optimum range shape for animals foraging from a central base, therefore, would be circular (Andersson 1981; Recher *et al.* 1987), rather than linear. Individuals of *P. norfolcensis* primarily focussed their ranges upon the linear remnants and their home ranges were largely linear and elongated in shape. The use of multiple den sites by individuals may be a response to foraging over long distances, thus negating the need to return to a central place and hence reduce energy demands (refer Chapter 6). In addition, gliding is a relative efficient form of locomotion (Norberg 1985) that may assist *P. norfolcensis* to forage over long ranges without experiencing excessive energetic costs.

A second response to linear home ranges by individuals may be the incorporation into their range of small woodland remnants within the adjacent agricultural matrix. While it appears that for most animals these paddock clumps are a supplement to their main range within linear strips, the frequency with which
Paddock clumps are visited suggest they provide important habitat. For example, 80% of the total fixes for one glider were recorded from within paddock clumps, and of the 46 individuals tracked, 80% incorporated paddock clumps into their activity areas. Paddock clumps ranged from single trees (living and dead) to patches of up to about six ha. These patches not only provide additional habitat in an otherwise highly-cleared landscape, but also allow gliders to 'round-out' their home range, thus potentially reducing foraging distances and energy expenditure. Other species occupying linear remnants in the same area, Grey Crowned Babbler *Postomatus temporalis* (Robinson *et al.* in press) and *P. tapoatafa* (van der Ree and Bennett 1999), also included paddock clumps in their foraging area, thereby reducing home range length, and potentially also energy expenditure.

Intersections of two or more linear habitats are potentially important landscape elements for plants and animals, and for energy flows through the landscape (Forman 1997). An 'intersection effect' may be evident, whereby intersections possess ecological characteristics that differ from the connecting corridors (Forman 1997). For example, several studies have found that bird and plant species richness is greater at intersections than along the adjoining corridor (Baudry 1984; Lack 1988; Riffell and Gutzwiller 1996). The distribution and group size of *P. temporalis* near Euroa was negatively correlated with distance to the nearest intersection (Robinson *et al.* in press). The significantly greater overlap of home ranges between gliders from adjacent social groups at intersections compared with those in linear habitats may be important for the species' long-term viability. Because more individuals encounter each other at intersections, the potential for gene mixing and gene flow across the landscape is enhanced. Within the Euroa floodplains, intersections provide the only opportunity for members of three or more social groups to interact while maintaining their territories. The network structure of linear remnants in this area may enhance gene flow and ensure habitat continuity in the face of catastrophe, by providing multiple pathways across the landscape (Forman 1991; Bennett 1999).

Increased size of home ranges at intersections may be a consequence of three factors. First, there is a higher density of *P. norfolcensis* in close proximity to
intersections than further away (Table 3.10), presumably to increase opportunity for social interaction with other gliders. The greater density of animals sharing limited resources may result in increased home range sizes. Second, intersections of linear remnants are often also the intersection between two roads. The clearing of vegetation and road maintenance activities to ensure human safety have resulted in a reduction in the number of trees bearing canopy hollows and in the basal area of *Eucalyptus* trees. This may represent a decline in the abundance of food, causing gliders to expand their home range to meet energy requirements. Finally, gliders may not be able to occupy territories and exclude other individuals as efficiently at intersections as in straight sections, effectively allowing greater overlap of ranges.

**Seasonal differences in home range size**

Studies of the diet of petaurid species have suggested that nectar and pollen are important food resources that provide energy and protein (Menkhorst and Collier 1987; Howard 1989; Goldingay 1990; Quin et al. 1996a). At Euroa, the staple dietary items for *P. norfolcensis* over a yearly period were inferred to be honeydew and manna (Holland 1998; G. Holland unpub. data), with nectar and pollen consumed when *Eucalyptus* trees were flowering. When these resources are abundant, animals may not need to move as far to forage and home range size may be reduced relative to other seasons. This appears to have occurred during autumn (when ranges were 19% smaller than summer estimates), which corresponded with the peak flowering period for *E. microcarpa*, the dominant overstorey species (R. van der Ree, unpub. data). Seasonal variation in home ranges of *P. norfolcensis* was not examined by Quin (1995) or Traill (1995) and hence comparisons cannot be made.
Area requirements and dispersal of juveniles

Juvenile gliders were very young animals (< 1 yr of age as estimated from tooth wear, body weight and size - see Chapter 4) when trapped and fitted with radiocollars. It is presumed that they still occupied their natal territory because they had not been captured elsewhere. An approximate dispersal age of 12.5 months recorded at Limeburners Creek (Quin 1995) suggests that dispersal had not yet occurred for these animals at Euroa. In addition, most juveniles nested with adult gliders and regularly associated with them while foraging, consistent with a parent-offspring relationship.

Home range shapes of juvenile gliders were similar to those of adults, being narrow, elongated and incorporating paddock clumps. Where juveniles belonged to known social groups, their ranges typically overlapped those of other group members. Despite a reduced tracking effort in comparison with adults, the largest and longest home ranges recorded at Euroa belonged to juveniles, probably reflecting exploratory forays outside the natal home range.

The size and length of home ranges of juvenile females were almost twice that of juvenile males, despite fewer locational fixes being obtained for females. The reason for this difference is not clear: if the large home range size is the result of exploratory forays, one might expect both sexes to undertake this behaviour, because both sexes are reported to disperse (Quin 1995). However, this result, considered in combination with a female bias in the number of > 2-year-old animals being recruited into the population (Table 4.3, Chapter 4), may indicate female-biased dispersal. This hypothesis, however, is tentative, given the small sample size. In addition, confirmed dispersal movements were not detected during this study, thus limiting comparisons between sexes.

A major limitation on identifying the dispersal distance, route and final destination was the high rate of predation on juveniles. High rates of juvenile mortality are typical among phalangeroids (Smith 1984b; Suckling 1984; Quin 1995), however the rate and likely cause of death have not been quantified in
other populations. In this study, seven of the 11 (64%) radiocollared juveniles died because of predation, most probably by owls (Chapter 4). This frequency is higher than those estimated in population viability analyses (PVA) for *P. gracilis* 25% (Jackson 1999) and *P. australis* (30 - 40%) (Goldingay and Possingham 1995). This is of concern if the rate of juvenile mortality at Euroa is typical for this species and of other petaurid populations, because these viability analyses (Goldingay and Possingham 1995; Jackson 1999) are then underestimating rates of juvenile survival, and potentially overestimating the viability of the populations modeled.

**CONCLUSIONS**

This study has identified a number of landscape features of importance to the conservation of *P. norfolcensis* in the linear network. First, the linear remnants support resident populations and provide the majority of habitat that *P. norfolcensis* requires. Intersections of linear remnants are key areas because they provide for the interaction of three or more social groups, and thus potentially enhance gene flow, while still maintaining stable territories between groups. Small patches of woodland embedded within the agricultural matrix were used by *P. norfolcensis*, even extensively by some individuals, as additional foraging habitat. The mean width of gaps in the overstorey canopy that gliders were observed to cross between woodland patches was 30 m, and the maximum was 70 m. Thus, even relatively small breaks in canopy cover may hinder movement, highlighting the importance of structural continuity and multiple pathways to move through the landscape.

Habitat quality appears to be responsible for the small sizes of home ranges reported in this study. First, remnant vegetation occurring on fertile soils is likely to have high foliar nutrient levels that support diverse and abundant fauna populations (Braithwaite *et al.* 1984; Kavanagh and Lambert 1990; Recher *et al.* 1996). Second, the abundance of large trees, which provide numerous hollows and diverse foraging substrates, is crucial for *P. norfolcensis* that relies on these
resources. Remnant woodland, and particularly an ongoing recruitment of large trees, is under threat in highly fragmented agricultural landscapes (Bennett et al. 1994b; Fisher and Harris 1999). Consequently, the conservation value of the network of linear woodland remnants for arboreal marsupials in the otherwise highly-cleared landscape of the Euroa floodplains is high.
CHAPTER 6
USE OF DEN TREES BY THE SQUIRREL GLIDER
PETAURUS NORFOLCENSIS, IN A NETWORK OF REMNANT LINEAR HABITATS

INTRODUCTION

In Australia, an estimated 400 species of birds, mammals, reptiles and amphibians rely on tree hollows for survival (Ambrose 1982; Saunders et al. 1982; Scotts 1991; Gibbons and Lindenmayer 1997). Tree hollows may be used to provide shelter and protection from adverse climatic conditions or potential predators; as well as provide a focal point for social behaviour, such as grooming or the rearing of young. For many hollow-dependant species, suitable tree hollows are considered a critical resource, and a decline in the availability of hollows below a critical threshold may be a factor limiting population size (Gibbons 1999). A positive relationship between the density of G. leadbeateri and the density of trees with hollows has been established (Smith and Lindenmayer 1988). In the agricultural region of south-west Western Australia, the long-term persistence of cockatoos is at risk due to a decline in the number of large hollow-bearing trees (Saunders et al. 1985). Concern about the consequences for wildlife regarding the loss of hollow-bearing trees, and indeed the loss of trees in general, from rural Australian landscapes has been raised (Saunders et al. 1993; Walker et al. 1993; Bennett et al. 1994b; Robinson and Traill 1996; Fisher and Harris 1999).

Studies of the use of hollow trees have been undertaken for a wide range of arboreal marsupials, including G. leadbeateri (Lindenmayer and Meggs 1996), Mountain Brushtail Possum Trichosurus caninus (Lindenmayer et al. 1996a; b; 1997b; 1998), T. vulpecula (Green and Coleman 1987; Cowan 1989), P. volans (Kehl and Borsboom 1984), and P. gracilis (Jackson 2000a). In all cases, individual animals used many trees - usually a small number were used often, with the remainder occupied less frequently. In addition, the trees selected for
occupation were usually preferentially selected from all potential den trees, suggesting that not all hollow-bearing trees are suitable for occupation. For example, two out of three potential den trees were considered unsuitable for occupation by *G. leadbeateri* (Smith and Lindenmayer 1988).

There is a net loss in the abundance of large trees with hollows in the temperate woodlands of Australia because the rate of loss exceeds the rate of recruitment (Bennett *et al.* 1994b; Robinson and Traill 1996). This is of particular concern in south-eastern Australia, because this region provides much of the habitat for *P. norfolcensis* (Menkhorst *et al.* 1988). The use of tree hollows by *P. norfolcensis* has been investigated in Queensland (Rowston 1998), coastal New South Wales (Quin 1995; Sharpe 1996) and north-eastern Victoria (Traill and Lill 1997). Of these studies, only Sharpe (1996) and Traill and Lill (1997) used radiotelemetry techniques to investigate the use of tree hollows. Consequently, there is still a paucity of data available concerning even the general patterns of den tree use by *P. norfolcensis* (Gibbons and Lindenmayer 1997). An understanding of the patterns of den tree use (e.g. co-occupancy, group size) can allow inferences to be made about the composition and dominance hierarchies of social groups. Furthermore, the flexibility in the social organisation of various species of petaurid (Quin 1995; Millis 2000) requires that a detailed study of den tree use be undertaken before the social structure of a particular population is inferred or assumed.

In the agricultural region of Euroa, north-eastern Victoria, a high density population of *P. norfolcensis* survives entirely within remnant *Eucalyptus* woodland occurring as linear strips along roads and scattered small patches within cleared farmland (Chapters 3 - 5). The arrangement of habitat into a network of linear strips raises important questions about the response of fauna to the distribution of hollow-bearing trees across the landscape. For example, what impact does the spatial arrangement of habitat have on the social organisation of *P. norfolcensis*, and are any changes reflected in the patterns of den tree use? Do gliders occupy multiple den trees scattered over the entire length of their elongated home ranges (see Chapter 5), or are den trees clustered together in the middle of the range? The number, location and arrangement of den trees may
have implications for energetic demands associated with foraging and territoriality by influencing the distances that need to be traveled to and from den sites. These implications may be exacerbated by a reduction in the availability of suitable hollows because hollow-bearing trees may decay and collapse more rapidly in linear strips of vegetation than in contiguous forest (Lindenmayer et al. 1997a). In addition, recruitment of hollow-bearing trees may be affected if floristic and structural changes to the vegetation at the edge of a remnant facilitate the growth of tree species that do not readily form hollows (Jackson 2000a).

The aim of this study was to investigate the use of den trees by *P. norfolcensis* within a network of linear woodland remnants. Specifically, the objectives of this study were to:

1) ascertain the number and spatial distribution of hollow-bearing trees used as den trees by individual gliders;
2) determine the spatial and temporal patterns in use of den trees; and
3) describe the physical characteristics of trees used as den sites.

**METHODS**

**Study area**

A population of *P. norfolcensis* was studied by trapping and radiotelemetry in a 30 km² area approximately 10 km west of the township of Euroa in the Northern Plains region of Victoria (36°45'S, 145°30'E). The composition of woodland vegetation and the spatial arrangement of habitats are described in Chapter 3.

**Trapping and radiotracking protocol**

Procedures for trapping *P. norfolcensis* are detailed in Chapter 3 and the radiotracking protocol is explained in Chapter 5. The methods, study area, and
individual gliders used in this study are identical to those used to investigate the spatial organisation of *P. norfolcensis* (Chapter 5).

The den tree occupied by each radiocollared animal was always located during daylight hours, usually around mid-day, using a receiver operating in the 150 MHz range with a collapsible 3-element Yagi antenna (Titley Electronics, Ballina, New South Wales). During 1997, den trees were usually located from three to five times during each 10 - 14 day trapping session undertaken to investigate habitat selection and population dynamics of arboreal marsupials (Chapters 3 and 4). During 1998, den trees were located on almost every day during each tracking period.

The accuracy of den tree locations or 'fixes' was regularly tested by stagwatching (Lindenmayer *et al.* 1990a) occupied den trees at dusk and recording the identity and number of emerging animals. On all occasions, radiotelemetry results concurred with stagwatching results and radio-collared gliders emerged from the identified tree. The possible movement of animals during daylight hours was also investigated by locating animals in the morning, followed later in the same day by again locating the animal in the afternoon or by stagwatching at dusk. On all occasions, animals remained in the same den tree throughout the daylight period.

Den trees were marked with a unique two-letter code stamped into a metal plate nailed to the trunk of each tree. The diameter at breast height (dbh) (measured to the nearest cm with a diameter tape), the species of tree, its life status (dead or alive), and location were recorded. The location was determined relative to previously established 100 m intervals along each linear habitat.

**Habitat assessments**

A detailed description of habitat assessment methods is given in Chapter 3. The same structural and floristic attributes of patches of woodland occurring within the cleared agricultural matrix (paddock clumps) were measured. Results from a
detailed study of movement patterns by *P. norfolcensis* (Chapter 5) were used to determine those patches in the agricultural matrix that were 'available' to gliders. The most distant location of a den from a linear remnant was 195 m, and the size of the largest gap that gliders were observed to cross was 70 m (from canopy edge to canopy edge). Therefore, all woodland habitat in farm paddocks, that was within 195 m from the nearest linear remnant where gliders were tracked, was assessed (provided that the largest gap to be crossed was less than 70 m). All trees in woodland patches less than 1.0 ha in size were counted and for patches greater than 1.0 ha, vegetation was sampled in 20 x 50 m quadrats positioned randomly within each patch. The number of quadrats per patch varied according to patch size. Patches from one to two ha had two quadrats; two to four ha, three quadrats; and greater than four ha, four quadrats.

Data analysis

Records of den trees used by animals on the same day that they were trapped and fitted with radiocollars were excluded from all analyses because a large proportion of such trees were never used during subsequent tracking, suggesting that gliders often 'escaped' into the nearest available hollow. The actual tree occupied by each glider could usually be identified. On occasions, a den tree could not be accurately identified when the crown and/or trunk of two or more adjacent trees were close together and the source of the signal did not clearly originate from one tree. When this occurred, it was termed a 'joint tree', and all such records were excluded from analyses in which the identity of the den tree was required.

The size and length of the denning range for each individual was calculated in the same way as home range size and length, to allow for direct comparison between these two measures. The techniques for measuring the home range (range length and grid cell estimator) are detailed in Chapter 5.

Chi-square goodness of fit tests were performed to compare the observed proportion of den trees with that expected based on the availability of trees of
differing size-class and species. One-way analysis of variance (ANOVA) was used to compare mean values for different parameters between groups (e.g. number of den trees used by males vs. females). When the assumption of homogeneous variances was violated, the non-parametric Mann-Whitney or Kruskal Wallis test was used to compare median values between groups (e.g. distance between consecutively used trees by males and females).

RESULTS

Twenty-four male and 27 female *P. norfolcensis* were radiotracked during the study. In total, 2238 diurnal fixes were obtained from these 51 individuals (mean number of diurnal fixes per individual was 43.9, range 18 - 114), with a total of 1162 locations for females and 1076 for males. Tracking effort varied throughout the study; the number of individuals tracked and the duration of each tracking period is detailed in Table 6.1. Within each tracking period, the number of males and females tracked, and the relative number of diurnal fixes per sex were similar (Table 6.1).

Number of trees used

The exact den tree occupied by radio-collared *P. norfolcensis* could be identified on 2081 occasions (males n = 1023, females n = 1058), representing 93% of the total number of diurnal fixes obtained. The remaining 7% of fixes were of locations where a single tree could not be confidently identified (joint trees). When the exact tree could be identified, 143 hollow-bearing trees were utilised by *P. norfolcensis* during the study. The number of different trees used by an individual throughout the study period ranged between one (F87, F94, n = 30 and 33 diurnal fixes, respectively), and 15 (M12, n = 79 diurnal fixes) (Fig 6.1). Most individuals used between two and six den trees (Fig. 6.1), with a mean of 5.29 (n = 51, s.e. 0.43) den trees per glider. There was no significant difference in the
mean number of den trees used by males or females (5.63 and 5.00 den trees respectively, One-way ANOVA, p = 0.48).

Table 6.1. Number of individuals and number of diurnal radio-tracking locations obtained for 51 *P. norfolcensis* radiotracked in linear remnants of woodland near Euroa, north-eastern Victoria.

<table>
<thead>
<tr>
<th>Tracking session</th>
<th>Gender</th>
<th>No. of individuals</th>
<th>No. of tracking days*</th>
<th>Total no. of tracking days</th>
</tr>
</thead>
<tbody>
<tr>
<td>1997</td>
<td>Male</td>
<td>3</td>
<td>36.0 ± 3.0</td>
<td>108</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>3</td>
<td>36.0 ± 0.6</td>
<td>108</td>
</tr>
<tr>
<td>Summer 1998</td>
<td>Male</td>
<td>10</td>
<td>39.6 ± 2.3</td>
<td>396</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>11</td>
<td>35.8 ± 3.2</td>
<td>394</td>
</tr>
<tr>
<td>Autumn 1998</td>
<td>Male</td>
<td>14</td>
<td>31.8 ± 2.9</td>
<td>445</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>16</td>
<td>32.2 ± 1.6</td>
<td>515</td>
</tr>
<tr>
<td>Winter 1998</td>
<td>Male</td>
<td>4</td>
<td>20.2 ± 0.9</td>
<td>81</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>5</td>
<td>19.2 ± 0.2</td>
<td>96</td>
</tr>
<tr>
<td>Spring 1998</td>
<td>Male</td>
<td>3</td>
<td>15.3 ± 0.3</td>
<td>46</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>3</td>
<td>16.3 ± 0.3</td>
<td>49</td>
</tr>
<tr>
<td>All sessions</td>
<td>Male</td>
<td>24</td>
<td>44.8 ± 4.4</td>
<td>1076</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>27</td>
<td>43.0 ± 4.4</td>
<td>1162</td>
</tr>
</tbody>
</table>

* Mean number of tracking days per glider for all sessions exceeds the values for each individual session because some individuals were tracked during two or more sessions.

The number of den trees used by each individual increased with tracking effort (Fig 6.2). For three of the four individuals tracked during three or four sessions (F4, M1, M12), the number of known den trees continued to increase over the full duration of the study (Fig 6.2). For some individuals, increases in the number of den trees coincided with the commencement of a new tracking session (e.g. M1, Fig 6.2). For others (e.g. M12), new den trees were regularly identified throughout the study period and the rate of increase showed no indication of
leveling off. It is interesting to note that both Male 1 and Male 12 shifted their home range during their final session of tracking (refer Chapter 5), and hence a new suite of den trees were identified for both individuals.

![Figure 6.1. Number of den trees used by individual P. norfolcensis in linear habitats near Euroa, north-eastern Victoria, as determined by radiotelemetry (n = 51 individuals).](image)

**Spatial distribution of den trees**

Seventeen gliders occupied den trees that occurred in patches of woodland ('paddock clumps') within the cleared agricultural matrix. The mean proportion of den tree fixes that originated in paddock clumps for these 17 gliders was 25.1% (range 0.9 - 66.7%). The location of all den trees occupied by the remaining 34 gliders was in roadside vegetation.

The size and length of the denning range in each session was determined for all gliders that occupied two or more den trees during that tracking session. The mean size of the denning range during each tracking session was uniformly small (Table 6.2) and ranged from 0.18 - 2.03 ha. Mean length of the denning range was more variable, with session means ranging between 75 and 833 m (Table 6.2). The size and length estimates of the long-term denning range for animals
tracked in three or four seasons in 1998 were larger (males, n = 2, 4.73 ha and 1137 m; females, n = 2, 2.28 ha, 560m, respectively).

Within each tracking session, the size and length of denning ranges were usually between 50 and 60% of the home range estimates (Table 6.2). Denning ranges during certain tracking sessions, including the long-term estimates, were up to 90% of the home range estimates. This indicates that den trees were often spatially distributed across a large proportion of an animal's home range.

Table 6.2. Characteristics of the denning range of *P. norfolcensis* in comparison with 95% home range estimates.

Only gliders tracked to two or more den trees during each session are included. Percentage of home range is the difference between the denning range and 95% home range estimate for each individual. 1997 home range estimates unpublished data and 1998 home range estimates in Chapter 5. Long-term estimates are for those gliders tracked in three or four sessions in 1998.

<table>
<thead>
<tr>
<th>Tracking session</th>
<th>Gender (sample size)</th>
<th>Denning range size (ha) Mean ± s.e.</th>
<th>% of home range</th>
<th>Denning range length (m) Mean ± s.e.</th>
<th>% of home range</th>
</tr>
</thead>
<tbody>
<tr>
<td>1997</td>
<td>Male (n = 3)</td>
<td>1.62 ± 0.35</td>
<td>58.6</td>
<td>603 ± 197</td>
<td>65.7</td>
</tr>
<tr>
<td></td>
<td>Female (n = 3)</td>
<td>1.98 ± 0.39</td>
<td>81.4</td>
<td>833 ± 282</td>
<td>88.8</td>
</tr>
<tr>
<td>Summer</td>
<td>Male (n = 10)</td>
<td>2.03 ± 0.29</td>
<td>70.9</td>
<td>652 ± 92</td>
<td>83.0</td>
</tr>
<tr>
<td>1998</td>
<td>Female (n = 9)</td>
<td>1.07 ± 0.25</td>
<td>44.4</td>
<td>372 ± 84</td>
<td>50.9</td>
</tr>
<tr>
<td>Autumn</td>
<td>Male (n = 14)</td>
<td>1.40 ± 0.45</td>
<td>47.7</td>
<td>457 ± 155</td>
<td>52.3</td>
</tr>
<tr>
<td>1998</td>
<td>Female (n = 15)</td>
<td>1.98 ± 0.65</td>
<td>63.9</td>
<td>639 ± 251</td>
<td>69.1</td>
</tr>
<tr>
<td>Winter</td>
<td>Male (n = 2)</td>
<td>0.18 ± 0.06</td>
<td>6.5</td>
<td>75 ± 45</td>
<td>7.7</td>
</tr>
<tr>
<td>1998</td>
<td>Female (n = 3)</td>
<td>0.69 ± 0.11</td>
<td>51.6</td>
<td>172 ± 27</td>
<td>51.6</td>
</tr>
<tr>
<td>Spring</td>
<td>Male (n = 3)</td>
<td>1.40 ± 0.44</td>
<td>65.1</td>
<td>373 ± 77</td>
<td>67.1</td>
</tr>
<tr>
<td>1998</td>
<td>Female (n = 3)</td>
<td>1.19 ± 0.6</td>
<td>91.2</td>
<td>292 ± 82</td>
<td>89.8</td>
</tr>
<tr>
<td>Long-term estimates</td>
<td>Male (n = 2)</td>
<td>4.73 ± 0.13</td>
<td>89.1</td>
<td>1137 ± 77</td>
<td>90.4</td>
</tr>
<tr>
<td></td>
<td>Female (n = 2)</td>
<td>2.28 ± 0.36</td>
<td>89.3</td>
<td>560 ± 100</td>
<td>94.4</td>
</tr>
</tbody>
</table>
Figure 6.2 The cumulative number of den trees used by four *P. norfolcensis* in relation to the number of den tree locations. Data are plotted for the four individuals with the maximum number of den tree fixes. Asterisk on horizontal axis denotes the commencement of each tracking session.
Figure 6.3. Proportional use of different den trees by female *P. norfolcensis* radiotracked in linear woodland remnants near Euroa, north-eastern Victoria.
Numbers above each column indicate the total number of tracking days. Only trees actually identified as den trees are included. The length of the column indicates the proportion of diurnal locations in different den trees. The most frequently used den tree is indicated by shading.

Figure 6.4. Proportional use of different den trees by male *P. norfolcensis* radiotracked in linear woodland remnants near Euroa, north-eastern Victoria.
Numbers above each column indicate the total number of tracking days. Only trees actually identified as den trees are included. The length of the column indicates the proportion of diurnal locations in different den trees. The most frequently used den tree is indicated by shading.
Spatial and temporal patterns in den tree use

Most animals utilised a small number of den trees frequently with their remaining den trees occupied infrequently. Throughout the study period, most animals used the same den tree on between 40 and 60% of tracking days, with a decreasing proportion of records coming from their remaining known den trees (Figs. 6.3 and 6.4).

To describe temporal and spatial patterns in den tree swapping behaviour, I only refer to data collected on consecutive days. In other words, a data point is the decision to remain in the same den tree or move to a different one. This reduces the number of den tree locations to those collected on consecutive days, but it ensures that swapping was known to occur from one day to the next. The mean number of den tree fixes collected on consecutive days across all sessions for each *P. norfolcensis* (*n*= 51) was 39.1 (range 9 - 103). On average, gliders remained in the same den tree for 4.9 consecutive days (range 1.4 - 32.0). Males spent fewer days consecutively in the same tree than females (3.3 vs. 6.3), but this difference was not significant (Mann-Whitney U-test, U = 224.5, *p* = 0.06).

The mean distance between den trees occupied by each individual on consecutive days was 247 m (range 0 - 1318 m). The mean maximum distance per individual glider between den trees occupied on consecutive days was 472 m (range 0 - 2335 m). There was no significant difference between males and females in the mean or maximum distance moved between den trees on consecutive days (Mann-Whitney, *U* = 261.0, *p* = 0.23 and *U* = 260.5, *p* = 0.23 respectively). Figures 6.5 - 6.8 show the location and sequence of occupation of den trees for four *P. norfolcensis*.

The majority of den trees (57%) were only ever occupied by one radiocollared individual during the study period (Table 6.3). A smaller proportion of den trees was occupied by two or three individuals (27% and 17% respectively). The maximum number of radio-tracked individuals utilising the same hollow tree at some stage during the study period was seven (Table 6.3).
Figure 6.5. Distribution of den trees (solid black squares) and the sequence of consecutive days (numbers) at each den tree for *P. norfolcensis* Female 17. Two-letter code refers to the identity of each den tree. Plotting 68 fixes: numbers 1 - 35 collected between 24/01/98 - 27/02/98, and numbers 36 - 68 collected between 29/04/98 - 31/05/98. Remnant woodland habitat is denoted by grey shading and cleared agricultural grasslands by white. Thick black line delineates the 95% home range.
Figure 6.6. Distribution of den trees (solid black squares) and the sequence of consecutive days (numbers) at each den tree for *P. norfolcensis* Female 93. Two-letter code refers to the identity of each den tree. Plotting 32 consecutive fixes collected between 26/01/98 - 26/02/98. Remnant woodland habitat is denoted by grey shading and cleared agricultural grasslands by white. Thick black line delineates the 95% home range.
Figure 6.7. Distribution of den trees (solid black squares) and the sequence of consecutive days (numbers) at each den tree for *P. norfolcensis* Male 32. Two-letter code refers to the identity of each den tree. Plotting 42 consecutive fixes collected between 17/04/98 - 28/05/98. Remnant woodland habitat is denoted by grey shading and cleared agricultural grasslands by white. Thick black line delineates the 95% home range.
Figure 6.8. Distribution of den trees (solid black squares) and the sequence of consecutive days (numbers) at each den tree for *P. norfolcensis* Male 1. Two-letter code refers to the identity of each den tree. Letters refer to the identity of each den tree. Plotting 90 consecutive fixes: nos. 1-36 collected 22/1/98 - 26/2/98, nos. 37-64 collected 29/4/98 - 26/5/98, nos. 65 - 77 collected 24/7/98 - 5/8/98, and nos. 78 - 90 collected 11/11/98 - 23/11/98. Remnant woodland habitat is denoted by grey shading and cleared agricultural grasslands by white. Thick black line delineates the 95% home range.
During the study period, 65 trees with hollows were stagwatched 105 times. On 83 occasions, *P. norfolcensis* were observed emerging from hollows at dusk and a total of 195 individuals was observed. Mean group size, based on the number of individuals emerging from occupied trees was 2.53 (range 1 - 6). Gliders formed clear social groups (Table 6.4) and rarely shared den trees with members of other social groups. Eight individuals from three adjacent social groups occupied 32 den trees during summer 1997-1998; on no occasion during this tracking session did gliders utilise den trees occupied by a different social group (Table 6.4). Over the long-term, the composition of social groups was dynamic, and individuals sometimes shifted social groups (refer Chapter 5). A summary of the composition of social groups in summer 1997-1998 is given in Table 4.5.

### Table 6.3. Number of radiocollared *P. norfolcensis* occupying each den tree during 1997 - 1998 as determined by radiotelemetry.

Diurnal locations where there was some uncertainty about tree identity ('joint-trees' - see text) are not included.

<table>
<thead>
<tr>
<th>Number of individuals that utilised a particular den tree</th>
<th>Number of den trees</th>
<th>Proportion of fixes (%) (n = 2081)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>82</td>
<td>18.7</td>
</tr>
<tr>
<td>2</td>
<td>27</td>
<td>18.3</td>
</tr>
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<td>3</td>
<td>17</td>
<td>18.3</td>
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<td>9.3</td>
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<td>5</td>
<td>8</td>
<td>19.8</td>
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<tr>
<td>6</td>
<td>2</td>
<td>7.9</td>
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<tr>
<td>7</td>
<td>1</td>
<td>7.7</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>143</strong></td>
<td><strong>100.0</strong></td>
</tr>
</tbody>
</table>
Table 6.4. Number of denning records in each den tree by eight radio-tracked *P. norfolcensis* occupying a continuous 2.1 km section of roadside vegetation in summer 1997-1998.

Two-letter code refers to the identity of each den tree. Den trees and social group members are arranged to allow ease of identification of social groups. M = males, F = females.

| Den tree | AQ | FY | IW | JK | KR | KT | AC | DA | AGDA | IB | IBIL | IL | AJ | AO | IA | IK | IK/KP | JH | HI | LI | MF | LK | LV | LK | MY | AF | AH | BU | FK | GF | GF/KZ | KZ | IM | IO | IP | JM |
|----------|----|----|----|----|----|----|----|----|------|----|------|----|----|----|----|----|------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| M1       | 5  | 1  | 2  | 21 | 6  | 8  |     |     |      |    |      |    |    |    |    |    |      |    |    |    |    |    |    |    |    |    |    |    |    |
| F17      | 25 | 1  | 9  |    |    |    |     |     |      |    |      |    |    |    |    |    |      |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| F6       | 8  | 1  | 2  |    |    |    |     |     |      |    |      |    |    |    |    |    |      |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| F7       | 7  | 3  | 1  | 1  | 5  | 1  | 17 | 1  | 1  | 6  |    |    |    |    |    |    |      |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| M9       | 1  | 8  | 1  | 1  | 1  | 3  | 20 | 9  |      |    |      |    |    |    |    |    |      |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| M12      | 1  | 12 | 1  | 1  | 2  | 17 | 4  | 1  | 2  |    |    |    |    |    |    |    |      |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| M10      |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |      |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |
| F4       |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |      |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |

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<th>F6</th>
<th>F7</th>
<th>M9</th>
<th>M12</th>
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<td>7</td>
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</tbody>
</table>
Characteristics of den trees

*Petaurus norfolcensis* utilised hollows in *E. microcarpa* (n = 117 trees), *E. polyanthemos* (n = 2), *E. leucoxylon* (n = 1), *E. blakelyi* (n = 8), *E. melliodora* (n = 5) and *E. camaldulensis* (n = 2) (Table 6.5). Den sites were also located in dead *Eucalyptus* trees (n = 6 trees). Within linear remnants, *P. norfolcensis* selected certain species of eucalypts as den trees more often than their proportional availability in the study area ($x^2 = 17.46$, d.f. = 7, $p < 0.05$) (Fig. 6.9a). It appears that *E. microcarpa* and *E. melliodora* are preferentially selected, and *E. blakelyi* appears to be selected less often than if by chance (Fig 6.9a). It is interesting to note that *E. microcarpa* is also the dominant overstorey species and occurs in almost all 50 m habitat sampling units (Chapter 3). In paddock clumps, gliders selected den trees of each species of eucalypt in proportion to their availability ($x^2 = 7.10$, d.f. = 6, $p > 0.25$) (Fig. 6.9b).

Dens were usually located in trees of large diameter, with a mean for all species of eucalypt combined of 88.5 cm (s.e. 2.1, range 24 - 156 cm). Large diameter trees (> 70 cm dbh) were selected by *P. norfolcensis* as den trees significantly more often than they occurred within linear remnants ($x^2 = 686.63$, d.f. = 3, $p < 0.001$) and within paddock clumps ($x^2 = 87.76$, d.f. = 3, $p < 0.001$) (Fig 6.10).

The health of living den trees varied from trees that were suffering severe levels of dieback (i.e. completely defoliated with just a few sprouting branchlets) to trees that appeared completely healthy. Entrances to hollows were often at the end of branches, as well as fissures or holes in the side of the trunk or major branches. Entrances to hollows were in both living and dead wood. The size of entrance holes were typically small, with an estimated range from a minimum size of four to six cm, increasing to approximately 10 to 15 cm. The height of entrance holes ranged from 2 m above the ground to approximately 20 m in the larger trees.
Table 6.5. Characteristics of den trees utilised by *P. norfolcensis*

Only data for known den trees are shown - joint trees are excluded because the exact tree could not be identified. DBH is the diameter at breast height of the den tree (cm).

<table>
<thead>
<tr>
<th>Parameter</th>
<th><em>E. microcarpa</em></th>
<th><em>E. camaldulensis</em></th>
<th><em>E. blakelyi</em></th>
<th><em>E. leucoxylon</em></th>
<th><em>E. polyanthemos</em></th>
<th><em>E. melliodora</em></th>
<th>Dead trees</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of den trees in linear remnants</td>
<td>99</td>
<td>2</td>
<td>5</td>
<td>1</td>
<td>4</td>
<td>5</td>
<td>4</td>
<td>120</td>
</tr>
<tr>
<td>Number of den trees in paddock clumps</td>
<td>18</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>23</td>
</tr>
<tr>
<td>Total number of den trees</td>
<td>117</td>
<td>2</td>
<td>8</td>
<td>1</td>
<td>4</td>
<td>5</td>
<td>6</td>
<td>143</td>
</tr>
<tr>
<td>Number of den tree fixes</td>
<td>1917</td>
<td>3</td>
<td>53</td>
<td>1</td>
<td>29</td>
<td>55</td>
<td>23</td>
<td>2081</td>
</tr>
<tr>
<td>Mean DBH ± s.e. (cm)</td>
<td>90.3 ± 2.3</td>
<td>83.0 ± 10.0</td>
<td>71.7 ± 6.7</td>
<td>93.0</td>
<td>78.7 ± 14.8</td>
<td>96.8 ± 5.9</td>
<td>76.5 ± 9.9</td>
<td>88.5 ± 2.1</td>
</tr>
<tr>
<td>Range in DBH (cm)</td>
<td>24 - 156</td>
<td>73 - 93</td>
<td>47 - 105</td>
<td>93</td>
<td>62 - 123</td>
<td>77 - 110</td>
<td>39 - 104</td>
<td>24 - 156</td>
</tr>
</tbody>
</table>
Figure 6.9. The percentage of den trees used by *P. norfolcensis* (open columns) and available trees (shaded columns) of each species within (A) linear remnants (n = 120 den trees) and (B) paddock clumps (n = 23). The tree species are *E. microcarpa* (E. mic), *E. blakelyi* (E. bla), *E. camaldulensis* (E. cam), *E. macrorhyncha* (E. mac), *E. melliodora* (E. mel), *E. leucoxylon* (E. leu), *E. polyanthemos* (E. pol), and dead trees (species not determined).
Figure 6.10. The percentage of den trees used by *P. norfolcensis* (open columns) and available trees (shaded columns) in each size class category (diameter at breast height) within (A) linear remnants (*n* = 120 den trees) and (B) paddock clumps (*n* = 23).
DISCUSSION

Characteristics of den trees

All dens of *P. norfolcensis* were located in hollows in *Eucalyptus* trees. Dens were located in trees of a range of sizes but they were invariably large old trees; the mean diameter of den trees was 88.5 cm. Dens occurred in all species of eucalypt that occurred within the study area. However, den trees were not selected at random, and gliders preferentially selected large diameter trees (> 70 cm dbh) and certain species (*E. microcarpa* and *E. melliodora*) as den trees.

The preference for large diameter trees may be because the number, size and type of hollows within a tree increases with tree diameter (Mackowski 1984; Lindenmayer *et al.* 1993; Bennett *et al.* 1994b; Soderquist 1999). As tree diameter and age are correlated (Stoneman *et al.* 1997), larger trees are older, and hence likely to contain more hollows than smaller, younger trees. In comparison with young trees, older trees are likely to have more large branches that are physically capable of forming hollows, and will have been exposed to a wider range of hollow-forming processes for a longer period (Mackowski 1984; Inions *et al.* 1989; Lindenmayer *et al.* 1993). Many studies have found that hollow-using fauna occupy large diameter trees (e.g. *T. vulpecula* Cowan 1989; *P. tapoatafa* van der Ree and Bennett 1999; *G. leadbeateri* Lindenmayer and Meggs 1996; Yellow-tailed Black-cockatoo *Calyptorhynchus funereus* Nelson and Morris 1994; and Gould's Long-eared Bat *Nyctophilus gouldi* Lunney *et al.* 1988). However, it is important to note that *P. norfolcensis* also occupied dens in small diameter trees (down to 24 cm), indicating that all trees with suitable hollows, even those with a small diameter, may be utilised.

Patterns in the selection of certain species as den trees are probably related to the propensity of different species of tree to form hollows (Saunders *et al.* 1982; Bennett *et al.* 1994b; Traill and Lill 1997). The preferential selection of certain species may also be due to their growth form and hence the relative proportion of hollows of a different form (e.g. fissure, hole) may vary between species. For example, *P. norfolcensis* often entered cavities via holes that occurred at the end
of branches. It is conceivable that *E. microcarpa* and *E. melliodora* supported more hollows of a particular form that *P. norfolcensis* preferred, although there was insufficient data to test this. In far north Queensland, dens of *P. gracilis* were also located more frequently in certain species of tree than expected from their abundance at the site, although no explanation was given (Jackson 2000a).

The number and rate of use of occupied trees

When the exact den tree could be identified (93% of 2238 locations), 51 gliders used a total of 143 different trees. Most gliders (49 out of 51) used two or more trees during the tracking period - the mean number of den trees used per individual was 5.3, and the maximum was 15. Moreover, the number of den trees that each glider occupied increased with tracking effort, indicating that the number of den trees utilised within an animal's lifetime is probably much greater. A steady increase in the number of dens used over time has also been found for *G. leadbeateri* (Lindenmayer and Meggs 1996), *P. volans* (Kehl and Borsboom 1984), *T. vulpecula* (Cowan 1989) and *T. caninus* (Lindenmayer *et al.* 1996b).

The number of den trees utilised by *P. norfolcensis* at Euroa is greater than that recorded for *P. norfolcensis* in coastal northern New South Wales (Quin 1995; Sharpe 1996) and north-east Victoria (Traill and Lill 1997). Most notably, the colony for which Quin (1995) had the most data remained in the same tree until the branch housing the colony collapsed, causing them to relocate to another tree; thus using two trees over a 30 month period. Sharpe (1996) reported that six glider groups used 16 known den trees over a six month period, and the maximum number of den trees utilised by a single group was four. At Chiltern in north-east Victoria, approximately 20 gliders used 26 tree hollows and 10 nest boxes (Traill and Lill 1997). These studies, however, are likely to have underestimated den tree usage because of methodological constraints. Quin (1995) did not use radiotelemetry, and while Sharpe (1996) did, his survey was only conducted intermittently over a six-month period. Traill and Lill (1997) used a combination of stagwatching and radiotelemetry - the latter technique confined to nine
individuals (Traill 1995). Consequently, it can not be confirmed whether the large number of den trees utilised in the Euroa area is typical for the species, or is an exceptional outcome that may be due to the shape or arrangement of habitat, the abundance of large trees with hollows, or alternatively, a reflection of the duration of this study.

At Euroa, gliders typically occupied a small number of trees frequently, with the remaining trees occupied less frequently. This parallels similar patterns in den tree use by other species of arboreal marsupials where two or three 'core' dens were identified (e.g. *T. caninus*, Lindenmayer *et al.* 1996b; *T. vulpecula*, Cowan 1989; and *P. volans*, Kehl and Borsboom 1984).

Gliders remained in the same den tree for an average of five consecutive days, with females remaining in the same den for almost twice as many consecutive days as males (6.3 vs. 3.3). Similarly, *T. caninus* typically used two or more den trees per week, with a maximum of six trees occupied by an individual during one week (Lindenmayer *et al.* 1996b). In New Zealand, *T. vulpecula* changed den sites on consecutive nights on 60% of occasions, with males changing dens from week to week significantly more frequently than females (Cowan 1989).

The use of multiple den trees, an apparent preference for particular den sites, and regular shifting between dens, appears to be a trait common to many other species of arboreal marsupial (e.g. *T. caninus*, Lindenmayer *et al.* 1996b; *P. volans*, Kehl and Borsboom 1984; *P. australis*, Henry and Craig 1984; *P. breviceps*, Suckling 1984; *P. tapoatafa*, Rhind 1996; van der Ree and Bennett 1999; *P. gracilis*, Jackson 2000; and *G. leadbeateri*, Lindenmayer and Meggs 1996). While the reasons for this behaviour are not understood, several hypotheses have been proposed.

First, the occupation of multiple dens may mitigate the risk of predation during emergence from the den at dusk. This may be achieved by exiting from different den trees on subsequent days. Potential predators of *P. norfolicensis* at Euroa include *N. strenua*, *N. connivens*, *F. catus* and *V. varius* (see Chapters 4 and 5). The observed rate of predation on juveniles (seven out of eleven radio-collared
individuals - see Chapter 4) suggests that at least for juveniles, the rate of predation may be high. However, the rate of predation on adult gliders appears low, and hence predation on gliders as they leave their den appears an unsatisfactory explanation.

Second, the regular swapping of dens may prevent the numbers of ectoparasites from building up in the dens and hence reduce transmission rates between group members. Swapping of den sites by the Brown Antechinus *A. stuartii* is believed to reduce the transmission and abundance of ticks between conspecifics (Cockburn and Lazenby-Cohen 1992). Similarly, a positive correlation was found between the abundance of ectoparasites on Pallid Bats *Antrozous pallidus* and their frequency of roost switching (Lewis 1996). The abundance of ectoparasites (unidentified fleas and mites) in the fur of *P. norfolcensis* was always low (R. van der Ree, pers. obs.) and appeared unlikely to be the primary cause of den-switching. Moreover, gliders spent almost 15% of their time outside the hollow engaged in grooming (Holland 1998), as well as an unknown proportion of their time within the den grooming, which probably assisted in keeping the observed abundance of ectoparasites low.

Third, different species of tree and hollows of different form and dimension are likely to posses varying thermal properties (e.g. humidity, temperature) (Calder *et al.* 1983; Tideman and Flavel 1987; Kalcounis and Brigham 1998). Animals may thus occupy particular tree hollows depending on the prevailing climate, which may also vary according to group size or behaviour, such as when vulnerable young are deposited in the nursery den while parents forage. For example, *P. tapoatafa* selects appropriate maternity dens where young are raised (Soderquist 1993b). *A. stuartii* also shows a high level of nest specificity, and mating nests, communal nests, natal nests and female refuges have been identified (Cockburn and Lazenby-Cohen 1992). However, fluctuations in ambient climatic conditions at Euroa appear unlikely to vary sufficiently over the average duration of time spent in the same den tree (five days) to explain the high frequency of den tree swapping. The influence of reproductive condition was difficult to test because during the study, only three reproductively active females were tracked (spring
While data are limited, each of the three females had pouch young and during 16 - 17 days of tracking, each used three different den trees.

Finally, the occupation of a large number of den trees within the home range, and in particular, the simultaneous occupation of multiple den trees by members of the same social group, may facilitate territory defense. This may be relevant at Euroa because of the high density of large and hollow-bearing trees (23 and 21 trees ha$^{-1}$, respectively, Chapter 3). Consequently, gliders may need to establish their presence in a large number of potential den trees in order to maintain a territory. In doing so, gliders may also increase their level of interaction with adjacent social groups and hence may be more aware of the composition of other groups and the reproductive condition of females. Goldingay and Kavanagh (1990) hypothesised that $P. australis$ may be aware of the composition of adjacent groups by vocalisations, and that neighbouring animals may be alerted to changes in group composition by altered levels of vocalisation. In contrast, $P. norfolcensis$ is largely silent (Traill 1998), and therefore may need to monitor its territory and the composition of adjacent groups by physically visiting the appropriate area.

An additional explanation that has received little attention in the scientific literature is that the use of den sites distributed throughout the home range may be a reflection of final foraging location before dawn. Thus, energy expenditure may be minimised by resting in the nearest suitable hollow, rather than returning to a centrally located den. The spatial distribution of den trees across a large proportion of the home range of $P. norfolcensis$ (up to 90.4% in this study) supports this explanation. This trend has been observed in studies of arboreal marsupials occupying continuous forest (e.g. $T. vulpecula$ and $P. gracilis$) where den trees were located throughout their home range, and tended to be distributed towards the perimeter of the range for some individuals (Ward 1978; Jackson 2000a). This may reduce energy expenditure because it may be more efficient to return to a nearby den rather than a centrally located one. The minimisation of energy may be particularly relevant for animals with low mobility, those occupying low quality habitat, or those resident in linear habitats because travel distances are longer than in continuous forest.
In addition, all-night observations of *P. norfolcensis* showed that at dawn, some gliders entered their hollow when there was enough natural light to see. Therefore, the risk of predation at dawn may be reduced by entering the nearest suitable hollow, rather than traversing the entire range to access a centrally located den.

Clearly, the reason for the use of multiple dens and the high frequency of den-swapping by *P. norfolcensis* is complex. The most likely explanation is a combination of social behaviour, the high availability of den trees and the linear arrangement of the habitat.

**CONCLUSIONS**

Large trees with hollows are an important component of the forests and woodlands of south-eastern Australia (Scotts 1991; Lindenmayer *et al.* 1993; Bennett *et al.* 1994b). They provide a diverse foraging substrate, as well as a diversity of hollows that provide shelter for many vertebrate species (Ambrose 1982). Large trees with hollows are a critical resource for *P. norfolcensis*. Individual gliders utilised up to 15 large diameter den trees that were distributed across a large proportion of their home range. Therefore, the conservation of *P. norfolcensis*, as well as the other hollow-dependent species living in sympatry, depends on an ongoing supply of trees with suitable hollows into the future. This requires the continual recruitment of new trees into large size-classes where hollows can form, as well as the protection and conservation of existing hollow-bearing trees, spatially distributed across the landscape.

The challenge in agricultural landscapes is to ensure a perpetual supply of hollow-bearing trees across the entire woodland mosaic (Saunders *et al.* 1993; Bennett *et al.* 1994b; Robinson and Traill 1996). At Euroa, gliders occupied trees that occurred throughout their home range area, implying a need for a relatively even distribution of hollow-bearing trees across the landscape. For hollow-dependent species, an even spatial distribution of suitable hollows ensures that the entire
linear strip and small patches may provide habitat and support resident populations, thus increasing overall population size. For territorial species of animals, sufficient hollow-bearing trees must occur within the territory of each social group. Hollows also need to be available in dispersal pathways to provide temporary shelter for dispersing individuals. Therefore, hollow-bearing trees need to be located in all areas of woodland that provide habitat or connectivity across the landscape, such as linear strips, small patches and scattered trees. This suggests that remnants of old-growth forest be retained wherever possible to maximise their value for fauna. In areas of regrowth where hollows are absent, the installation of nest-boxes may raise the value of the habitat for fauna.
CHAPTER 7
SYNTHESIS OF RESULTS AND IMPLICATIONS FOR MANAGEMENT

INTRODUCTION

The preceding chapters treated aspects of the ecology of arboreal marsupials in a fragmented woodland mosaic as separate topics. However, rather than reiterate the conclusions of each chapter, this synthesis addresses four themes. The first theme reviews and documents the widespread occurrence of linear landscape elements in anthropogenically modified landscapes throughout the world. The second summarises the value of linear landscape elements as habitat for fauna. The third theme identifies the landscape and habitat features that appear to be important for the persistence of arboreal marsupials in a network of linear habitats. Finally, this chapter concludes with a discussion of the implications of these results for the management and conservation of arboreal marsupials in temperate woodlands of Australia.

PATTERNS IN THE SPATIAL CONFIGURATION OF HABITAT

Linear landscape elements are characteristic of many anthropogenically-modified landscapes throughout the world (Burel 1996; Forman 1997). These features differ structurally and often floristically from the surrounding landscape. They include open corridors or rights-of-way, such as roads and pipeline easements through forest-dominated landscapes, or strips of trees, shrubs or other vegetation types in otherwise-cleared landscapes.

The origins of linear landscape elements are diverse and five corridor types have been identified (Forman and Godron 1986; Forman 1997). Natural corridors
usually follow topographic or environmental contours, such as watercourses and riparian vegetation. Remnant corridors are created when the surrounding environment is cleared or disturbed, leaving the strip relatively intact within the modified matrix. Regenerated corridors spontaneously develop following disturbance, and include many hedges and fencerows growing in uncultivated field margins. Planted corridors include windbreaks, shelterbelts, hedgerows and fencerows that have been intentionally planted by humans. Disturbance corridors are strips of cleared land through continuous habitat such as roads, trails and powerline easements that require ongoing levels of disturbance to maintain the opening.

This synthesis focusses primarily on the structure and function of wooded or shrubby linear features that dissect and form an abrupt boundary with cleared agricultural land. Known variably as fencerows, hedgerows, windbreaks, shelterbelts, wildlife corridors, roadside vegetation or streamside strips, these linear elements are conspicuous components of many agricultural landscapes (Harris and Scheck 1991; Burel 1996; Forman 1997; Bennett 1999).

Linear strips of trees and shrubs are common in many agricultural regions around the world, including eastern and western Europe (Wauters et al. 1994; Burel 1996; Kotzageorgis and Mason 1997; Sarlöv Herlin and Fry 2000), North America (Merriam 1990; Keller et al. 1993; Warner 1994; Haas 1995) and Australia (Bennett 1990a; Saunders et al. 1993; Laurance and Laurance 1999). In these production landscapes, large or continuous patches of wooded habitat rarely occur and the conservation of woodland-dependent species is reliant on small or linear strips of wooded habitat (Forman and Baudry 1984; Firbank 1997). For example, 87% of the woodland cover in the Euroa floodplains area occurs as linear strips along roads and streams (Chapter 2).

There is concern in temperate North America and Europe that the intensification and specialisation of modern agriculture will reduce the suitability of agricultural landscapes for conservation of plants and animals (Warner 1994; Burel and Baudry 1995; Freemark 1995; Firbank 1997). A major, though by no means the only problem, is the reduction of landscape heterogeneity as smaller fields are
consolidated into larger ones with a concomitant decrease in the extent of hedgerows and other linear landscape elements (Burel 1996). The rate of hedgerow removal in England has increased dramatically since the mid-1800's (Conyers 1986; Mason et al. 1987; Barr and Parr 1994), and between 1984 and 1990, approximately 4,000 km per year has been cleared (Firbank 1997).

The level of research on the function and value of certain types of linear landscape elements varies according to location and type. For example, hedgerows and fencerows in North America and Europe have received considerable attention (e.g. Watt and Buckley 1994; Merriam 1995; Burel 1996). More recently, roadside vegetation has been the focus of research effort in south-western and south-eastern Australia (e.g. Bennett 1990a; Cale 1990; Lynch et al. 1995). Investigations into other types of linear strips (e.g. planted shelterbelts or wildlife corridors) are less extensive and represent a specific gap in the current state of knowledge. This lack of comprehensive knowledge about the functioning of linear landscape elements extends to all types, and has recently been highlighted for hedgerows (Hooper 1994), despite them being the most extensively researched type of linear strip.

In summary, linear strips of wooded vegetation are, a) common in many anthropogenic landscapes around the world; b) represent a large proportion of the mosaic of 'natural' or wooded habitat occurring and; c) many are under threat due to removal or neglect. Therefore, it is essential that the value of linear strips of natural vegetation be investigated and documented.

LINEAR LANDSCAPE ELEMENTS AS HABITAT FOR FAUNA

During this study, five species of arboreal marsupial (T. vulpecula, P. peregrinus, P. breviceps, P. norfolcensis, P. cinereus) and two species of scansorial marsupial (P. tapoatafa and A. flavipes) were detected utilising the linear strips of woodland at Euroa. This represents seven out of eight species of arboreal marsupial known to occur in the Northern Plains region of Victoria (Bennett et al. 1991; Bennett et
The species not observed during the study was *A. pygmaeus*, however, it is difficult to detect because of its small size and cryptic nature (Henry 1995), and hence may have gone undetected. Further, at least three species established breeding populations within the linear strips (*P. norfolcensis*, Chapter 4; *T. vulpecula*, Murphy 1997; *P. tapoatafa*, van der Ree and Bennett 1999).

Internationally, linear strips of vegetation have been observed to provide habitat for various species of animal in many agricultural landscapes. Small mammals have been recorded as resident in fencerows, hedgerows, shelterbelts, and roadside and streamside strips (Pollard and Relton 1970; Wegner and Merriam 1979; Yahner 1983; Henderson *et al.* 1985; Bennett 1990a; Bennett *et al.* 1994a; Wauters *et al.* 1994; Downes *et al.* 1997a; Kotzageorgis and Mason 1997; Bright 1998; de Lima and Gascon 1999). Numerous species of birds have also been recorded resident in linear strips (Wegner and Merriam 1979; Osborne 1984; Shalaway 1985; Lack 1988; Arnold and Weeldenburg 1990; Cale 1990; Leach and Recher 1993; Haas 1995; Bentley and Catterall 1997). Invertebrates, including beetles, ants, and butterflies have been recorded in linear strips of habitat (Pollard 1968; Burel 1989; Vermeulen 1993; Hill 1995; Major *et al.* 1999c). Data on the use of linear habitats by amphibians is scant but 12 species of frog have been recorded in retained riparian strips in the Amazon Basin (de Lima and Gascon 1999). Therefore, it is clear that linear strips of vegetation can provide habitat for a wide range of species.

There is, however, evidence to suggest that linear strips may not provide habitat for all species of animal. For example, in the temperate woodlands of south-eastern Australia, roadside strips of vegetation supported 69% of ant species and 64% of beetle species that were present in large patches of adjacent habitat (Major *et al.* 1999c). Similarly, between 74% and 88% of the avifaunal species occurring in the highly fragmented woodlands of the wheatbelt district of Western Australia were observed in roadside strips (Arnold and Weeldenburg 1990; Cale 1990; Lynch and Saunders 1991). In addition, between 22% and 27% of the bird species recorded were detected only once or twice (Cale 1990; Lynch and Saunders 1991). Lynch and Saunders (1991) found that the occurrence of bird species occurring in roadside verges was correlated with their tendency to occur at
the margins (as opposed to the interior) of large patches. They (Lynch and Saunders 1991) concluded that small-bodied birds and those reliant on native vegetation for all their nesting, food and shelter requirements were less common in linear remnants. In contrast, species that utilised cleared agricultural land for foraging and woodland mainly for nesting and roosting were more commonly detected in the linear strips.

At Euroa, the linear remnants supported a similarly rich and abundant arboreal marsupial fauna to the non-linear remnants nearby (Chapter 2). Therefore, the linear remnants, in comparison with the largest remaining patches of continuous habitat nearby, do not appear to be 'sink' habitats that are only capable of supporting a depauperate community of arboreal marsupials (Pulliam 1988). Similar results have been found in some of the studies that have compared species richness or overall abundance of fauna between linear and non-linear habitats (Bentley and Catterall 1997; de Lima and Gascon 1999; Major et al. 1999c).

Population density is an estimate of the number of individuals per unit area and is directly influenced by the relative rates of immigration, emigration, natality and mortality (Krebs 1999). The ecological carrying capacity of an area or specific patch of habitat is the natural limit of a population set by the availability of resources (Caughley and Sinclair 1994) which influences population density. The maintenance of high density or large populations is important because such populations are more resilient to the vagaries of stochastic events that may cause the population decline or extinction (Shafer 1981; Caughley 1994). At Euroa, the density of the population of *P. norfolcensis* was at least equal to the maximum recorded for the species anywhere else in Australia (Chapter 4). Similarly, the density of *T. vulpecula* in roadside habitat at Euroa was up to twice that recorded in continuous tracts of forest (Murphy 1997). However, assessing habitat suitability based on estimates of abundance or density may be misleading (Van Horne 1983) and additional biological and ecological studies are required.

The size and shape of habitat patches has been shown to influence aspects of the ecology, behaviour or population dynamics of various species (van Schagen *et al*. 1992; Bennett *et al*. 1994a; Lindenmayer *et al*. 1994; Collins and Barrett 1997;
Downes et al. 1997a; Downes et al. 1997b; Major et al. 1999a). For example, Downes et al. (1997a, b) working in south-eastern Australia, found that female Bush Rats *Rattus fuscipes* and male and female *A. stuartii* had lower body weights in strips of forest than in large patches of continuous forest. In Canada, transient and resident Eastern Chipmunks *Tamias striatus* captured in fencerows responded to different landscape and habitat variables (Bennett et al. 1994a). In the temperate woodlands of eastern Australia, the density of male Red-capped Robins *Petroica goodenovii* was significantly lower and the proportion of yearling males significantly higher in linear than non-linear remnants (Major et al. 1999a).

At Euroa, detailed studies of the ecology of *P. norfolcensis* (Chapters 4) revealed that the linear habitats supported resident, self-sustaining populations. Sex ratios did not differ significantly from parity, and the rates of reproduction, recruitment and mortality were similar to those recorded from populations in continuous habitats. Consequently, the age-structure of the population was stable, indicating that sufficient resources were consistently available over time to allow the development of similarly structured age groups.

Home range size of *P. norfolcensis* (Chapter 5) was small, indicating that sufficient resources were available. Furthermore, it appears that the linear remnants themselves provided most of the gliders' requirements, as the home ranges of most gliders were centered on the linear strips, resulting in elongated, narrow home ranges. Perhaps as an adaptation to long home ranges, gliders nested in hollow-bearing trees that were distributed throughout a large proportion of their ranges, thus reducing the need to return to a central nest site.

**IMPORTANT LANDSCAPE AND HABITAT FEATURES**

The results of this study clearly indicate that linear remnants at Euroa provide high quality habitat for a number of species of arboreal marsupial. Quality of the habitat within a linear strip will influence its suitability as habitat or movement corridor and hence may modify metapopulation persistence by influencing rates of
extinction and recolonisation (Henein and Merriam 1990). At Euroa, there appears to be a number of environmental factors that influence the quality of the habitat. These include the high density of large diameter trees, the spatial arrangement of the habitat, the landscape position on soils with high nutrient levels and the abundance of an Acacia shrub midstorey. These factors act to provide sufficient resources to sustain populations of arboreal marsupials.

**Large diameter trees**

Large trees are important components of forests and woodlands (Ambrose 1982; Dickman 1991; Scotts 1991; Bennett et al. 1994b; Gibbons and Lindenmayer 1997) because they provide a range of resources for animals. Tree hollows are required by arboreal marsupials for shelter and raising young (Gibbons and Lindenmayer 1997), and the abundance and diversity of hollows generally increases with tree diameter (Mackowski 1984; Bennett et al. 1994b; Soderquist 1999). Large trees have a relatively larger surface area and a greater diversity of microhabitats for foraging which may provide more efficient and higher quality foraging opportunities for animals than smaller trees (Recher 1991). Moreover, large trees probably support a richer and more abundant invertebrate community than smaller trees because they typically contain more decorticating bark and dead wood than small trees (Recher 1991; Hooper 1996). Large trees supply logs and fallen branches in a greater range of sizes and stages of decay than do smaller trees, and these provide habitat for ground-dwelling species (Williams and Faunt 1996). Finally, large trees may flower significantly more than smaller trees (Wilson and Bennett 1999), and thus supply a greater and more reliable source of nectar and pollen.

Large diameter trees and trees with hollows were identified as important habitat components for various species of arboreal marsupial throughout this study. For example, the frequency of captures of *T. vulpecula* was significantly correlated with the number of hollow-bearing trees (Table 3.9). Large trees (> 70 cm DBH) were preferentially selected as den trees by *P. norfolcensis* (Chapter 6).
Furthermore, _P. norfolcensis_ preferentially selected large trees for foraging, moving and social behaviour (Holland 1998).

Not only are large trees important _per se_, but their density may also influence habitat quality (Smith and Lindenmayer 1988; Pasinelli 2000). The occupation of multiple den trees by individuals over time appears to be a characteristic trait of many species of arboreal marsupial (Kehl and Borsboom 1984; Lindenmayer _et al._ 1996b; van der Ree and Bennett 1999; Jackson 2000a). At Euroa, an individual of _P. norfolcensis_ occupied at least 15 den trees over three seasons, and a social group of four gliders occupied a combined total of 16 den trees over 40 tracking days in summer 1997 - 1998 (Chapter 6). These results highlight the necessity of adequate densities of large trees to support viable populations and assemblages of hollow-dependent species.

The linear woodland remnants at Euroa contain a high density of large trees (approximately 23 ha\(^{-1}\), Chapter 3) – an order of magnitude greater than that found in the intensively harvested box-ironbark forests of central Victoria (ECC 1997; NRE 1998). Consequently, the abundance of large trees and suitable hollows that currently exist in the Euroa area is probably a major factor contributing to the high quality habitat for arboreal marsupials.

**Understorey characteristics**

A major determinant of the composition and richness of vertebrate communities in _Eucalyptus_ forests and woodlands are the characteristics of the mid- and understories (Recher 1991; Woinarski _et al._ 1997). Nectar, pollen, foliage and exudates from a variety of shrub species, mostly from within the genera _Acacia_ and _Banksia_, have been reported in the diet of many species of arboreal and scansorial marsupial (Smith 1982; Smith 1984a; Statham 1984; Turner 1984; Menkhorst and Collier 1987; Howard 1989; Scarff _et al._ 1998). A well-developed litter and shrub layer may also be critical for species that spend time foraging at ground-level, by providing foraging substrates and shelter (Dickman 1991).
Furthermore, leaf-litter and logs provide habitat for ground-dwelling invertebrates, as well as breeding areas for species of invertebrate that colonise trees as adults (Recher 1991), and which arboreal insectivores may consume.

It is likely that the resources utilised by a species in contiguous habitat will still be required within linear strips of habitat. For example, radiotracking studies of White-footed mice *Peromyscus leucopus* in Canada showed that transients (individuals translocated into alien fencerows) preferentially used structurally complex fencerows (Merriam and Lanoue 1990). This corresponded to some of the known resource requirements of the species occupying large woodland patches as well as potentially reduced risk of mortality (Merriam and Lanoue 1990). The size of populations of bank voles *Clethrionomys glareolus* resident in English hedgerows was found to be positively related with ground cover (Eldridge 1971; Kotzageorgis and Mason 1997), which may be related to resource requirements or predation. Studies of the movement and dispersal patterns of mice (*Mus musculus*) also indicated a preference for movement within structurally complex hedgerows (Lorenz and Barrett 1990). Within fencerows in North America, the density and diversity of bird nests increased with shrub abundance, reflecting protection from predators, a suitable substrate for nesting-building and increased foraging habitat (Shalaway 1985).

At Euroa, the abundance of *A. pycnantha*, *A. verticillata* and *A. implexa* were identified as significant explanatory variables influencing the abundance of *P. norfolcensis* and *T. vulpecula* (Tables 3.9 and 3.10). This may be a reflection of their dietary requirements as both species include *Acacia* in their diet (Statham 1984; Menkhorst and Collier 1987; Evans 1992; Holland 1998). Alternatively, the abundance of *Acacia* may be a surrogate measure of other parameters or processes (e.g. disturbance levels or grazing intensity), to which arboreal marsupials are responding. This is evidenced by the high correlation between grazing intensity and the abundance of *A. pycnantha* (Chapter 3). In addition, the abundance of *Acacia* may contribute to forest health through their nitrogen fixing ability (Adams and Attiwill 1984).
Position on productive soils

The species richness and abundance of birds, arboreal marsupials and invertebrates has been linked to foliar nutrient levels, which is in turn related to soil nutrient levels (Braithwaite et al. 1984; Kavanagh and Lambert 1990; Majer et al. 1990; Majer et al. 1992; Recher et al. 1996). In addition, sites with greater productivity (arising from availability of both moisture and nutrients) have an extended growing season and tend to support larger trees (Nix 1993; Woinarski et al. 1997; Robinson et al. in press).

The settlement of the temperate Eucalyptus woodlands for agriculture targeted areas of high soil fertility, which were then preferentially cleared (Hobbs and Saunders 1993; Prober and Thiele 1993; Muir et al. 1995; Robinson and Traill 1996). Consequently, vegetation communities naturally occurring on fertile soils are often severely depleted (e.g. Prober and Thiele 1995). The fertile alluvial soils of the Euroa floodplains (ECC 1997) were recognised for their suitability for agriculture and consequently, the woodland vegetation has been extensively cleared – from at least 76% tree cover in 1869 (estimated for the entire Northern Plains, Bennett and Ford 1997) to less than 5% today (Chapter 2). Most of the remnant woodland that survived in the Euroa area was spared from clearing because it occupied public land (e.g. road reserves, stream frontages) and not because it was on poor soils. Indeed, these remnants generally occur on high productivity soils. This is in contrast with much of the forests and woodlands of central Victoria which remain uncleared because they occupy poor and rocky soils (ECC 1997).

Spatial configuration of woodland habitat

The structural connectivity of a fragmented landscape is influenced by factors such as the size and number of gaps between linkages, the presence of multiple alternative pathways and the presence and abundance of nodes and stepping-
stones (Forman and Godron 1981; Forman and Godron 1986; Noss and Harris 1986; Bennett 1990b; Bennett 1999). There has been extensive discussion about the optimum arrangement of habitat required to achieve adequate levels of connectivity (Noss 1987; Simberloff and Cox 1987; Harris and Scheck 1991; Hobbs 1992; Hess 1994; Bennett 1999). There can be little debate, however, that 'populations, communities and natural ecological processes (are) more likely to be maintained in landscapes that comprise an interconnected system of habitats, than in landscapes where habitats occur as dispersed ecologically-isolated fragments' (Bennett 1999, p. 7).

An interconnected network of linear remnants
As individual units, linear remnants may enhance the movement of individuals if they connect between patches (Forman 1997; Bennett 1999), but their ability to provide habitat may be limited by the typically narrow and elongated shape. The arrangement of linear remnants into an interconnected network is likely to even further improve levels of landscape connectivity and enhance the conservation potential of the landscape (Forman and Godron 1981; Forman 1997; Bennett 1999). A network may be more effective in achieving conservation goals than single linear remnants because it can fulfill a number of important ecological functions that isolated remnants can not. Multiple alternative pathways for movement are available, potentially allowing the recolonisation of patches and thus enhancing the viability of a metapopulation (Fahrig and Merriam 1985). A network will be more resilient to perturbation and may continue to provide structural connectivity in the event of a catastrophe (Forman and Godron 1981; Noss 1993; Fleury and Brown 1997). The intersection of linear strips may also be important structural components of the network for flora and fauna (Forman 1997). Many networks, particularly in developed landscapes, are anthropogenic in origin (e.g. fencerows, hedgerows, road and trail networks) and therefore may traverse or include a variety of habitat types (Forman 1997), potentially providing a wider range of resources for animals.

The arrangement of linear remnants in the trapping grid area at Euroa provides a structurally continuous habitat for arboreal marsupials. This is likely to be
important for species' persistence in the landscape because it effectively increases
the size of populations and hence reduces their risk of extinction (Shafer 1981). The linear shape of habitat may limit movement patterns and opportunity for social interactions (Chapter 5), but the continuous interconnected arrangement of the habitat increases the likelihood that gene flow across the landscape can occur. Preliminary results from further work at Euroa (van der Ree and Taylor, unpub. data) indicate that there were no major differences in allele frequency between individuals of *P. norfolcensis* occurring at each end of the trapping grid (ca. four to six km), suggesting that at this spatial scale, interchange of genetic material is uninhibited. The arrangement of the linear remnants as a network increases the likelihood that individuals will find a suitable pathway for dispersal to new areas. This is an important consideration because several studies have highlighted the barrier effect of discontinuities in linear habitats or corridors (Andreassen *et al.* 1996b; Kotzageorgis and Mason 1997; Bright 1998).

In large tracts of contiguous habitat, adjacent territories of groups or individuals potentially abut or overlap at many locations (Covich 1976). Within the straight linear strips at Euroa, the potential for interaction between adjacent social groups of *P. norfolcensis* is greatly reduced and is limited to each end of the territory or home range (Chapter 5). Intersections of two or more wooded linear strips appear to be important locations because they provide the only opportunity for three or more social groups to interact whilst maintaining normal home ranges or territories. Moreover, there was a greater capture rate of *P. norfolcensis* in close proximity to intersections (Chapter 3), suggesting that this area was not dominated by an individual animal or social group, but rather was occupied by a number of individuals. In landscapes dominated by linear habitats, intersections may be important areas for gene flow and dispersal. If sufficiently large to support a social group, paddock clumps or nodes of trees adjacent to linear remnants may also fulfill the same function.

Intersections may possess ecological characteristics that differ from those in the adjacent linear strips (Forman 1997). This has been termed an 'intersection effect'. Species richness of birds and some plants has been found to be greater at an intersection than further away (Baudry 1984; Lack 1988; Riffell and Gutzwiller
1996). For other species, intersections may provide access to additional foraging habitat (Robinson et al. in press). The intersection effect is generally considered to be a positive influence because it may reduce edge effects; for example by creating a mesic microclimate more typical of 'interior' conditions (Forman 1997). However, it appears that at Euroa, the quality of the habitat at intersections was lower than within adjacent straight sections. Because of road maintenance activities, linear remnants within 100 m of an intersection were more likely to contain fewer large trees and a lower basal area of eucalypts (Chapter 5), presumably reducing habitat quality. This factor, as well as increased population densities, may also account for the significantly larger home ranges of P. norfolcensis at intersections than in straight sections (Chapter 5).

Paddock clumps
Fragments of natural vegetation, planted woodlots and other small patches of habitat are common components of agricultural landscapes around the world, including Australia (Saunders et al. 1993; Barrett et al. 1994; Prober and Thiele 1995; Law and Dickman 1998), United Kingdom (Helliwell 1976; Fitzgibbon 1993; Usher et al. 1993), continental Europe (Verboom and van Apeldoorn 1990; van Apeldoorn et al. 1994; Wauters et al. 1994) and North America (Wegner and Merriam 1979; Weddell 1991). In many intensively managed landscapes, opportunities to conserve and manage large reserves for conservation no longer exist, hence raising the value and relative importance of small patches. Patches may provide habitat for resident animals, or assist in the provision of connectivity across the landscape by acting as 'stepping stones'. In doing so, fragments may offer an alternative route to the linear remnants, highlighting the concept that corridors are not the only way to achieve connectivity across landscapes (Bennett 1999).

In the Euroa floodplains, patches of woodland greater than 1 ha in size accounted for just 17% of tree cover (Chapter 2). In addition to these woodland patches, single trees and paddock clumps (typically < 0.5 ha in size) were widespread across the landscape. Radiotelemetry studies (Chapters 5 and 6) revealed that gliders utilise the entire woodland mosaic for foraging and denning. All
woodland occurring within the otherwise-cleared agricultural matrix, regardless of tree health or patch size, was utilised by *P. norfolcensis* if it could be reached by gliding. However, these clumps of woodland were of insufficient size to support resident populations because the majority of radio-locations of most radiotracked individuals occurred from within the linear remnants (Chapter 5). Nonetheless, these small patches of woodland appear to be important for *P. norfolcensis* because they provide supplementary habitat and potentially connectivity across the landscape.

Connectivity with other habitat is likely to be a major influence on recolonisation and extinction rates in fragments by enabling new individuals to reach and supplement otherwise isolated populations (Fahrig and Merriam 1985). For example, many studies have found that species richness or abundance in a patch is positively related to proximity to other patches of habitat and the number of 'corridors' connected to it (Verboom and van Apeldoorn 1990; Weddell 1991; Usher *et al.* 1993; van Apeldoorn *et al.* 1994). The species richness, turnover and population size of small passerines in small woodland fragments in cleared agricultural land in south-western Australia was negatively related with increasing distance from the nearest vegetated roadside (Fortin and Arnold 1997). Therefore, patches of woodland may act as stepping stones provided the gap-size does not exceed a critical distance (Desrochers and Hannon 1997; Bright 1998; Grubb and Doherty 1999).

*Edge effects and width*

Width of a linear strip may influence its suitability as habitat or as a movement corridor in a number of ways (Forman 1997; Bennett 1999). First, the total area of available habitat for a given length is directly proportional to its width. A wider strip, therefore, not only provides more habitat *per se*, but it may also include a wider variety of habitat types by sampling a larger area of land. Consequently, wider strips are more likely to support greater species richness and more viable populations because of their larger population size (Shalaway 1985; Lynch 1987; Leach and Recher 1993; Laurance and Laurance 1999). At Euroa, the abundance of *P. norfolcensis*, *T. vulpecula* and all arboreal marsupials
combined, as revealed by trapping, was significantly related to canopy width (Tables 3.9 and 3.10). This was most likely due to a greater abundance of animals in the wider habitat, rather than an artifact of trap density because there was no significant difference in the capture rates of individual animals in strips of different width (Chapter 3).

Second, the amount of core area remaining less-affected by edge effects is increased in wider strips (Laurance 1991b; Paton 1994; Collinge 1996; Lidicker 1999). Animals may respond to structural or floristic changes in the vegetation at edges (Cale and Hobbs 1991; Beer and Fox 1997; Hansson 2000), or to altered microclimate (Kapos 1989; Turton and Freiburger 1997), or increased soil nutrient levels (Cale and Hobbs 1991; McIntyre and Lavorel 1994; Majer et al. 2000) that occur at the edge of a remnant because of exposure to the adjacent matrix (Saunders et al. 1991). Certain species of arboreal marsupial may benefit because food resources may increase due to proximity of the matrix. For example, the abundance and growth rates of leaf-eating invertebrates (Coleopterans) may be elevated in woodlands in close proximity to pasture (e.g. edges of large patches or small or narrow strips (Landsberg and Wylie 1983; Landsberg et al. 1990). *P. norfolcensis*, *P. breviceps* and *P. tapoatafa* may be particularly advantaged because Coleopterans form a major component of their diet (Smith 1982; Menkhorst and Collier 1987; Scarff et al. 1998).

Finally, animals may perceive wider habitat not as a linear strip, but rather as a 'patch' shaped habitat, thus allowing animals to form foraging territories that are more optimal in shape (Covich 1976; Pyke et al. 1977; Recher et al. 1987). This did not actually occur for *P. norfolcensis* at Euroa because the linear remnants were either 20 or 40 m in width.

The optimum width for linear strips that are designed to act as movement corridors remains open to debate (Harris and Scheck 1991; Soulé and Gilpin 1991; Beier and Loe 1992; La Polla and Barrett 1993; Wilson and Lindenmayer 1995; Andreassen et al. 1996a). It has been suggested that the optimum width may be best determined by measuring the minimum width of the home range of the target species in continuous habitat (Harrison 1992). This approach, however,
does not consider the ability of individuals to adapt their spatial organisation to the available habitat. For example, average home range width of *P. norfolcensis* at Euroa was the width of the linear remnant - 20 to 40 m wide and up to 2580 m in length (Chapter 5). Similarly, the home ranges of four species of bird radiotracked in roadside strips in south-western Australia were as wide as the strips of available habitat (10 - 50 m) and approximately 1000m in length (Lynch *et al.* 1995).

Computer simulations and experimental studies indicate that the design (i.e. width, length, shape) of linear strips that act as habitat may differ from those designed to act solely as movement corridors (Soulé and Gilpin 1991; La Polla and Barrett 1993; Ruefenacht and Knight 1995; Andreassen *et al.* 1996a). Wider or convoluted corridors may impede linear progress because the opportunity for cross-directional movement or 'getting lost' is greater (Soulé and Gilpin 1991; Andreassen *et al.* 1996a). In addition, the rate of entry into narrow corridors may be lowered because dispersing animals are more likely to miss the entrance (Andreassen *et al.* 1996a). However, a study of dispersing Deermice *Peromyscus maniculatus* found that habitat variables (e.g. tree density, log density) had a greater influence on the number of passes in the corridor than corridor width and size of gaps (Ruefenacht and Knight 1995).

**IMPLICATIONS FOR MANAGEMENT AND CONSERVATION**

This study demonstrates that within highly cleared and fragmented landscapes, linear strips of wooded vegetation, especially if comprising old-growth forest, can provide high quality habitat for some species of woodland dependent fauna. Furthermore, it highlights the need to recognise that the conservation network consists of the entire woodland mosaic, including linear strips, small patches and isolated trees. At Euroa, linear strips provided core habitat for resident animals while other woodland configurations (small patches and single trees) provided additional resources for foraging, shelter or movement. The value of the woodland fragments for conservation is heightened because such a small
percentage of the original extent remains. Moreover, if small patches have been managed appropriately, they can contain some of the most-intact examples of pre-European vegetation communities that remain (Prober and Thiele 1995).

Single fragments of habitat are unlikely to support viable populations of all extant species in perpetuity (Saunders 1989; Recher and Serventy 1991; Hobbs 1993a; Hobbs et al. 1993b; Goldney et al. 1995; Law and Dickman 1998; Bennett 1999). Therefore, a coordinated conservation system must be designed at the landscape or catchment scale that incorporates patches of varying size and shape across a range of vegetation communities (Barrett et al. 1994; Bennett et al. 1998; Thiele and Prober 1999). The reserve system must also recognise that in production landscapes, opportunities for reserving large areas of natural habitat on publicly owned land for conservation purposes are scant. Consequently, habitat occurring in production landscapes, including privately owned land must be included in the conservation network and managed appropriately (Bennett et al. 1995; Hale and Lamb 1997; Thiele and Prober 1999). This will also recognise that much of the within-remnant functioning in fragmented landscapes is driven by processes occurring within the matrix (Laurance 1991a; Loney and Hobbs 1991; Saunders et al. 1991).

This approach views the whole of the landscape as the biological resource, not just the individual patches (Barrett et al. 1994; Thiele and Prober 1999). This is essential because corridors or linear strips of vegetation, in the absence of larger patches, will never be sufficient to conserve all biodiversity (Soulé and Gilpin 1991; Hobbs 1993a; Goldney et al. 1995; Harrison and Bruna 1999). For example, Major et al. (1999a) cautioned that excessive attention on wildlife corridors at the expense of large areas within the woodlands of New South Wales may see the decline of certain species, such as *P. goodenovii*. Conversely, Barrett et al. (1994) who also worked in woodlands of New South Wales, suggested that focussing management on just the very large patches, at the expense of managing all remnant vegetation across the landscape, may see the extinction of bird species that are at present considered secure.
The persistence of species in the landscape at present does not mean that populations are viable in the long-term. Numerous species have disappeared from even relatively large conservation reserves in the wheatbelt of Western Australia (Saunders 1989; Hobbs et al. 1993a). For example, *T. vulpecula*, a common species at Euroa, disappeared over a 10-year period from a 1030 ha woodland reserve in south-western Australia (Hobbs et al. 1993a). Consequently, remnant vegetation requires management to maintain or enhance habitat quality and increase extent (Loney and Hobbs 1991). Passive or benign management (i.e. 'do nothing' approach) will ultimately lead to further loss and degradation of habitats, ultimately resulting in the decline and extinction of elements of the biota.

At Euroa, any reduction in habitat quality, area of habitat, or level of connectivity is likely to be detrimental for the conservation of woodland dependent species. The first step in ensuring that the conservation potential of the landscape does not decline is to protect all remnants that currently exist, from further habitat clearing, stock grazing and other threatening processes. Habitat restoration and revegetation are complementary to protection and should focus on enlarging patch size, restoring connections across the landscape and widening linear strips.

Overgrazing by domestic stock and introduced herbivores is a major threat to the persistence of woodland communities (Robinson and Traill 1996). Overgrazing can change the species composition of woodlands by preferentially consuming more-palatable species (Lunt 1990; Sivertsen 1993; McIntyre and Lavorel 1994; Prober and Thiele 1995; Yates et al. 2000). Grazing may also affect the long-term persistence of woodlands by preventing regeneration of the overstorey, ultimately resulting in a senescent landscape (Abensperg-Traun and Smith 1993; Bennett et al. 1994b). As grazing is typically widespread throughout most agricultural landscapes (Wilson 1990) (e.g. 89% of 1200 woodland remnants surveyed in New South Wales showed signs of grazing, Sivertsen 1993), this lack of regeneration is likely to occur over large areas. Moreover, grazing may also affect ecological processes such as cycling of organic matter and nutrients and erosion by altering the structure of soil and leaf litter, soil temperature, and moisture levels in soil and leaf litter (Bromham et al. 1999; Yates et al. 2000). Specifically, grazing in
woodland remnants at Euroa, especially those with relatively intact understories, should be phased out and remnants protected from further grazing by fencing.

The extent of clearing of temperate woodlands since European settlement has been massive, and in some regions almost 95% has been removed (Robinson and Traill 1996). However, rates of clearing in some districts are still high, especially in western New South Wales and Queensland (Sivertsen 1993; DEST 1995). The rate of habitat loss in many already cleared landscapes has slowed by virtue of the small amount that remains, but incremental loss still occurs. However, the incremental loss of small amounts of habitat may have consequences beyond that predicted from the size of the patch alone. Bennett and Ford (1997) suggested that the loss of habitat from an already highly cleared landscape will result in the extinction of more species of bird than if the same amount of habitat were cleared from a landscape containing more tree cover. Therefore, the loss of very small patches or even single trees in landscapes like that of Euroa will result in a reduction in foraging and denning habitat, potentially decreasing population size.

At a landscape scale, 10% tree cover has been recommended as a minimum first step to achieving conservation and maintain productive agricultural systems in the Northern Plains region of Victoria (Bennett and Ford 1997). In order to achieve this, the existing habitat mosaic must be retained and a large-scale restoration and revegetation effort is required across the entire temperate woodland zone (Robinson and Traill 1996). Restoration procedures will necessarily be site-specific but guiding principles are available (Hobbs and Yates 1997). Revegetation efforts must focus on consolidating existing remnants by increasing patch size, and in the case of linear remnants, increasing width and connectivity. If the spatial configuration of habitat is not sufficient to meet the needs of fauna, strategic linkages across the landscape (e.g. corridors, stepping stones) can be established. If patches are absent from the landscape, nodes along corridors and plantings at intersections are effective places to start.

The conservation of biota and maintenance of agricultural productivity in the wheat and sheep belt of temperate Australia is reliant on healthy, functioning ecosystems. At present, the Euroa floodplains support a diverse and abundant
assemblage of arboreal marsupials, including a number of rare and threatened species. However, the future potential of the district for conservation and sustainable agriculture is not secure and urgent action is required to counter the deleterious effects of habitat clearing and land degradation (Robinson and Traill 1996). The current and potential value of remnant vegetation for conservation and sustainable agriculture will only be realised with appropriate management by land managers and sufficient financial support and incentive from government. Significant efforts by landholders in many districts is evident (e.g. Orsini et al. 1995; Williams 1995) and highlights even further that conservation and agriculture can indeed be compatible.
REFERENCES


ash forest in the central highlands of Victoria, southeastern Australia. 


APPENDICES

BARBED WIRE FENCING AS A HAZARD FOR WILDLIFE


HOME RANGE USE BY THE BRUSH-TAILED PHASCOGALE
PHASCOGALE TAPOATAFA (MARSUPIALIA) IN HIGH-QUALITY,
SPATIALLY LIMITED HABITAT

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