

# **Ecological Value of Riparian Zones to Birds in Forest Landscapes**

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**DEAKIN UNIVERSITY**  
**CANDIDATE DECLARATION**



I certify that the thesis entitled

***Ecological Value of Riparian Zones to Birds in Forest Landscapes***

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## Preface

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The thesis chapters have been designed such that each can be readily modified as manuscripts for publication. As a result, the thesis is designed such that each chapter is self-contained. This has resulted in some repetition between chapters, however this is minimised where possible, particularly in methods sections, by referring to earlier descriptions and findings where appropriate. References for all chapters have been compiled and listed at the end of the thesis.

One chapter of this thesis has been published with Andrew Bennett as a co-author.

The chapter published is:

### Chapter 2

Palmer, G.C. and Bennett, A.F. (2006). Riparian zones provide for distinct bird assemblages in forest mosaics of south-east Australia. *Biological Conservation* **130**, 447-457.

I have authored a further paper which encompassed data gathered for this study:

Palmer, G.C. (2005). Habitat use and distribution of the Beautiful Firetail *Stagonopleura bella* in foothill forests of the Victorian Highlands, Australia. *Emu* **105**, 233-239.

A copy of this paper is provided in the Appendix of this thesis.

### Research Permit

Permission was granted to conduct scientific research in Kinglake National Park and Bunyip State Park pursuant to the provisions of the *National Parks Act* 1975, under permit number 10001565.

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# Contents

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<b>Preface.....</b>	<b>i</b>
<b>Acknowledgements.....</b>	<b>ii</b>
<b>Contents .....</b>	<b>iv</b>
<b>List of tables .....</b>	<b>xi</b>
<b>List of figures.....</b>	<b>xiv</b>
<b>Abstract .....</b>	<b>xviii</b>
<b>1 General introduction.....</b>	<b>1</b>
1.1 Riparian zones in the landscape.....	2
1.2 Riparian zones – locally rich habitats for birds .....	3
1.3 What features of riparian zones are attractive to birds?.....	5
1.4 Landscape factors that influence the importance of riparian habitats to birds...	7
1.5 Riparian zones as corridors .....	9
1.6 The role of riparian zones in the conservation of birds.....	10
1.7 Research needs .....	12
1.8 Aims and structure of this thesis .....	13
1.8.1 Aims and scope .....	13
1.8.2 Study area .....	13
1.8.3 Study sites .....	18

1.8.4	Thesis outline .....	22
<b>2</b>	<b>Riparian zones provide for distinct bird assemblages in forest mosaics of south-east Australia.....</b>	<b>25</b>
2.1	Introduction.....	26
2.2	Methods.....	27
2.2.1	Study area .....	27
2.2.2	Study sites.....	28
2.2.3	Habitat characteristics.....	29
2.2.4	Bird survey.....	30
2.2.5	Data analysis.....	31
2.3	Results.....	32
2.3.1	Habitat characteristics.....	32
2.3.2	Bird assemblages.....	33
2.4	Discussion .....	43
2.4.1	Landscape pattern and bird assemblages.....	43
2.4.2	Habitat characteristics and bird assemblages .....	46
2.4.3	Implications for conservation .....	47
<b>3</b>	<b>Seasonal patterns of variation in the structure of riparian and non-riparian bird assemblages in a forest mosaic.....</b>	<b>49</b>
3.1	Introduction.....	50
3.2	Methods.....	52

3.2.1	Study area .....	52
3.2.2	Study sites .....	52
3.2.3	Bird surveys.....	52
3.2.4	Movement groups.....	53
3.2.5	Dietary groups .....	53
3.2.6	Data analysis .....	54
3.3	Results.....	56
3.3.1	Bird assemblages.....	56
3.3.2	Seasonal changes in the structure of bird assemblages.....	62
3.3.3	Seasonal changes in the species composition of bird assemblages .....	65
3.3.4	Seasonal variation in movement groups.....	69
3.3.5	Seasonal variation in dietary groups.....	74
3.3.6	Seasonal variation in individual species .....	76
3.4	Discussion .....	78
3.4.1	Riparian zones and the structure of bird assemblages through time.....	78
3.4.2	Riparian zones and the composition of bird assemblages through time .	80
3.4.3	Implications for conservation .....	83
<b>4</b>	<b>Structure and ecological characteristics of bird assemblages: differences between riparian and non-riparian habitats in eucalypt forest .....</b>	<b>85</b>
4.1	Introduction.....	86
4.2	Methods.....	87



4.2.1	Study area .....	87
4.2.2	Study sites .....	87
4.2.3	Bird surveys.....	87
4.2.4	Foraging observations.....	87
4.2.5	Foraging groups .....	88
4.2.6	Nest type .....	89
4.2.7	Body mass.....	90
4.2.8	Data analysis.....	90
4.3	Results.....	92
4.3.1	Bird assemblages.....	92
4.3.2	Foraging groups .....	97
4.3.3	Comparison of foraging groups between riparian and non-riparian sites	98
4.3.3.1	Number of foraging groups .....	98
4.3.3.2	Richness within foraging groups .....	100
4.3.3.3	Relative abundance of birds in foraging groups .....	100
4.3.4	Comparison of nest-type groups between riparian and non-riparian sites .....	101
4.3.4.1	Number of nest-type groups.....	101
4.3.4.2	Richness of species within nest-type groups.....	102
4.3.4.3	Abundance of birds within nest-type groups.....	103

4.3.5	Comparison of body mass groups between riparian and non-riparian sites .....	104
4.3.5.1	Number of body mass groups .....	105
4.3.5.2	Richness of species within body mass groups .....	106
4.3.5.3	Abundance of birds within body mass groups .....	106
4.3.6	Are there differences in foraging patterns between riparian and non-riparian sites? .....	107
4.3.7	Do foraging patterns of species differ between riparian and non-riparian sites? .....	111
4.4	Discussion .....	116
4.4.1	A greater number of ecological groups are represented in riparian assemblages. ....	117
4.4.2	Species richness within ecological groups is greater in riparian assemblages .....	120
4.4.3	Ecological mechanisms promoting richness in riparian assemblages ...	123
<b>5</b>	<b>Resource dynamics in riparian and non-riparian habitats and the relationship to bird assemblages in a eucalypt forest landscape .....</b>	<b>125</b>
5.1	Introduction .....	126
5.2	Methods .....	128
5.2.1	Study area .....	128
5.2.2	Study sites .....	128
5.2.3	Bird surveys .....	128

5.2.4	Resource availability and dynamics .....	128
5.2.4.1	Food and foraging resources .....	128
5.2.4.1.1	Tree flowering .....	129
5.2.4.1.2	Bark shed .....	129
5.2.4.1.3	Mistletoes .....	130
5.2.4.1.4	Shrub flowering .....	130
5.2.4.2	Shelter and nest site resources .....	130
5.2.4.2.1	Tree hollows .....	130
5.2.5	Tree productivity .....	131
5.2.6	Data analysis .....	131
5.3	Results .....	133
5.3.1	Tree flowering .....	133
5.3.2	Shrub flowering .....	138
5.3.3	Bark shed .....	142
5.3.4	Mistletoes .....	147
5.3.5	Tree hollows .....	147
5.3.6	Productivity trends in riparian and non-riparian habitats .....	153
5.4	Discussion .....	155
5.4.1	Comparison of resource availability between riparian and non-riparian sites .....	155
5.4.2	Temporal reliability of resources .....	157

5.4.3	Bird patterns and community structure .....	159
5.4.4	Implications for conservation .....	160
<b>6</b>	<b>Synthesis of results and implications for conservation .....</b>	<b>162</b>
6.1	Overview .....	163
6.1.1	Structure of riparian and non-riparian bird assemblages .....	166
6.1.2	Seasonal dynamics in riparian and non-riparian bird assemblages.....	167
6.1.3	Ecological characteristics of bird assemblages .....	169
6.1.4	Resource availability and dynamics between riparian and non-riparian habitats .....	171
6.2	Conservation value of riparian zones and implications for management in forest landscapes .....	172
	<b>References .....</b>	<b>177</b>
	<b>Appendix .....</b>	<b>197</b>

## List of tables

---

### Chapter 2

Table 2-1	Description of habitat variables measured at riparian and non-riparian sites in the Victorian Highlands .....	30
Table 2-2	Habitat variables characteristic of riparian and non-riparian habitats in the Victorian Highlands ..	34
Table 2-3	The relative abundance of bird species (individuals ha <sup>-1</sup> ) recorded during point counts at riparian and non-riparian sites in the Victorian Highlands .....	36

### Chapter 3

Table 3-1	Relative abundance (individuals ha <sup>-1</sup> ) of birds occurring in riparian (R) and non-riparian (NR) habitats (n = 30), each season between July 2001 and December 2002.....	57
Table 3-2	Repeated measures ANOVA comparing the mean species richness per survey of bird assemblages at riparian and non-riparian habitats among seasons... ..	63
Table 3-3	Repeated measures ANOVA comparing the mean abundance of birds occurring between riparian and non-riparian habitats among seasons. ....	64
Table 3-4	Summary of repeated measures ANOVA comparing seasonal differences in the proportion of resident birds within riparian and non-riparian bird assemblages. ....	69
Table 3-5	Bird movement groups association with riparian and non-riparian habitats between seasons.....	71
Table 3-6	Bird diet groups association with riparian and non-riparian habitats between seasons..	71

Table 3-7	Bird species that had the greatest influence on dissimilarities (SIMPER) between riparian and non-riparian assemblages, July 2001 to December 2002...	77
-----------	---	----

## Chapter 4

Table 4-1	Foraging group definitions for bird assemblages in the Victorian Highlands, south-east Australia. ....	89
Table 4-2	Foraging group, nest-type classification and body mass of bird species (n = 88) recorded at riparian (Rip) and non-riparian (NR) sites during the field survey. ....	93
Table 4-3	Species richness and relative abundance of birds (individuals ha <sup>-1</sup> ) for each foraging group occurring in riparian and non-riparian assemblages. ....	101
Table 4-4	Species richness and relative abundance of birds (individuals ha <sup>-1</sup> ) for each nest-type group occurring in riparian and non-riparian assemblages. ....	103
Table 4-5	Species richness and relative abundance of body mass groups occurring in riparian and non-riparian bird assemblages. ....	105
Table 4-6	Comparison of the proportional use (% of observations) of structural features of habitat in riparian (Rip) and non-riparian (NR) sites for six commonly recorded birds. ....	112
Table 4-7	Comparison of the proportional use (% of observations) of foraging substrates in riparian (Rip) and non-riparian (NR) sites for six commonly recorded birds. ....	113
Table 4-8	Comparison of the proportional height of foraging attempts in riparian (Rip) and non-riparian (NR) sites for six commonly recorded birds. ....	114

## Chapter 5

Table 5-1	Timing and distribution of flowering events observed for tree species in riparian and non-riparian habitats. ....	134
-----------	---	-----

Table 5-2	Results of repeated measures ANOVA comparing eucalypt flowering intensity between riparian and non-riparian sites (site type) over six sampling periods from February 2002 to December 2002.....	136
Table 5-3	Results of repeated measures ANOVA used to compare shrub flowering intensity between riparian and non-riparian sites (site type) over five sampling periods from April 2002 to December 2002.....	138
Table 5-4	Results of repeated measures ANOVA comparing the amount of bark peel between riparian and non-riparian sites (site type) over six sampling periods from February 2002 to December 2002.....	143
Table 5-5	Results of repeated measures ANOVA comparing the amount of bark hang between riparian and non-riparian sites (site type) over six sampling periods from February 2002 to December 2002.....	145
Table 5-6	Distribution and abundance of tree hollows at riparian and non-riparian sites. ....	151
Table 5-7	Site type and sampling period differences in productivity of all eucalypts, and of Messmate <i>E. obliqua</i> and Narrow-leaved Peppermint <i>E. radiata</i> , showing <i>F</i> -values for a repeated measures ANOVA of site type (riparian or non-riparian) X sampling period (April, June, August, October, December).....	154

## Chapter 6

Table 6-1	Summary of objectives and key findings of study.....	164
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## List of figures

---

### Chapter 1

- Figure 1-1 Geographic position of forest areas surveyed in this study in the Victorian Highlands – Southern Fall (green) and – Northern Fall (purple) bioregions, south-east Australia..... 14
- Figure 1-2 Vegetation map of Bunyip State Park, showing location of paired study sites (01-20)..... 19
- Figure 1-3 Vegetation map of Kinglake National Park, showing location of paired study sites (21-25)..... 20
- Figure 1-4 Vegetation map of Marysville State Forest, showing location of paired study sites (26-30)..... 21

### Chapter 2

- Figure 2-1 Ordination of bird assemblages occurring at sites in the Victorian Highlands (stress = 0.1). ..... 42

### Chapter 3

- Figure 3-1 A generalised diagram of the large-scale movement patterns displayed by birds in eastern Australia (adapted from Griffioen and Clarke (2002)) that were used to classify species into large-scale movement groups. .... 54
- Figure 3-2 Mean values ( $\pm$  standard deviation) of species richness (species/visit) among riparian (■) and non-riparian sites (□) through time. .... 62
- Figure 3-3 Mean values ( $\pm$  standard deviation) of bird abundance (birds ha<sup>-1</sup>) among riparian (■) and non-riparian sites (□), winter 2001 to summer 2002..... 64
- Figure 3-4 Ordination of seasonal bird assemblages occurring at riparian (solid) and non-riparian sites (open) in the Victorian Highlands..... 66



Figure 3-5	Ordination of seasonal bird assemblages occurring at riparian (A) and non-riparian sites (B). .....	67
Figure 3-6	Similarity of bird assemblages in riparian (■) and non-riparian habitats (□) in the Victorian Highlands through time, July 2001 to December 2002. Based on Bray-Curtis similarity index. ....	68
Figure 3-7	Proportion of individuals in movement groups contributing to bird assemblages at riparian (a) and non-riparian (b) sites between seasons, winter 2001 to summer 2002. ....	73
Figure 3-8	Proportion of individuals in dietary groups contributing to bird assemblages at riparian (a) and non-riparian (b) sites between seasons, winter 2001 to summer 2002. ....	75

## Chapter 4

Figure 4-1	Ordination of species based on empirical data on structural features of habitats and substrates used during foraging attempts (stress = 0.19). ....	98
Figure 4-2	Number of riparian (black) and non-riparian sites (grey) at which representatives of foraging groups were recorded. ....	99
Figure 4-3	Number of riparian (black) and non-riparian sites (grey) at which representatives of nest-type groups were recorded. ....	102
Figure 4-4	Relative abundance of individuals within nest-type groups for riparian (black) and non-riparian (grey) bird assemblages. ....	104
Figure 4-5	Number of riparian (black) and non-riparian sites (grey) at which representatives of body mass groups were recorded. ....	106
Figure 4-6	Relative abundance of individuals in body mass groups for riparian (black) and non-riparian bird assemblages (grey). ....	107

Figure 4-7	Use of structural features of habitats (% of observations) by birds during foraging attempts in riparian (black) and non-riparian (grey) habitats in foothill eucalypt forest. ....	108
Figure 4-8	Use of substrates (% of observations) by birds during foraging attempts in riparian (black) and non-riparian (grey) habitats in foothill eucalypt forest.. ....	109
Figure 4-9	Proportional height of foraging attempts (% of observations) by birds in riparian (black) and non-riparian (grey) habitats in foothill eucalypt forest.. ....	110
Figure 4-10	Magnitude of difference in niche breadth between riparian and non-riparian sites for structural features of habitat, substrates and heights used by species. ....	116

## Chapter 5

Figure 5-1	Mean flowering intensity of eucalypt trees (all species) in riparian (black) and non-riparian (grey) habitats. ....	135
Figure 5-2	Number of nectarivores at riparian (black) and non-riparian sites (grey) and relationship to eucalypt flowering events.....	137
Figure 5-3	Flowering index of major shrub species at riparian and non-riparian sites. ....	139
Figure 5-4	Number of nectarivores at riparian (black) and non-riparian (grey) sites (n = 30) and the relationship to shrub flowering events in <i>Banksia</i> (□) and <i>Hakea</i> (x) at non-riparian sites. ....	140
Figure 5-5	Abundance of Red Wattlebird (top), Eastern Spinebill (middle) and Crescent Honeyeater (bottom) at riparian (■) and non-riparian sites (□) and flowering of <i>Banksia</i> (▲) at non-riparian sites.....	142
Figure 5-6	Timing and extent of bark peel at riparian (black) and non-riparian sites (grey). ....	142

Figure 5-7	Extent of hanging bark at riparian (black) and non-riparian sites (grey) through the annual cycle.....	144
Figure 5-8	Patterns of bark shed in <i>Symphyomyrtus</i> (■) and <i>Monocalyptus</i> (□) eucalypts through the annual cycle, for all sites pooled. A) bark peel index and, B) bark hang index.....	146
Figure 5-9	Proportion of trees containing hollows for tree size-classes in riparian (black) and non-riparian (grey) habitats.....	148
Figure 5-10	Proportion of trees containing small hollows (entrance <10 cm diameter) for tree size-classes in riparian (black) and non-riparian (grey) habitats... ..	149
Figure 5-11	Proportion of trees containing large hollows (>10 cm entrance diameter) for tree size-classes in riparian (black) and non-riparian (grey) habitats... ..	149
Figure 5-12	Relationship between the number of tree hollows and the total number of hollow-dependent birds at riparian (■) and non-riparian sites (□) during the breeding season.....	153
Figure 5-13	Productivity index scores for riparian (closed symbols; upwards, solid error bars = s.d.) and non-riparian habitats (open symbols; downwards, dashed error bars = s.d.) for all eucalypts (■), Messmate <i>E. obliqua</i> (●) and Narrow-leaved Peppermint <i>E. radiata</i> (▲) during 2002.....	154

## Abstract

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Riparian zones are a characteristic component of many landscapes throughout the world and increasingly are valued as key areas for biodiversity conservation. Their importance for bird communities has been well recognised in semi-arid environments and in modified landscapes where there is a marked contrast between riparian and adjacent non-riparian vegetation. The value of riparian zones in largely intact landscapes with continuous vegetation cover is less well understood. This research examined the importance of riparian habitats for avifauna conservation by investigating the ecological interactions contributing to the pattern of bird assemblages in riparian and adjacent non-riparian habitats. Specifically, the focus is on the bird assemblages of riparian zones and those of adjacent non-riparian vegetation types and the influence that associated differences in resource availabilities, habitat structure and conditions have on observed patterns.

This study was conducted in the foothill forests of the Victorian Highlands, south-east Australia. Mixed-species eucalypt (genus *Eucalyptus*) forests dominate the vegetation of this region. Site selection was based on the occurrence of suitable riparian habitat interspersed within extensive, relatively undisturbed (i.e. no recent timber harvesting or fire events) forest mosaics. A series of 30 paired riparian and non-riparian sites were established among six stream systems in three forest areas (Bunyip State Park, Kinglake National Park and Marysville State Forest). Riparian sites were positioned alongside the stream and the non-riparian partner site was positioned on a facing slope at a distance of approximately 750 m. Bird surveys were carried out during 29 visits to each site between July 2001 and December 2002.

Riparian sites were floristically distinct from non-riparian sites and had a more complex vegetation structure, including a mid-storey tree layer mostly absent from non-riparian sites, extensive fine litter and coarse woody debris, and dense ground-layer vegetation (e.g. sedges and ground ferns). The characteristic features of non-riparian habitats included a relatively dense canopy cover, a ground layer dominated by grasses and fine litter, and a high density of canopy-forming trees in the smaller size-classes.

Riparian zones supported a significantly greater species richness, abundance and

diversity of birds when compared to non-riparian habitats. The composition of bird assemblages differed significantly between riparian and non-riparian habitats, with riparian assemblages displaying a higher level of similarity among sites. The strongest contributors to observed dissimilarities between habitat types included species that occurred exclusively in either habitat type or species with large contrasts in abundance between habitat types. Much of the avifauna (36%) of the study area is composed of species that are common and widespread in south-east Australia (i.e. forest generalists). Riparian habitats were characterised by a suite of species more typical of wetter forest types in south-east Australia and many of these species had a restricted distribution in the forest mosaic. Some species (7%) occurred exclusively in riparian habitats (i.e. riparian selective species) while others (43%) were strongly linked to these habitats (i.e. riparian associated species). A smaller proportion of species occurred exclusively (2%) in non-riparian habitats (i.e. non-riparian selective species) or were strongly linked to these habitats (10%; i.e. non-riparian associated species).

To examine the seasonal dynamics of assemblages, the variation through time in species richness, abundance and composition was compared between riparian and non-riparian sites. Riparian assemblages supported greater richness and abundance, and displayed less variation in these parameters, than non-riparian assemblages at all times. The species composition of riparian assemblages was distinct from non-riparian assemblages throughout the annual cycle. An influx of seasonal migrants elevated species richness and abundance in the forest landscape during spring and summer. The large-scale movement pattern (e.g. coastal migrant, inland migrant) adopted by migrating species was associated with their preference for riparian or non-riparian habitats in the landscape. Species which migrate north-south along the east coast of mainland Australia (i.e. coastal migrants) used riparian zones disproportionately; eight of eleven species were riparian associated species. Species which migrate north-south through inland Australia (i.e. inland migrants) were mostly associated with non-riparian habitats. The significant differences in the dynamics of community structure between riparian and non-riparian assemblages shows that there is a disproportionate use of riparian zones across the landscape and that they provide higher quality habitat for birds throughout the annual cycle.

To examine the ecological mechanisms by which riparian assemblages are richer and

support more individual birds, the number of ecological groups (foraging, nest-type and body mass groups) represented, and the species richness of these groups, was compared between riparian and non-riparian assemblages. The structurally complex vegetation and distinctive habitat features (e.g. aquatic environments, damp sheltered litter) provided in the riparian zone, resulted in the consistent addition of ecological groups to riparian assemblages (e.g. sheltered ground – invertebrates foraging group) compared with non-riparian assemblages. Greater species richness was accommodated in most foraging, nest-type and body mass groups in riparian than non-riparian assemblages. Riparian zones facilitated greater richness within ecological groups by providing conditions (i.e. more types of resources and greater abundance of resources) that promoted ecological segregation between ecologically similar species. For a set of commonly observed species, significant differences in their use of structural features, substrates and heights were registered between riparian and non-riparian habitats.

The availability and dynamics of resources in riparian and non-riparian habitats were examined to determine if there is differential availability of particular resources, or in their temporal availability, throughout the annual cycle. Riparian zones supported more abundant and temporally reliable eucalypt flowering (i.e. nectar) than non-riparian habitats throughout the annual cycle. Riparian zones also supported an extensive loose bark resource (an important microhabitat for invertebrates) including more peeling bark and hanging bark throughout the year than at non-riparian sites. The productivity of eucalypts differed between habitat types, being higher in riparian zones at most times for all eucalypts combined, and for some species (e.g. Narrow-leaved Peppermint *Eucalyptus radiata*). Non-riparian habitats provided an abundant nectar resource (i.e. shrub flowering) at particular periods in the annual cycle. Birds showed clear relationships with the availability of specific food (i.e. nectar) and foraging resources (i.e. loose bark). The demonstration of a greater abundance of resources and higher primary productivity in riparian zones is consistent with the hypothesis that these linear strips that occupy only a small proportion of the landscape have a disproportionately high value for birds.

Riparian zones in continuous eucalypt forest provide high quality habitats that contribute to the diversity of habitats and resources available to birds in the forest

mosaic, with positive benefits for the landscape-level species pool. Despite riparian and non-riparian habitat supporting distinct assemblages of birds, strong linkages are maintained along the riparian-upslope gradient. Clearly, the maintenance of diverse and sustainable assemblages of birds in forest landscapes depends on complementary management of both riparian and non-riparian vegetation.

# 1 General introduction

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Typical view of the forest landscape in the Victorian Highlands, south-east Australia



## 1.1 Riparian zones in the landscape

Throughout recorded history, streams have been used by humans for purposes including water supply, transport and as a source of food and other resources. They have also long been appreciated for their aesthetic values. Intimately linked with streams is the riparian zone – those parts of the landscape adjacent to a waterway that extend from the water's edge to the upland boundary of periodic inundation. This zone typically supports plant species and/or life forms that differ from the surrounding non-riparian environment (Szaro 1980; Malanson 1993). Riparian zones are characterised by greater water availability and nutrient-rich soils, which provides for a greater structural and biological diversity than occurs in adjacent upland habitats, such as on slopes and ridges (Recher *et al.* 1991).

Riparian zones are prominent features in the landscape, being directly associated with the flow of water across the land surface. The riparian zone is generally viewed as a terrestrial component of the landscape and, along with streams and rivers, is commonly considered to be an element of the landscape mosaic. Recognition of the heterogeneity in the internal structure of rivers, including the riparian zone, has also lead to consideration of river systems as landscapes in their own right (Wiens 2002).

Riparian zones represent a place of active exchange between terrestrial and aquatic systems that varies in intensity, both temporally and spatially. This results in great heterogeneity in environmental conditions and diversity of habitats in a relatively confined area (Lachavanne 1997). While the natural boundaries of the riparian zone are defined more by valleys and hill slopes than by the stream alone (Forman 1995), the distinctiveness of the riparian zone often reflects a gradient in available moisture (Malanson 1993). In mesic regions, riparian vegetation more closely resembles the surrounding non-riparian vegetation because differences in moisture availability through the landscape are more subtle. In drier, semi-arid or arid regions, a sharp gradient in water availability away from the stream limits productivity and creates distinct boundaries.

Riparian zones form a hierarchical pattern of linear habitats imposed on the landscape, from small intermittent drainage lines to mid-order streams and large rivers (Bren 1995;

Forman 1995; Bennett 1999). In forested landscapes, riparian zones generally form natural corridors that vary greatly in width, habitat heterogeneity and distinctiveness from surrounding non-riparian habitats due to variation in topography, steepness of slopes and the sharpness of the riparian-upland gradient (Voller 1998). For example, on the broad floodplains of major rivers the riparian zone may be kilometres wide, such as is observed for River Red Gum *Eucalyptus camaldulensis* forests along the Murray River, Australia (Land Conservation Council 1985). In contrast, in complex terrain (e.g. mountain ranges, canyons) the riparian zone may be limited to areas immediately fringing the waterway and its width measured in metres. The extent of the riparian zone in the landscape can be relatively large when the entire stream network is considered. For example, the streambeds of a dendritic stream network in a catchment in foothill forests of the Great Dividing Range, south-east Australia, occupied approximately 0.49% (0.32 km<sup>2</sup> of 65.4 km<sup>2</sup>) of the catchment area (Bren 1995). If the riparian zone was assumed to encompass a mean of 8.5 m either side of the streambed (a very modest estimate), then approximately 5% of the catchment would be riparian zones (Bren 1995).

Throughout the world, vegetation communities associated with riparian zones, especially floodplains, have been targeted for agricultural development. The selective clearing of vegetation along drainage lines and across floodplains is a consequence of these habitats occurring on the richest soils and having high primary productivity (Recher and Lim 1990; Robinson and Traill 1996). Riparian zones in Australia continue to be threatened by poor land management and a range of processes, including weed invasion, salinity, and water diversion and impoundment (Hancock *et al.* 1996; Jansen and Robertson 2001).

## 1.2 Riparian zones – locally rich habitats for birds

Riparian zones are widely recognised for supporting a disproportionately high richness, abundance and diversity of bird species, relative to their extent in the landscape. Indeed, due to their importance they have been aptly described as the ‘aorta of an ecosystem’ in recognition of the contribution such habitats make to biodiversity at local, landscape and regional scales (Knopf and Samson 1994). For example, in the western U.S.A., approximately 82% of bird species occur in riparian habitats (Knopf 1985), while

in the south-west >50% of the species are dependent on riparian habitats and 47% (78/160) of species that breed in the area are restricted to these habitats (Johnson *et al.* 1977).

The promotion of riparian zones as key habitats for birds has generally been based on the high number of species (England *et al.* 1984; Decamps *et al.* 1987; Brown *et al.* 1989) and individuals (Johnson and Haight 1985; Szaro and Jakle 1985; Smith and Schaefer 1992; Mac Nally *et al.* 2000; Pearson and Manuwal 2001) occurring locally. For example, in a heavily cleared, agricultural landscape in South Dakota, U.S.A., where the remaining 2.6% wooded vegetation cover is distributed among riparian woodlands, remnant forest patches, shelterbelts and woodlots, bird species richness was significantly higher in all seasons in riparian woodlands than in other vegetation types (Emmerich and Vohs 1982). Likewise, in box-ironbark forests in Victoria, Australia, sites in gullies (*viz.* riparian zones) had a significantly greater density of birds (54% greater) than sites in habitats on surrounding ridges in this dry forest landscape (Mac Nally *et al.* 2000).

The species composition of riparian bird assemblages is often distinctive (Szaro and Jakle 1985; Gates and Giffen 1991; McGarigal and McComb 1992). Birds that occur exclusively in riparian zones and those that occur more commonly in riparian habitats than in surrounding vegetation strongly contribute to such distinctiveness (e.g. Mac Nally *et al.* 2000; Tzaros 2001). Australia has very few riparian-specialists among its terrestrial birds. One example, the Purple-crowned Fairy-wren *Malurus coronatus* is confined to dense vegetation that fringes permanent streams in northern Australia, rarely being found further than 10 m from the water (Rowley 1993). Species that occur exclusively in riparian habitats frequently depend on stream-edge habitats and fringing vegetation (e.g. Whitaker and Montevicchi 1999). Some species depend on riparian zones during particular stages in their life cycle. In south-east Australia, Regent Parrots *Polytelis anthopeplus* rely on River Red Gum trees in the riparian zone for breeding, and nest only in trees within 60 metres of water (Burbidge 1985). Other species move into the riparian zone in response to seasonal variation in resources, such as nectar (e.g. Woinarski *et al.* 2000; French *et al.* 2003).

The trend for riparian zones to support a greater richness and abundance of birds may not be upheld in all environments. In the mesic forests associated with mountain

ranges in the Pacific Northwest, U.S.A., riparian zones were less important than adjacent upland habitats in enhancing the avifauna of intact forest – in total, 91% of species were observed in non-riparian habitats compared with 67% in riparian zones (McGarigal and McComb 1992). Mean species diversity, richness and abundance per site were greater in non-riparian habitats (McGarigal and McComb 1992). Likewise, in the Appalachian Mountains, U.S.A., species richness and relative abundance of birds was similar in riparian zones and upland forests (Murray and Stauffer 1995). Ultimately, the importance of riparian zones to birds may depend on the nature of the gradient that distinguishes them from the rest of the landscape. Where the gradient is more subtle, the value of the riparian zone may be diminished.

### **1.3 What features of riparian zones are attractive to birds?**

Features of riparian zones that make them more important for birds include their proximity to free water, structural complexity of the vegetation, abundance of food resources, edge-associated effects and conditions in the surrounding matrix. Many of these features are interrelated, and birds commonly respond to more than one (Naiman and Decamps 1997; Woinarski *et al.* 2000).

Water is probably the single most important feature of riparian zones that contributes to their value as wildlife habitat (Rochelle *et al.* 1988). The availability of water supports the productive vegetation communities that are typical of these landscape elements. Habitats with available free water tend to have higher bird species diversity than similar habitats without water (MacArthur and MacArthur 1961). Streams provide a source of water, an essential requirement for many birds, and some birds move to riparian zones from surrounding environments on a daily basis to obtain water. The aquatic environment also supports potential prey items including invertebrates (Jackson and Fisher 1986), fish (Gende and Willson 2001) and amphibians (Parris and McCarthy 1999), on which birds in riparian zones may feed.

In response to variation in soil moisture and nutrient regimes, soil types and disturbance associated with flooding, a complex mosaic of vegetation associations occurs within the riparian zone, including different age-classes of habitats (Gregory *et al.* 1991; Malanson 1993; Naiman and Decamps 1997). Multiple edge effects associated with the gradient

in vegetation types from the water's edge to upland habitats, also act to increase habitat heterogeneity (Bull 1978). Riparian zones often have a complex mid-storey structure (e.g. Stamp 1978; Stauffer and Best 1980; Murray and Stauffer 1995), diverse low storey and ground vegetation (e.g. Stamp 1978; Bentley and Catterall 1997; Sanders and Edge 1998) and horizontal patchiness (e.g. Meents *et al.* 1981; Gates and Giffen 1991; Saab 1999). Benefits for birds associated with increased structural complexity of vegetation include a greater array of foraging opportunities, shelter and protection from predators, a greater number of nesting substrates and increased opportunities for resource utilisation (MacArthur and MacArthur 1961; Bull and Skovlin 1982).

Resources specific to the riparian zone are important for some bird species. The natural accumulation of piles of coarse woody debris associated with the flow of water provides an important resource for birds (Steel *et al.* 1999; Mac Nally *et al.* 2001). They use these piles for foraging, perching, territorial displays and shelter (Steel *et al.* 1999). Birds, otherwise characteristic of the non-riparian matrix, that are seeking specific resources in the landscape, such as water, food, nesting and perch sites may use riparian zones on a daily or seasonal basis. In central Australia, for example, the breeding of raptors is largely confined to riparian zones because this is where large trees are concentrated (Aumann 2001).

Riparian zones may provide enhanced or distinct food resources for birds. Invertebrates associated with the aquatic environment may be particularly important for terrestrial birds (Gray 1993; Gende and Willson 2001; Lynch *et al.* 2002). Emergent aquatic prey accounted for approximately 26% of the annual total energy demand of the bird community in temperate deciduous forests in Japan, with forest birds being strongly dependent on this prey source during leafless periods (Murakami and Nakano 2001). Some food resources may only be available in riparian zones. For instance, in Douglas-Fir forests of north-west U.S.A., the presence of berry-producing shrubs found in riparian habitats was positively correlated with the number of riparian-associated birds (Pearson and Manuwal 2001). Other food resources may be restricted to riparian habitats in the landscape at particular times. In eastern New South Wales, populations of the endangered Regent Honeyeater *Xanthomyza phrygia* depend on reliable nectar flows of the mistletoe *Amyema cabbagei* in riparian vegetation at a time when other resources in the landscape are limited (Geering and French 1997).

Conditions in riparian zones tend to be independent of those operating in the surrounding landscape. Malanson (1993) likened riparian zones to mountains in that they are diverse in structure and function among regions while responding to the same primary factors. In the riparian zone, conditions allow for greater productivity, including more consistent and sustained plant growth (Gregory *et al.* 1991; Malanson 1993), which likely contributes to resource dynamics that do not coincide with those operating in surrounding landscapes. The mobility of birds allows them to track resources at large spatial scales, such that they can move into riparian habitats in response to unseasonal availability of resources that are in short supply in the surrounding landscape.

Riparian zones may be particularly important for the development of large trees in the landscape because the deep, nutrient-rich soils and consistent soil moisture provide favourable conditions for tree growth (Malanson 1993). This is a significant issue for birds in Australia, because many species require tree hollows for breeding (Gibbons and Lindenmayer 2002). Shallower soils and lower productivity in slope and ridge habitats restrict the development of large trees away from riparian areas (Lindenmayer 1996). Buffering from fire in riparian zones also contributes to a greater concentration of large, old trees in these areas for any given forest or woodland. Large trees are also concentrated in riparian zones in timber production landscapes due to the protection of these strips in buffers excluded from harvesting.

#### **1.4 Landscape factors that influence the importance of riparian habitats to birds**

As a distinctive element in the landscape, riparian zones have several functional attributes that influence bird populations and assemblages and shape interactions between riparian and non-riparian assemblages.

1. The interface with the surrounding matrix is extensive due to the linearity of the riparian zone;
2. Riparian zones share boundaries with a range of vegetation types along their length;
3. Riparian systems provide a hierarchical network of natural linear habitats

across large areas;

4. Riparian zones bisect and connect patches of vegetation throughout the landscape;
5. Riparian zones provide ecological connections between high and low elevations across landscapes and regions.

Landscape context and the nature of the surrounding environment, the biogeographic situation and the spatial dimensions of the riparian corridor, all influence the level of interaction between riparian and non-riparian bird assemblages. While there is evidence from a variety of settings throughout the world that riparian zones support rich bird assemblages, including in temperate and tropical forests and woodlands (Mac Nally *et al.* 2000; Woinarski *et al.* 2000; Catterall *et al.* 2001), deserts (Shurcliff 1980; Szaro and Jakle 1985), agricultural areas (Crome *et al.* 1995; Bentley and Catterall 1997; Fisher and Goldney 1997; Saab 1999) and urban landscapes (Small and Hunter 1989; Rottenborn 1999; Miller *et al.* 2003), some authors have justifiably expressed caution in generalising this response to all landscapes because of the influence that matrix habitats can have on riparian bird assemblages (McGarigal and McComb 1992; Croonquist and Brooks 1993; Murray and Stauffer 1995; Pearson and Manuwal 2001). A regional study in Australia's tropical savannas found that the association of birds with riparian zones was driven by landscape context, being much more pronounced in low rainfall areas (Woinarski *et al.* 2000). This related, in part, to a vegetation gradient from relatively extensive canopy cover in riparian zones in high rainfall areas, to reduced canopy cover in low rainfall non-riparian areas (Woinarski *et al.* 2000).

The nature of the surrounding matrix can strongly influence the pattern and distinctiveness of riparian bird assemblages (Strong and Bock 1990; Bentley and Catterall 1997; Saab 1999). Contrasts between assemblages of riparian zones and non-riparian habitats are likely to be less marked where a greater similarity occurs in the structure and floristic composition of vegetation in these habitats. Saab (1999) concluded that the surrounding matrix, rather than microhabitat features (e.g. vegetation characteristics) or macrohabitat features (e.g. patch size, shape, edge), was the most important predictor of high species richness and the frequency of occurrence for individual birds in riparian zones in Idaho, U.S.A. Riparian zones in agricultural

areas supported distinctly different assemblages from those within large areas of natural vegetation, due to an influx of birds associated with agricultural land-use (Saab 1999). Similar patterns have been reported in Australia (Bentley and Catterall 1997; Fisher and Goldney 1997).

Both riparian and non-riparian habitats attract species from the landscape 'pool'. Regionally, the most diverse avifauna may occur in the more extensive non-riparian habitats, despite locally rich riparian assemblages (e.g. Knopf 1985; Tzaros 2001). The amount of interaction between adjacent assemblages may be a function of landscape context and the similarity between riparian and adjacent vegetation types; however, the structure of surrounding bird assemblages can also be important. In south-west U.S.A., the extent to which riparian breeding birds utilised adjacent non-riparian habitat was driven by the diversity of birds in such adjacent habitats – non-riparian habitats with high diversity were less utilised by riparian breeding species (Carothers *et al.* 1974). Similarly, Shurcliff (1980) found bird assemblages in riparian areas to be most similar to those of directly adjacent habitats, compared with those of other vegetation types in the landscape. This was attributed to the indistinct boundaries between adjoining vegetation types and the limited size of riparian zones that preclude them from exclusively supporting many bird species at the landscape level.

## 1.5 Riparian zones as corridors

Riparian zones are commonly perceived to facilitate movements at various scales, including daily, seasonal and migratory movements of birds through the landscape (Stevens *et al.* 1977; Warkentin *et al.* 1995; Skagen *et al.* 1998). The benefits of riparian corridors to wildlife in general have been widely discussed (Bennett 1999). Machtans *et al.* (1996) demonstrated that retained strips of riparian vegetation that connect forest patches were used by forest bird species for movement, thus reducing the impacts of habitat fragmentation. Others have established the importance of riparian habitat in providing stopover habitat for migrating birds (Stevens *et al.* 1977; Wauer 1977; Motroni 1984; Skagen *et al.* 1998). Investigations of the corridor function of riparian zones have largely focused on remnant strips that occur in modified landscapes. Their function as corridors in large, intact landscapes is largely unknown.



Riparian corridors facilitate the persistence of some species in otherwise hostile landscapes, and expansions of the geographic range of species along riparian corridors have been documented. In south-east Australia, a suite of mesic forest-adapted birds (e.g. Crimson Rosella *Platycercus elegans*, Crested Shrike-tit *Falcunculus frontatus*, Bassian Thrush *Zoothrea lunulata*) extend their distribution into semi-arid regions along the riparian zone associated with the Murray River (Tzaros 2001). Similarities in the avifauna decreased with increasing separation of sites along the climatic gradient through which the river flows; however, the change was less for the riparian zone than in the surrounding landscape (Tzaros 2001). Likewise, the riparian zone provides the sole or main access into areas of low rainfall for many birds associated with higher rainfall environments in northern Australia (Woinarski *et al.* 2000).

The spatial characteristics of the riparian corridor also influence the structure of bird assemblages. Species richness of birds tends to increase with increasing width of the riparian zone (Stauffer and Best 1980; Spackman and Hughes 1995; Hodges and Krementz 1996). Associated with this is an increase in richness and abundance of birds with increasing river order; greater width of the riparian zone coincides with larger rivers (Knopf 1985; Lock and Naiman 1998). While this relationship represents a classic species-area response, the trend appears to be maintained even in large, non-fragmented forest environments (Kilgo *et al.* 1998). Enhanced width is likely to contribute to increased heterogeneity of vegetation in the riparian zone, in response to complex moisture gradients and mechanical disturbance caused by water flows (Gregory *et al.* 1991; Malanson 1993).

## 1.6 The role of riparian zones in the conservation of birds

Several attributes of the relationship between terrestrial birds and riparian zones contribute to the riparian zone being a high priority habitat for wildlife conservation in Australia.

Riparian zones provide key habitat for a number of species and taxa of conservation concern in Australia (Garnett and Crowley 2000) such as Sooty Owl *Tyto tenebricosa* (Smith 1984), Crimson Finch *Neochmia phaeton evangelinae* (Garnett and Crowley 2000), Regent Parrot (Burbidge 1985) and Regent Honeyeater (Oliver *et al.* 1999).

Another, the critically endangered Helmeted Honeyeater *Lichenostomus melanops cassidix*, is restricted to a small number of sites in swampy Mountain Swamp Gum *Eucalyptus camphora*, open forest, which occurs along creeks in the foothills of the Yarra Valley, Victoria (Pearce and Minchin 2001).

Riparian zones are particularly important to bird assemblages in heavily cleared agricultural landscapes where retained streamside vegetation often represents a large proportion of the remnant vegetation to provide habitat for wildlife populations (Bennett 1995; Darveau *et al.* 1995; Hagar 1999). In cleared landscapes in particular, riparian vegetation is likely to have a critical role in forming habitat networks for wildlife, providing linkages across the landscape that aid wildlife movements (Bennett 1999). Such linkages are potentially important in facilitating dispersal of species, recolonisation of isolated patches of habitat, and to maintain gene flow among populations.

Habitats in riparian zones can also provide refuge for birds as conditions (e.g. food availability, water availability) deteriorate in the surrounding landscape during times of environmental stress (e.g. drought, fire) (Nix 1993; Morton *et al.* 1995). The generally wetter conditions experienced in the riparian zone could also be important in buffering riparian habitats from fire (Kelsey and West 1998), providing temporary refugia and then functioning as a source of recolonising individuals for the recovering landscape. Riparian zones may be crucial in species' response to future climate change. Effects caused by predicted climate change (see Hughes 2003), are likely to be subtly different between riparian and non-riparian habitats due to the interactions between factors such as topography, moisture availability and temperature.

Riparian zones have been a focus of restoration and revegetation programs throughout Australia and the value of such efforts for wildlife are now being assessed (e.g. Merritt 2002; Thompson *et al.* 2002). In the extensively cleared Murrumbidgee Catchment of New South Wales, populations of Brown Treecreeper *Climacteris picumnus* and Superb Fairy-wren *Malurus cyaneus*, and the composition of the overall bird community displayed obvious signs of recovery 10 years after being fenced to exclude livestock grazing (Thompson *et al.* 2002). The positive response of bird assemblages to such actions means that riparian zones are an effective location to focus revegetation, restoration and conservation efforts in modified landscapes.

## 1.7 Research needs

There are several constraints in our current understanding of the relationship between terrestrial birds and riparian zones in the landscape. First, much of the conceptual understanding of the importance of riparian zones to birds has emanated from research conducted in arid environments (McGarigal and McComb 1992; Catterall 1993; Lock and Naiman 1998). Such generalisations may not be directly applicable to more mesic environments, where the gradient between riparian and upland habitats is less severe. Second, research has been conducted primarily at the local level (Knopf and Samson 1994). There is little understanding of the use and value of riparian zones to birds at the landscape or regional scale, or for whole stream systems. Third, remarkably little attention has been given to the dynamics of bird communities in riparian habitats in relatively intact landscapes (Woinarski *et al.* 2000). Research in extensive, intact landscapes will help to identify the fundamental attributes of bird-riparian relationships better, controlling for the impacts of confounding processes such as fragmentation, degradation and modification to both riparian and non-riparian habitats.

There is little information on the dynamics of bird communities between riparian zones and adjacent non-riparian habitats in the landscape. Woinarski *et al.* (2000) described the 'knitting' of riparian and surrounding areas in the temporal cycle of birds responding to resource fluctuations (e.g. nectar availability), emphasising the interdependence of these landscape components. The importance of these landscape elements in providing seasonal habitat for birds, including their role in providing crucial refuge during drought and following wildfire needs to be assessed and quantified.

The ecological processes that drive relationships between riparian zones and terrestrial bird species, and wildlife in general, continue to be poorly understood, particularly in Australia (Catterall 1993; Lock and Naiman 1998; Lynch and Catterall 1999). Observations of high species richness and abundance have been made (Shurcliff 1980; Fisher and Goldney 1997; Mac Nally *et al.* 2000; Jansen and Robertson 2001), but empirical studies of the ecological basis for this relationship are limited. There has been surprisingly little quantitative research on resource dynamics within riparian habitats, severely hampering knowledge of the use of riparian zones by birds.

## **1.8 Aims and structure of this thesis**

### *1.8.1 Aims and scope*

This study focused on understanding the ecological mechanisms that underpin the pattern of bird assemblages in riparian and adjacent non-riparian habitats. Birds were selected as the subject of study because they have relatively high diversity and display a wide range of ecological, life history and functional characteristics. Due to their mobility, birds can rapidly respond to changing environmental conditions. They are conspicuous and easily sampled. As a result, the structure of bird assemblages has been well studied, which facilitates comparisons with other studies, both in Australia and abroad, and in a wide range of landscape settings.

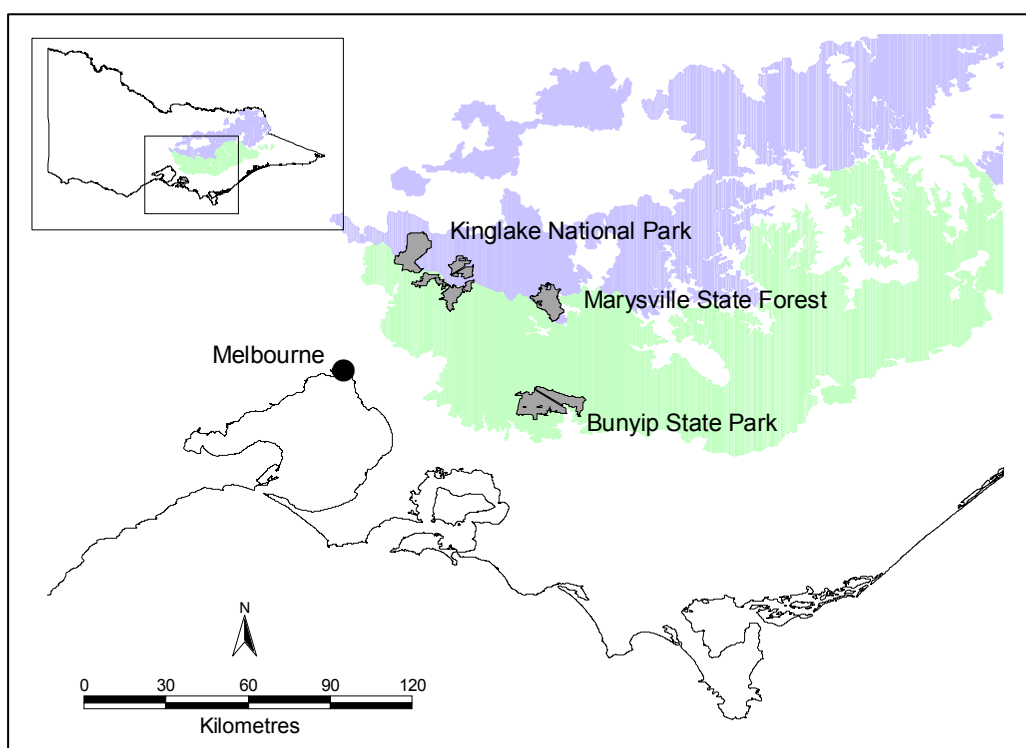
The main aim of this thesis is to examine the bird assemblages of riparian zones and those of adjacent non-riparian vegetation types and the influence that associated differences in resource availabilities, habitat structure and conditions have on observed patterns. This research was carried out in an extensive, temperate forest landscape. The riparian-upslope gradient in these forests was characterised by a continuous canopy of eucalypts. This presented significant opportunities to investigate the fundamental features of riparian zones that make them key areas in the landscape for wildlife.

### *1.8.2 Study area*

The study area was located in the Victorian Highlands – Southern Fall and Victorian Highlands – Northern Fall bioregions in south-east Australia (Figure 1-1). The study area covers about 8 400 km<sup>2</sup> in the Bunyip and Goulburn River basins. Townships closest to study sites are Gembrook (Bunyip State Park), Kinglake (Kinglake National Park) and Narbethong (Marysville State Forest). The region has a temperate climate. Summers are generally warm to hot (25°C January average daily maxima) and winters cool to cold (12°C July average daily maxima). Rainfall occurs throughout the year (900-1400 mm annually), with the majority of the annual rainfall occurring during winter and spring.

The dominant feature of the region is the mountain ranges and associated foothills of

the Great Dividing Range. The Victorian Highlands bioregions maintain an extensive eucalypt forest cover (approximately 75% of the bioregion retains native vegetation cover). Biodiversity, including the operation of ecological processes, is in relatively good to very good condition across the landscape, particularly in extensive forest areas (Commonwealth and Victorian Regional Forest Agreement Steering Committee 1997).



**Figure 1-1** Geographic position of forest areas surveyed in this study in the Victorian Highlands – Southern Fall (green) and – Northern Fall (purple) bioregions, south-east Australia.

A wide range of eucalypt-dominated ecological vegetation classes (EVC) occur across the study area. On protected south-facing slopes tall, moist forest EVCs preside with diverse understoreys of ferns, grasses and tall shrubs. These vegetation classes include Wet Forest, Damp Forest and Shrubby Foothill Forest. On drier north-facing aspects low open forests and woodlands with dense shrub understoreys occur including Heathy Woodland and Heathy Dry Forest. Medium to tall forests with a grass, herb and shrub understorey occur on intermediate slopes (e.g. Lowland Forest and Herb-rich Foothill Forest).

Major stream networks in the study area are the Acheron River, Yarra River, Yea River and Bunyip River. In forest areas, these rivers and their tributaries are in good to excellent condition (Mitchell 1990). These dendritic stream networks support riparian vegetation that is generally in very good to excellent condition (Mitchell 1990). Riparian zones are limited in extent, and occur as relatively narrow, linear strips of vegetation interspersed in the forest mosaic. The streamside vegetation is typically classified as Riparian Forest.

The region includes several major conservation reserves including the Yarra Ranges, Dandenong Ranges and Kinglake National Parks and Bunyip State Park. Other major forest-based land-uses in the study area include timber harvesting and water production. Forests in the study area have supported timber harvesting since the late 1800s and they continue to be important for timber production in Victoria (Commonwealth and Victorian Regional Forest Agreement Steering Committee 1997).



**Plate 1 Riparian site (Riparian site 17, Bunyip State Park)**



**Plate 2 Riparian site (Riparian site 10, Bunyip State Park)**





**Plate 3 Non-riparian site (Non-riparian site 02, Bunyip State Park)**



**Plate 4 Non-riparian site (Non-riparian site 07, Bunyip State Park)**



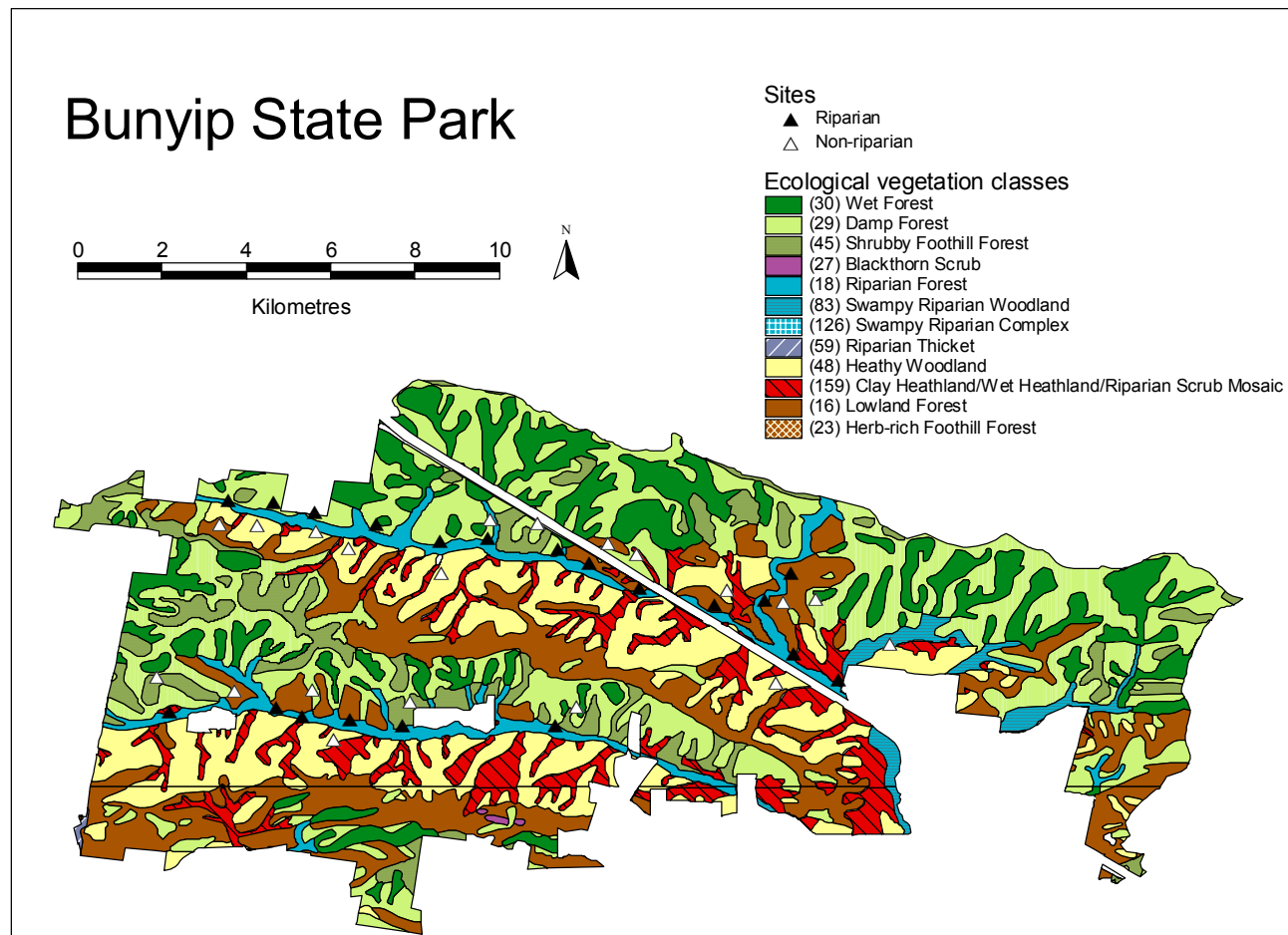
### 1.8.3 Study sites

As described above, the importance of riparian zones to birds may depend on the steepness of the riparian-upslope gradient, particularly in relation to water availability. To moderate any influence of moisture availability on observed patterns of the use of riparian zones by birds, this study was carried out in a temperate region with relatively high annual rainfall. Bird communities in riparian zones also suffer substantial impacts from modifications to surrounding upland habitats (Machtans *et al.* 1996; Fisher and Goldney 1997; Saab 1999). To ensure that any observed riparian effects were not compounded by external processes (e.g. fragmentation, habitat loss, habitat disturbance), it was important that this study be carried out in a relatively intact landscape.

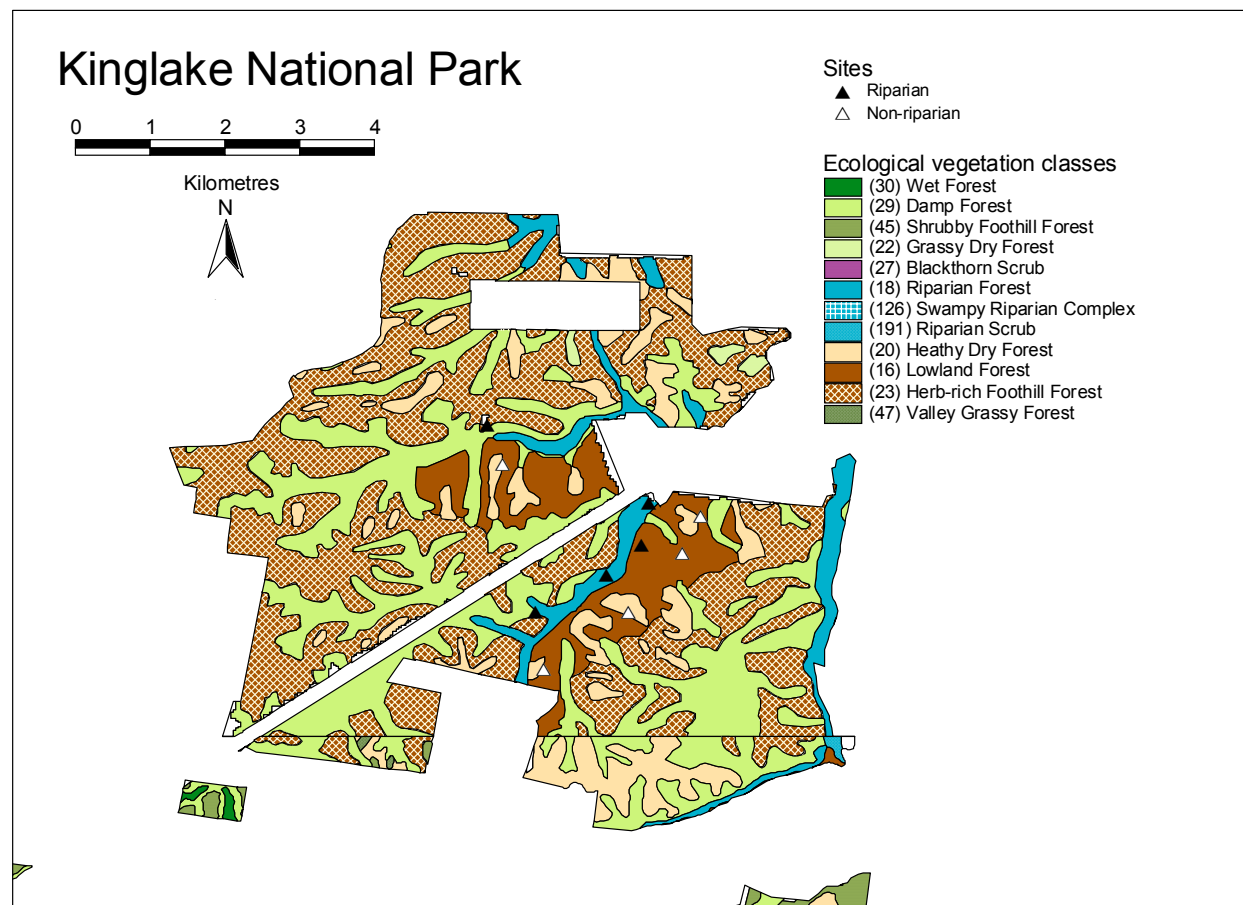
Sites were selected that met the following criteria:

1. Perennial, third or fourth order streams
2. Continuous eucalypt canopy along the gradient from riparian to non-riparian sites
3. Paired sites must occur in relatively undisturbed vegetation
4. Approximately 1 km distance between site pairs
5. Riparian sites positioned immediately adjacent to the stream channel
6. Non-riparian sites positioned approximately 750 m from the stream channel on a surrounding slope

Six stream systems distributed in three forest areas were selected that meet these criteria. The three forest areas used were Bunyip State Park (37°56'S, 145°35'E), Kinglake National Park (37°29'S, 145°22'E) and Marysville State Forest (37°34'S, 145°41'E). Data for the study were collected from 30 paired riparian and non-riparian sites. The location of sites and vegetation communities (i.e. ecological vegetation classes) for each forest area are shown in Figure 1-2 (Bunyip State Park), Figure 1-3 (Kinglake National Park) and Figure 1-4 (Marysville State Forest).

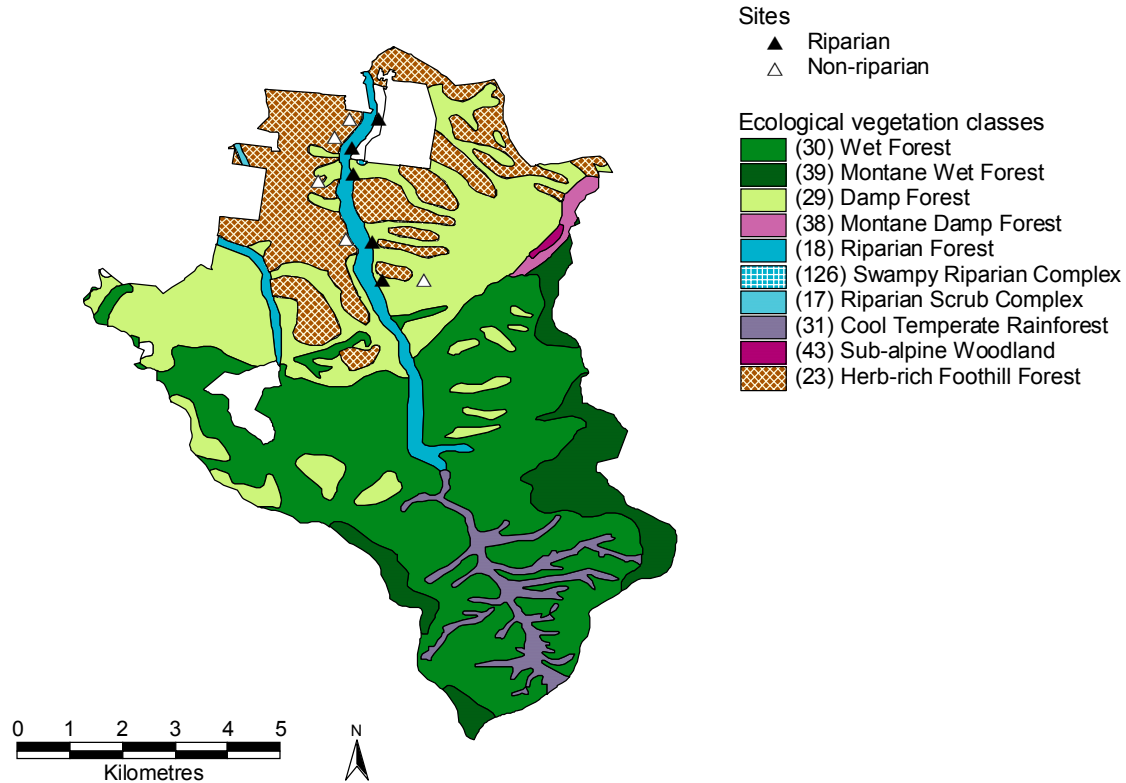


**Figure 1-2** Vegetation map of Bunyip State Park, showing location of paired study sites (01-20).



**Figure 1-3**      **Vegetation map of Kinglake National Park, showing location of paired study sites (21-25).**

## Marysville State Forest



**Figure 1-4** Vegetation map of Marysville State Forest, showing location of paired study sites (26-30).

#### 1.8.4 Thesis outline

In examining the value of riparian zones to bird assemblages, the thesis begins with a review of worldwide research on the relationships between terrestrial birds and the riparian zone (see **Chapter 1**). This provides a background to the research and, importantly, gives context to the contribution that the thesis makes in addressing key knowledge gaps and enhancing understanding of the ecology of this relationship. The thesis then investigates four specific themes relating to the use of riparian zones by birds in the forested landscape.

##### 1. The structure of bird assemblages in riparian and non-riparian habitats

The species richness, abundance, diversity and composition of bird assemblages are compared between riparian and non-riparian sites (see **Chapter 2**). The principal objectives are to:

1. Compare the structural and floristic features of riparian and non-riparian vegetation to identify attributes that may contribute to distinctive habitats for birds.
2. Quantify the bird assemblages of riparian and non-riparian habitats to investigate any differences in species richness and abundance between habitat types.
3. Compare the composition of avifaunal assemblages between riparian and non-riparian habitats to identify the strength of species' relationships with the riparian zone.

This component of the research examines the pattern of riparian and non-riparian bird assemblages in the forest landscape, and investigates how species contribute to the dissimilarities between these assemblages. The habitat structure and floristics of riparian and non-riparian sites are also examined.

## 2. Seasonal variation in the structure of bird assemblages in riparian and non-riparian habitats

The seasonal patterns in species richness, abundance and composition of bird assemblages occurring in riparian and non-riparian habitats are investigated (see **Chapter 3**). The principal objectives are to:

1. Compare the temporal variation in the structure (richness, abundance) of bird assemblages between riparian and non-riparian sites.
2. Compare the temporal variation in the species composition of bird assemblages between riparian and non-riparian sites.

This component of the research examines the temporal patterns in riparian and non-riparian bird assemblages and considers the influence that migratory and nomadic species have on assemblages.

## 3. Ecological characteristics of the structure of riparian and non-riparian bird assemblages

The richness of ecological groups (foraging, nest-type, body mass), and the species richness within these groups, in riparian and non-riparian assemblages are examined (see **Chapter 4**). Two hypotheses to account for greater richness in riparian zones are investigated:

1. Riparian habitats are more structurally complex and diverse and therefore there are more opportunities (i.e. niches) available. This hypothesis predicts that assemblages in riparian sites will be composed of species representing a greater number of ecological groups than are present in assemblages in non-riparian sites.
2. Riparian habitats support a similar number of niches to non-riparian habitats but there is greater species packing within ecological groups. This hypothesis predicts that there is no difference between riparian and non-riparian sites in the number of ecological groups present, but that on average there will be more species per group in riparian sites.

This component of the research examines how additional species are accommodated in riparian assemblages, and the ecological mechanisms (resource partitioning, species packing) that underlie this pattern. Species foraging ecology is also examined to address how changes in niche breadth affect resource use between habitat types.

4. Resource availability and dynamics between riparian and non-riparian habitats

Explicit contrasts of resource availability (eucalypt flowering, eucalypt bark shed, mistletoes, shrub flowering, tree hollows) and vegetation productivity are conducted between riparian and non-riparian sites over an annual cycle (see **Chapter 5**). Three hypotheses are tested:

1. Riparian habitats provide a greater abundance of resources used by birds than non-riparian sites.
2. There is greater reliability in the seasonal availability of resources in riparian habitats than non-riparian sites.
3. Primary productivity is greater and more reliable at riparian sites than non-riparian sites.

This part of the research seeks to determine whether there is differential availability of particular resources, or in their temporal availability throughout the annual cycle, between riparian and non-riparian habitats in the landscape. This quantitative assessment of resource availability is used to examine the ecological value of riparian zones to birds.

The final section of this thesis draws together the major findings of the research (see **Chapter 6**). The implications of these findings for the maintenance of avifauna in the landscape are discussed. Particular reference is made to the role of riparian zones in enhancing the avifauna by providing high quality habitats in the landscape. The applicability of these findings to other situations is discussed. The interdependence of riparian and surrounding non-riparian habitats is also recognised.

## 2 Riparian zones provide for distinct bird assemblages in forest mosaics of south-east Australia

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Rufous Fantail *Rhipidura rufifrons* (T. Wilson)



## 2.1 Introduction

Riparian habitats are a distinctive component in many landscapes. Their topographic position, dendritic structure, high amount of edge area and connectivity through the landscape are characteristic features (Malanson 1993; Forman 1995). The value of riparian habitats for terrestrial wildlife has been investigated on a number of continents (Stauffer and Best 1980; Decamps *et al.* 1987; Doyle 1990; Warkentin *et al.* 1995; Fisher and Goldney 1997; Robertson *et al.* 1998), and frequently they have been reported to harbour a rich and abundant fauna in comparison with that of surrounding non-riparian habitats (Thomas *et al.* 1978; Knopf and Samson 1994; Lynch and Catterall 1999; Woinarski *et al.* 2000). Further, in heavily modified or cleared landscapes, riparian habitats often are prominent examples of the remaining natural or semi-natural vegetation available to native biota (Gregory *et al.* 1991; Malanson 1993; Lachavanne 1997; Martin *et al.* 2006). Consequently, throughout the world riparian zones are increasingly being promoted as key areas for biodiversity conservation (Knopf *et al.* 1988a; Catterall 1993; Malanson 1993).

The value of riparian zones for birds has been well demonstrated in semi-arid and arid landscapes (Anderson and Ohmart 1977; Shurcliff 1980; Szaro 1980; Knopf 1985; Szaro and Jakle 1985; Fleishman *et al.* 2002). In these situations, conditions in the riparian zone (e.g. moisture regimes, nutrient availability) often contrast strongly with those predominating in the surrounding non-riparian matrix (Gregory *et al.* 1991; Malanson 1993). This leads to distinct patterning of vegetation associations in the landscape (Austin *et al.* 1996) and birds respond positively to such diversity of habitats (Cody 1993; Borchert 2003). Riparian habitats in managed landscapes, such as remnant vegetation along streams in agricultural areas (Crome *et al.* 1995; Fisher and Goldney 1997; Kilgo *et al.* 1998; Jansen and Robertson 2001; Martin *et al.* 2006) and among plantation forests (Friend 1982; Armstrong and van Hensbergen 1994; Hodges and Krementz 1996; Lindenmayer *et al.* 2002; Conner *et al.* 2004) have also been a focus for research effort and are considered important for avifaunal conservation. In these environments too, there is a marked contrast between the vegetation of the riparian zone and that of adjacent land.

Less attention has been given to the role of riparian habitats in largely intact

landscapes, where riparian and adjacent non-riparian habitats maintain continuous vegetation cover (Catterall 1993; Murray and Stauffer 1995; Woinarski *et al.* 2000). In continuous forests in mesic environments, for example, there may be less contrast between riparian zones and adjacent vegetation as habitat for birds, due to the greater availability of moisture across the landscape and the continuity of forest cover. Some studies in such environments have found bird assemblages in non-riparian habitats to have equal or greater species richness and diversity than nearby riparian assemblages (McGarigal and McComb 1992; Pearson and Manuwal 2001; Shirley and Smith 2005).

In this study the use of riparian zones by birds in continuous forest landscapes in mesic south-east Australia was investigated. The study was based on explicit contrasts of the avifauna and habitat characteristics at 30 pairs of riparian and adjacent non-riparian sites in extensive foothill forests in the Victorian Highlands. There were three main objectives:

1. To compare structural and floristic features of riparian and non-riparian vegetation to identify attributes that may contribute to distinctive habitats for birds.
2. To quantify the bird assemblages of riparian and non-riparian habitats to investigate any differences in species richness and abundance between habitat types.
3. To compare the composition of avifaunal assemblages between riparian and non-riparian habitats to identify the strength of species' relationships with the riparian zone.

## 2.2 Methods

### 2.2.1 Study area

The study was conducted in the Victorian Highlands, south-east Australia. Three extensive forest areas were investigated: Bunyip State Park (37°56'S, 145°35'E), Kinglake National Park (37°29'S, 145°22'E) and Marysville State Forest (37°34'S, 145°41'E). Mean annual rainfall in the study area is 900–1400 mm, with most rain

falling between April and September. The area experiences dry, hot summers (25°C January average daily maxima) and cool, damp winters (12°C July average daily maxima).

Riparian zones are interspersed in the mixed-*Eucalyptus* forest mosaic as relatively narrow bands of vegetation along the dendritic stream network that drains both the coastal and inland fall of the Great Dividing Range in this region. The streamside vegetation is typically classified (by the Department of Sustainability and Environment, Victoria) as Riparian Forest ecological vegetation class (EVC). A wide range of other vegetation associations occur in upland areas of the landscape. On protected south-facing slopes there are tall, moist forest associations (Wet Forest, Damp Forest and Shrubby Foothill Forest ecological vegetation classes) (Commonwealth and Victorian Regional Forest Agreement Steering Committee 1997). Low, heathy forests and woodlands dominate on the drier, gently sloping north-facing aspects, and characteristically support a dense shrub layer. Tall open forests with a grass, herb and shrub understorey occur on intermediate slopes. Notably, throughout the landscape a continuous eucalypt tree canopy is maintained along the gradient from riparian to upland habitats.

### 2.2.2 Study sites

Site selection was driven by the availability of extensive riparian zones located in forested catchments that displayed no evidence of recent disturbance. Potential sites were identified from vegetation maps (Ecological Vegetation Classes) of the region. Stretches of continuous Riparian Forest that fringed perennial mid-order stream systems (stream order 3 to 5, stream width 1–8 m) and were greater than 5 000 m in length were sought. Of potential stream systems, six were selected and a total of 30 sites was located as follows: Black Snake Creek (n = 10 sites), Bunyip River (4), Diamond Creek (6) (all in Bunyip State Park), Island Creek (4), Captain Creek (1) (both Kinglake National Park) and Acheron River (5) (Marysville State Forest). Riparian sites were positioned alongside the stream, with the site boundary within 10 m of the stream edge.

Non-riparian sites were positioned parallel to their riparian partner on a facing slope at a distance of approximately 750 m. Non-riparian sites represent a range of ecological

vegetation classes; Wet Forest (n = 1 in Bunyip State Park), Damp Forest (4 Bunyip State Park and Marysville State Forest), Shrubby Foothill Forest (4 Bunyip State Park), Herb-rich Foothill Forest (4 Marysville State Forest), Lowland Forest (6 Bunyip State Park and Kinglake National Park), Heathy Dry Forest (3 Kinglake National Park) and Heathy Woodland (8 Bunyip State Park). A distance of at least 1 000 m was maintained between site-pairs.

### 2.2.3 *Habitat characteristics*

Data on habitat structure and floristic composition were gathered at all sites (Table 2-1). Habitat structure assessments were based on vegetation life-forms. All trees were identified to species level, counted and determined to be either canopy forms or mid-storey forms, within a 0.25 ha quadrat (100 m x 25 m) at each site. The diameter-at-breast-height (dbh) of each tree was measured and assigned to one of six size-classes ( $\leq 10$  cm dbh, 11–20 cm, 21–40 cm, 41–60 cm, 61–80 cm,  $\geq 81$  cm). The cover (%) of the canopy and mid-storey tree layers was visually estimated. Dead standing trees were similarly measured and counted, and categorised into two size-classes ( $\leq 10$  cm dbh,  $> 10$  cm). Trees bearing mistletoe (*Amyema* spp.) or with hollows visible from the ground were tallied. For shrub assessments, a randomly placed 25 m x 25 m quadrat was used. Shrubs were identified, counted and assigned to one of three height classes ( $< 1$  m, 1–2 m,  $> 2$  m). The cover (%) of each shrub species was also recorded in each height class. The cover (%) of a suite of vegetation life-forms (e.g. tree ferns, low ferns, grasses, sedges) was also visually estimated in 10% intervals within this quadrat (Table 2-1). Cover of bare ground, fine litter and ground vegetation was assessed in four 25 m<sup>2</sup> (5 m x 5 m) quadrats and average values generated for each site. The extent of coarse woody debris in two size categories ( $\leq 50$  cm diameter,  $> 50$  cm diameter) was measured as the number of intercepts along a 100 m transect centrally positioned at each site.

**Table 2-1 Description of habitat variables measured at riparian and non-riparian sites in the Victorian Highlands.**

Variable	Description
Tree density	Density of trees by size-class ( $\leq 10$ cm; 11-20 cm; 21-40 cm; 41-60 cm; 61-80 cm; $\geq 81$ cm diameter) summed across all species (number $\text{ha}^{-1}$ )
Tree hollows	Number of trees containing visible hollows (number $\text{ha}^{-1}$ )
Mistletoes	Number of trees with visible mistletoes (number $\text{ha}^{-1}$ )
Dead standing trees	Density of dead trees by size-class ( $\leq 10$ cm; $> 10$ cm) summed across all species (number $\text{ha}^{-1}$ )
Canopy height	Representative height (m) of tree layer
Canopy cover	Projective crown foliage cover (%)
Mid-storey trees	Projective mid-storey foliage cover (%)
Shrub richness	Number of shrub species
Shrub cover	Estimate of percentage cover of shrub species by size-class ( $< 1$ m, 1 - 2 m, $> 2$ m)
Tree ferns	Cover of tree ferns (%)
Ground ferns	Cover of ground ferns (%)
Grass trees	Cover of grass trees (%)
Grasses	Cover of grasses (%)
Sedges	Cover of sedges (%)
Herbs	Cover of herbs (%)
Creepers	Cover of creepers (%)
Ground vegetation	Cover of ground vegetation $\leq 10$ cm high (%)
Fine litter	Cover of fine litter ( $< 6$ cm diameter) (%)
Bare ground	Cover of bare ground (%)
Coarse woody debris	Abundance of coarse woody debris ( $> 10$ cm diameter and $> 100$ cm long) by size-class (CWD $\leq 50$ cm, CWD $> 50$ cm diameter)

### 2.2.4 Bird survey

Bird assemblages were sampled using a fixed-point count method (Pyke and Recher 1984). Fixed-points were centrally located 50 m apart in two adjoining plots, each 50 m x 50 m, yielding a combined sampling area of 0.5 ha at a site. At each fixed-point the survey time was standardised to 8 min. Upon completion of the survey at the first point, the observer moved to the next point and commenced another 8 min count, a standard 2 min after completion of the first. All birds seen or heard within the two plots were recorded. Occurrence of birds within plots and movements between plots were

closely monitored to avoid duplication of individual observations wherever possible. All surveys and observations were completed by the author (GP). The data reported here were pooled from both plots at each site. The taxonomy for bird species follows Christidis and Boles (1994).

During the study, each site was visited on 29 occasions, a total of 3 480 point counts across the 60 sites. Each site was surveyed five times per season (winter, spring, summer and autumn) between July 2001 and December 2002. Surveys were conducted throughout the day in suitably still and dry conditions. Nocturnal surveys were not undertaken and therefore species active at night (e.g. owls and nightjars) were poorly sampled. Due to the constraints posed by geographic separation, sites were grouped by stream units and the order of site-pair surveys was randomised within these units.

### 2.2.5 *Data analysis*

Differences between the habitat structure of riparian and non-riparian habitats were tested by using analysis of similarity (ANOSIM) in the PRIMER software package (Clarke and Gorley 2001). For all analyses, a significance level of  $p = 0.05$  was employed. A related procedure, similarity percentage (SIMPER), was then used to identify the physiognomic variables that contribute most to the similarities within site groups (i.e. riparian, non-riparian) and to the dissimilarities between groups based on contributions of variables to the Bray-Curtis similarity matrix (PRIMER software package) (Clarke and Gorley 2001). Habitat variables were standardised for analyses because they were measured on different scales.

To investigate floristic associations of sites, a modified 'importance value' (Mueller-Dombois and Ellenberg 1974) was employed. For tree species, this index was calculated by summing the proportional contribution of each species at a site to the total basal area (relative dominance) and total stem density (relative density). For shrubs, the index generated for each species at a site was the sum of the percentage of total shrub cover and percentage of total number of shrubs. Importance indices, therefore, have values from 0–200 for identified plant species at a given site. Importance values for tree and shrub species at each site were tabulated and converted to a similarity-by-site matrix using the Bray-Curtis similarity measure. The ANOSIM and SIMPER

procedures were then used for comparisons between riparian and non-riparian sites, using  $\sqrt{}$ -root transformed variables to reduce the influence of abundant species.

Bird species observations were compiled and pooled for all 29 visits to each site. Species richness values were analysed by using a paired *t*-test to compare between riparian and non-riparian sites for each pair. Species abundance and species diversity (Shannon-Weiner diversity index) values were also analysed using paired *t*-tests. ANOSIM and SIMPER procedures (Clarke and Gorley 2001) were used to test for differences in species composition between riparian and non-riparian sites and to identify species contributing most to the similarity within site types (riparian or non-riparian) and the dissimilarity between site types (riparian v non-riparian). Again, variables were  $\sqrt{}$ -root transformed to reduce the influence of abundant species and give greater weight to less-common species.

An ordination of bird assemblages at each site was constructed by using multidimensional scaling (MDS), based on a Bray-Curtis similarity matrix. To assist in interpreting the ordination, Spearman rank correlations were calculated between the ordination dimensions and all measured physiognomic and floristic variables for each site. This enabled the variables most strongly correlated with each of the MDS dimensions to be identified.

## 2.3 Results

### 2.3.1 *Habitat characteristics*

Habitat structure differed significantly (ANOSIM,  $R = 0.656$ ,  $p < 0.001$ ) between riparian and non-riparian sites. The most distinctive features of riparian habitats were the taller canopy height, a ground layer with extensive cover of fine litter and ground vegetation, large amounts of coarse woody debris ( $\leq 50$  cm diameter) and a dense cover of mid-storey trees (Table 2-2). The characteristic features of non-riparian habitats included a relatively dense canopy cover, a ground layer dominated by ground vegetation and fine litter, high cover of grasses and a high density of canopy-forming trees in the smaller size-classes (Table 2-2).

Variables that contributed to the similarities within riparian and non-riparian habitats

also contributed to the dissimilarities between these habitat types (Table 2-2). In particular, contrasts between habitat types were derived from dissimilarities in the structure of the tree layers. Riparian habitats were near exclusive in containing a mid-storey tree layer dominated by species such as Scented Paperbark *Melaleuca squarrosa*, Hazel Pomaderris *Pomaderris aspera*, Blackwood *Acacia melanoxylon* and Silver Wattle *Acacia dealbata* (Table 2-2). The distribution of tree size-classes also contributed strongly to dissimilarities, with the density of canopy trees in the size-classes  $\leq 10$  cm, 11–20 cm and 21–40 cm diameter being almost twenty, nine and three times, respectively, greater in non-riparian habitats (Table 2-2). Other variables that contributed to the dissimilarities between habitat types included cover of ground ferns (twice as great in riparian habitats) and cover of sedges (three times greater in riparian habitats) (Table 2-2).

Differences in the floristic composition of riparian and non-riparian habitats were highly significant (ANOSIM,  $R = 0.814$ ,  $p < 0.001$ ). Five species of trees and shrubs contributed approximately 70% of the similarity within riparian habitats (Table 2-2). None of these were included in the eight species contributing to 70% of the similarity in non-riparian habitats (Table 2-2). Dissimilarity between riparian and non-riparian sites was generated either by the unique occurrence of tree and shrub species in one habitat type or from large disparity in importance values of species between types (Table 2-2).

### 2.3.2 Bird assemblages

Eighty-eight bird species were recorded at sites during surveys (Table 2-3). The Brown Thornbill and Striated Thornbill (see Table 2-3 for scientific names) were recorded at all riparian and non-riparian sites. Other species recorded at >90% of sites included Grey Fantail, Spotted Pardalote, Yellow-faced Honeyeater, Crimson Rosella, Golden Whistler, Eastern Spinebill, Grey Shrike-thrush, White-throated Treecreeper and Red Wattlebird (Table 2-3). Fifteen species were recorded only at riparian sites; of these, Australian Shelduck, Sulphur-crested Cockatoo, Yellow-tufted Honeyeater, Pink Robin, Satin Bowerbird, Red-browed Finch and Swamp Harrier were recorded at more than one site (Table 2-3). Of ten species recorded exclusively at non-riparian sites, only Wedge-tailed Eagle, Buff-rumped Thornbill and Yellow Thornbill were recorded at multiple sites (Table 2-3).



**Table 2-2 Habitat variables characteristic of riparian and non-riparian habitats in the Victorian Highlands. Values represent the percentage contributions to similarity within riparian (RIP) and non-riparian (NR) sites, and dissimilarities between riparian and non-riparian sites (RIP v NR) based on Bray-Curtis indices (SIMPER). Analyses were conducted separately for structural variables and floristic composition of trees and shrubs.**

Variable	Similarity		Dissimilarity	Variable means	
	RIP	NR	RIP v NR	RIP	NR
Structural variables					
Canopy height	8.0	6.2		39.5	30.6
Fine litter	7.6	6.6	3.5	44.7	44.5
Coarse woody debris (≤50 cm)	7.2	5.2		140.0	103.6
Ground vegetation	7.1	6.7	4.1	43.8	51.7
Mid-storey trees	6.7		8.5	37.0	3.0
Sedges	6.2		5.5	39.0	12.2
Ground ferns	5.6		5.7	35.3	17.8
Tall shrubs	4.9			25.7	23.0
Tree ferns	4.0		5.2	16.0	2.3
Bare ground	3.8			13.5	9.7
Grasses	3.0	6.3	5.6	14.7	50.0
Canopy cover		8.7		35.5	56.0
Tree density (21-40 cm dbh)		6.7	4.9	44.8	164.0
Shrub cover (≤1 m)		4.5	4.5	4.2	22.8
Dead trees (≤10 cm)		4.3	3.2	38.8	95.6
Shrub cover (≥2 m)		4.2	3.5	25.7	23.0
Tree density (≤10 cm)		5.1	7.3	7.6	137.6
Tree density (11-20 cm)		5.0	5.7	12.0	118.4
Shrub cover (1 - 2 m)		4.9	3.6	9.7	25.0
Tree and shrub species (Importance Values)					
Coprosma quadrifida	31.4		9.4	120.9	9.2
Pomaderris aspera	16.3		5.7	41.0	0.8
Acacia melanoxylon	9.3		3.5	16.4	0.1
Acacia dealbata	7.9		3.0	12.3	0.8
Eucalyptus viminalis	6.5		3.7	25.3	
Eucalyptus radiata		23.33	5.4	16.8	66.3
Eucalyptus obliqua		13.34	4.5	16.8	48.1
Hakea sericea		8.1	3.3	14.0	10.4
Banksia spinulosa		6.9	2.9	0.8	15.9

**Table 2.2** continued

Variable	Similarity		Dissimilarity	Variable means	
	RIP	NR	RIP v NR	RIP	NR
Tree and shrub species (Importance Values)					
<i>Eucalyptus sieberi</i>		6.8	3.5		29.0
<i>Eucalyptus baxteri</i>		5.5	3.2	1.0	25.4
<i>Lomatia ilicifolia</i>		4.1	1.9		7.8
<i>Leptospermum continentale</i>		3.9	2.8		19.9
<i>Melaleuca squarrosa</i>			3.1	22.8	
<i>Eucalyptus camphora</i>			2.5	23.2	
<i>Spyridium parvifolium</i>			2.3		19.1
<i>Platylobium formosum</i>			2.2	6.0	11.1
<i>Epacris impressa</i>			1.9	0.6	7.6
<i>Leptospermum lanigerum</i>			1.4	14.9	

Bird assemblages of riparian zones were significantly richer in species compared with non-riparian habitats (paired  $t = 10.16$ , d.f. = 29,  $p < 0.001$ ). The mean species richness of assemblages in riparian habitats was 36.9 species ( $\pm 4.94$  SD, range 28–46), compared with 25.5 ( $\pm 3.92$  SD, range 18–33) for non-riparian habitats. In all cases, riparian sites supported higher species richness than occurred at their non-riparian site partner.

**Table 2-3      The relative abundance of bird species (individuals ha<sup>-1</sup>) recorded during point counts at riparian and non-riparian sites in the Victorian Highlands. The number of sites (n = 30) in riparian or non-riparian habitat at which each species was recorded is also presented.**

The distribution pattern of each species is identified. Only species recorded at ≥4 sites are included. Classification based on an abundance index discriminating between predominantly riparian and predominantly non-riparian species. Groups are: Forest generalist (Fg) = recorded evenly in both habitat types; Riparian selective (Rs) = only recorded at riparian sites; Riparian associated (Ra) = ≥75% of individuals recorded at riparian sites; Non-riparian selective (Ns) = only recorded at non-riparian sites; Non-riparian associated (Na) = ≥75% of individuals recorded at non-riparian sites.

Common name	Species name	Riparian			Non-riparian			Distribution pattern
		Sites	Mean	SE	Sites	Mean	SE	
Australian Shelduck	<i>Tadorna tadornoides</i>	2	0.01	0.01	-	-	-	
Australian Wood Duck	<i>Chenonetta jubata</i>	1	<0.01	<0.01	-	-	-	
Pacific Black Duck	<i>Anas superciliosa</i>	1	0.01	0.01	-	-	-	
Whistling Kite	<i>Haliastur sphenurus</i>	1	<0.01	<0.01	-	-	-	
Brown Goshawk	<i>Accipiter fasciatus</i>	6	0.02	0.01	2	<0.01	<0.01	Ra
Collared Sparrowhawk	<i>Accipiter cirrhocephalus</i>	1	<0.01	<0.01	1	<0.01	<0.01	
Wedge-tailed Eagle	<i>Aquila audax</i>	-	-	-	2	0.01	0.01	
Little Eagle	<i>Hieraaetus morphnoides</i>	1	<0.01	<0.01	2	0.01	0.01	
Swamp Harrier	<i>Circus approximans</i>	2	<0.01	<0.01		0.00	0.00	
Peregrine Falcon	<i>Falco peregrinus</i>	-	-	-	1	<0.01	<0.01	
Brush Bronzewing	<i>Phaps elegans</i>	-	-	-	1	<0.01	<0.01	
Yellow-tailed Black-Cockatoo	<i>Calyptrorhynchus funereus</i>	8	0.08	0.03	8	0.06	0.02	Fg
Gang-gang Cockatoo	<i>Callocephalon fimbriatum</i>	14	0.10	0.02	8	0.07	0.03	Fg
Sulphur-crested Cockatoo	<i>Cacatua galerita</i>	8	0.08	0.03	-	-	-	Ra
Musk Lorikeet	<i>Glossopsitta concinna</i>	2	<0.01	<0.01	1	<0.01	<0.01	
Little Lorikeet	<i>Glossopsitta pusilla</i>	2	0.01	0.01	1	<0.01	<0.01	
Purple-crowned Lorikeet	<i>Glossopsitta porphyrocephala</i>	1	<0.01	<0.01	-	-	-	

**Table 2–3      continued.**

Common name	Species name	Riparian			Non-riparian			Distribution pattern
		Sites	Mean	SE	Sites	Mean	SE	
Australian King Parrot	<i>Alisterus scapularis</i>	12	0.06	0.02	10	0.04	0.01	Fg
Crimson Rosella	<i>Platycercus elegans</i>	30	0.51	0.07	28	0.47	0.11	Fg
Eastern Rosella	<i>Platycercus eximius</i>	8	0.03	0.01	9	0.07	0.02	Fg
Swift Parrot	<i>Lathamus discolor</i>	1	<0.01	<0.01	-	-	-	
Pallid Cuckoo	<i>Cuculus pallidus</i>	1	<0.01	<0.01	1	<0.01	<0.01	
Fan-tailed Cuckoo	<i>Cacomantis flabelliformis</i>	13	0.04	0.01	11	0.04	0.01	Fg
Shining Bronze-Cuckoo	<i>Chrysococcyx lucidus</i>	20	0.07	0.01	10	0.03	0.01	Fg
Southern Boobook	<i>Ninox novaeseelandiae</i>	1	<0.01	<0.01	-	-	-	
Australian Owlet-nightjar	<i>Aegotheles cristatus</i>	-	-	-	1	<0.01	<0.01	
White-throated Needletail	<i>Hirundapus caudacutus</i>	1	<0.01	<0.01	5	0.06	0.03	Na
Laughing Kookaburra	<i>Dacelo novaeguineae</i>	19	0.11	0.03	15	0.08	0.02	Fg
Sacred Kingfisher	<i>Todiramphus sanctus</i>	10	0.04	0.01	1	<0.01	<0.01	Ra
Superb Lyrebird	<i>Menura novaehollandiae</i>	15	0.08	0.02	6	0.03	0.02	Fg
White-throated Treecreeper	<i>Cormobates leucophaeus</i>	30	0.54	0.05	26	0.43	0.06	Fg
Red-browed Treecreeper	<i>Climacteris erythrops</i>	27	0.50	0.09	9	0.08	0.03	Ra
Superb Fairy-wren	<i>Malurus cyaneus</i>	23	0.40	0.07	23	0.46	0.09	Fg
Southern Emu-wren	<i>Stipituris malachurus</i>	4	0.03	0.02	15	0.24	0.07	Na
Spotted Pardalote	<i>Pardalotus punctatus</i>	30	0.80	0.07	29	0.40	0.05	Fg
Striated Pardalote	<i>Pardalotus striatus</i>	30	1.31	0.15	23	0.17	0.03	Ra
White-browed Scrubwren	<i>Sericornis frontalis</i>	30	2.75	0.12	17	0.37	0.10	Ra
Large-billed Scrubwren	<i>Sericornis magnirostris</i>	22	0.23	0.05	1	<0.01	<0.01	Ra
White-throated Gerygone	<i>Gerygone olivacea</i>	1	<0.01	<0.01	-	-	-	
Brown Thornbill	<i>Acanthiza pusilla</i>	30	5.61	0.21	30	2.29	0.25	Fg

**Table 2–3 continued.**

Common name	Species name	Riparian			Non-riparian			Distribution pattern
		Sites	Mean	SE	Sites	Mean	SE	
Buff-rumped Thornbill	<i>Acanthiza reguloides</i>	-	-	-	4	0.09	0.05	Ns
Yellow Thornbill	<i>Acanthiza nana</i>	-	-	-	5	0.03	0.02	Ns
Striated Thornbill	<i>Acanthiza lineata</i>	30	4.52	0.37	30	3.16	0.31	Fg
Red Wattlebird	<i>Anthochaera carunculata</i>	28	0.54	0.10	27	1.21	0.27	Fg
Noisy Miner	<i>Manorina melanocephala</i>	-	-	-	1	<0.01	<0.01	
Lewin's Honeyeater	<i>Meliphaga lewinii</i>	15	0.15	0.03	1	<0.01	<0.01	Ra
Yellow-faced Honeyeater	<i>Lichenostomus chrysops</i>	30	2.03	0.15	29	0.28	0.05	Ra
White-eared Honeyeater	<i>Lichenostomus leucotis</i>	22	0.17	0.03	7	0.03	0.02	Ra
Yellow-tufted Honeyeater	<i>Lichenostomus melanops</i>	5	0.30	0.16	-	-	-	Rs
Brown-headed Honeyeater	<i>Melithreptus brevirostris</i>	21	0.22	0.06	12	0.09	0.04	Fg
White-naped Honeyeater	<i>Melithreptus lunatus</i>	29	4.33	0.74	15	0.15	0.05	Ra
Crescent Honeyeater	<i>Phylidonyris pyrrhoptera</i>	28	0.60	0.09	15	0.17	0.05	Ra
New Holland Honeyeater	<i>Phylidonyris novaehollandiae</i>	7	0.09	0.06	1	<0.01	<0.01	Ra
Eastern Spinebill	<i>Acanthorhynchus tenuirostris</i>	28	0.51	0.07	29	0.63	0.10	Fg
Scarlet Robin	<i>Petroica multicolor</i>	2	0.01	0.01	19	0.16	0.04	Na
Flame Robin	<i>Petroica phoenicea</i>	-	-	-	3	0.01	0.01	
Rose Robin	<i>Petroica rosea</i>	30	0.40	0.03	5	0.03	0.02	Ra
Pink Robin	<i>Petroica rodinogaster</i>	6	0.02	0.01	-	-	-	Rs
Eastern Yellow Robin	<i>Eopsaltria australis</i>	30	0.98	0.09	21	0.25	0.05	Ra
Eastern Whipbird	<i>Psophodes olivaceus</i>	19	0.19	0.04	1	<0.01	<0.01	Ra
Varied Sittella	<i>Daphoenositta chrysoptera</i>	21	0.21	0.04	17	0.18	0.04	Fg
Crested Shrike-tit	<i>Falcunculus frontatus</i>	16	0.08	0.02	1	<0.01	<0.01	Ra
Olive Whistler	<i>Pachycephala olivacea</i>	21	0.11	0.02	3	0.01	0.00	Ra

**Table 2–3**      **continued.**

Common name	Species name	Riparian			Non-riparian			Distribution pattern
		Sites	Mean	SE	Sites	Mean	SE	
Golden Whistler	<i>Pachycephala pectoralis</i>	30	0.90	0.08	28	0.20	0.03	Ra
Rufous Whistler	<i>Pachycephala rufiventris</i>	15	0.08	0.02	26	0.24	0.04	Na
Grey Shrike-thrush	<i>Colluricincla harmonica</i>	28	0.21	0.03	28	0.27	0.03	Fg
Leaden Flycatcher	<i>Myiagra rubecula</i>	-	-	-	1	<0.01	<0.01	
Satin Flycatcher	<i>Myiagra cyanoleuca</i>	22	0.19	0.04	6	0.03	0.01	Ra
Rufous Fantail	<i>Rhipidura rufifrons</i>	28	0.37	0.04	5	0.02	0.01	Ra
Grey Fantail	<i>Rhipidura fuliginosa</i>	30	1.84	0.11	29	0.63	0.08	Fg
Black-faced Cuckoo-shrike	<i>Coracina novaehollandiae</i>	11	0.04	0.01	13	0.08	0.02	Fg
Olive-backed Oriole	<i>Oriolus sagittatus</i>	4	0.02	0.01	13	0.06	0.01	Na
Dusky Woodswallow	<i>Artamus cyanopterus</i>	2	0.09	0.07	2	0.01	0.01	Ra
Grey Butcherbird	<i>Cracticus torquatus</i>	1	<0.01	<0.01	3	0.03	0.02	Na
Australian Magpie	<i>Gymnorhina tibicen</i>	1	<0.01	<0.01	-	-	-	
Pied Currawong	<i>Strepera graculina</i>	7	0.05	0.02	9	0.09	0.04	Fg
Grey Currawong	<i>Strepera versicolor</i>	9	0.04	0.01	8	0.03	0.01	Fg
Australian Raven	<i>Corvus coronoides</i>	6	0.03	0.02	2	0.01	0.01	Ra
White-winged Chough	<i>Corcorax melanorhamphos</i>	-	-	-	1	0.02	0.02	
Satin Bowerbird	<i>Ptilonorhynchus violaceus</i>	4	0.07	0.04	-	-	-	Rs
Red-browed Finch	<i>Neochmia temporalis</i>	3	0.01	0.01	-	-	-	
Beautiful Firetail	<i>Stagonopleura bella</i>	16	0.17	0.04	2	0.01	0.01	Ra
Mistletoebird	<i>Dicaeum hirundinaceum</i>	8	0.02	0.01	9	0.03	0.01	Fg
Welcome Swallow	<i>Hirundo neoxena</i>	4	0.04	0.02	3	0.02	0.01	Fg
Tree Martin	<i>Hirundo nigricans</i>	22	0.71	0.24	5	0.04	0.02	Ra
Silvereye	<i>Zosterops lateralis</i>	30	1.58	0.17	23	0.19	0.05	Ra

**Table 2–3      continued.**

Common name	Species name	Riparian			Non-riparian			Distribution pattern
		Sites	Mean	SE	Sites	Mean	SE	
Bassian Thrush	<i>Zoothera lunulata</i>	19	0.13	0.03	4	0.01	0.01	Ra
*Common Blackbird	<i>Turdus merula</i>	12	0.05	0.01	-	-	-	Rs

\* = Introduced species

The relative abundance of birds recorded in riparian habitats, 35.5 individuals ha<sup>-1</sup> ( $\pm 8.12$  SD, range 21.3–50.3), was also significantly greater (paired  $t = 12.17$ , d.f. = 29,  $p < 0.001$ ), than that registered in non-riparian habitats, 14.0 individuals ha<sup>-1</sup> ( $\pm 4.95$  SD, range 5.7–23.5). The diversity of bird assemblages was also significantly greater (paired  $t = 2.93$ , d.f. = 29,  $p = 0.003$ ) in riparian habitats ( $H' = 3.09$ , SD  $\pm 0.23$ ) compared with that in non-riparian habitats ( $H' = 2.28$ , SD  $\pm 0.31$ ).

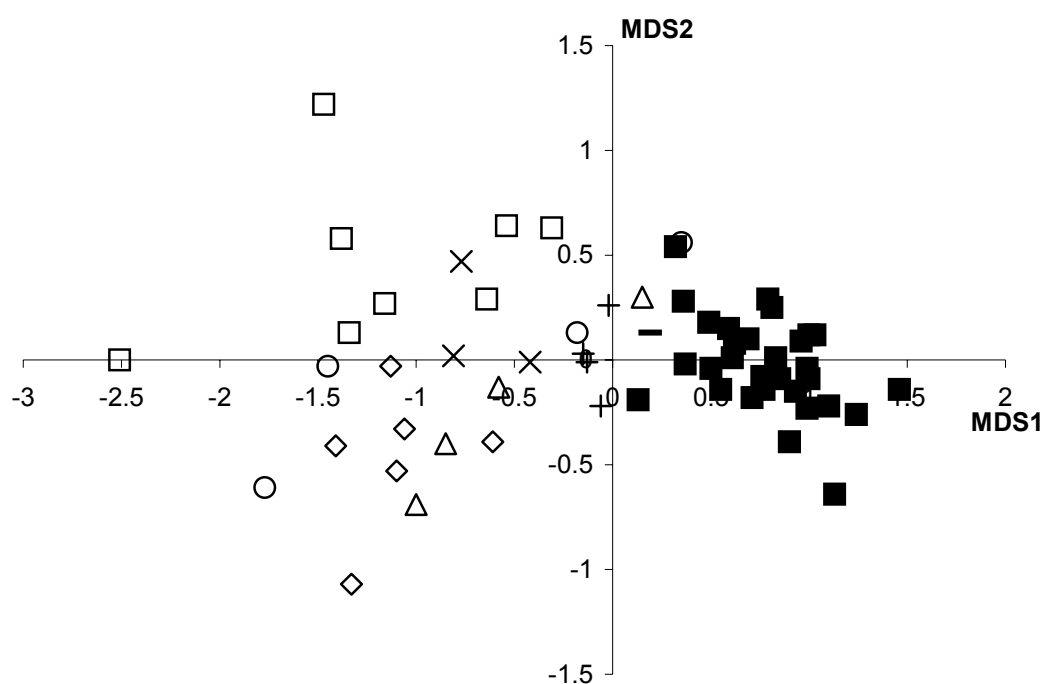
The species composition of bird assemblages differed significantly between riparian and adjacent non-riparian habitats (ANOSIM,  $R = 0.713$ ,  $p < 0.001$ ) (Figure 2-1). A SIMPER analysis showed that for riparian sites, 13 bird species contributed approximately 70% of the similarity among assemblages occurring at these sites. Those contributing most to the similarity of riparian assemblages included Brown Thornbill (10.9%), Striated Thornbill (8.9%), White-browed Scrubwren (7.5%), Yellow-faced Honeyeater (6.0%) and Grey Fantail (5.9%). Eleven species contributed to 70% of the similarity among assemblages at non-riparian sites. The greatest contributors were Striated Thornbill (15.8%), Brown Thornbill (12.8%), Red Wattlebird (6.3%), Grey Fantail (6.2%) and Eastern Spinebill (5.4%). Half (7 of 14 species) of the species contributing most to the similarities within riparian or non-riparian habitats were common to both: Brown Thornbill, Striated Thornbill, Yellow-faced Honeyeater, Grey Fantail, Spotted Pardalote, Golden Whistler and White-throated Treecreeper.

Twenty-seven species accounted for 70% of the dissimilarity between bird assemblages of riparian and non-riparian habitats. The greatest contributors were White-naped Honeyeater (6.7%), White-browed Scrub-wren (5.7%), Brown Thornbill (4.3%), Yellow-faced Honeyeater (4.1%) and Silvereye (3.9%). By comparing the mean abundance of birds in each habitat type (Table 2-3) it is evident that species contributions to dissimilarities were predominantly generated by those with large contrasts in relative abundance between habitat types. Species more abundant in riparian habitats included White-naped Honeyeater, Brown Thornbill, White-browed Scrubwren, Silvereye and Yellow-faced Honeyeater (Table 2-3). Overall 36% ( $n = 32$ ) of species attained a greater abundance in riparian habitats. Those with higher abundance in non-riparian habitats, and contributing strongly to dissimilarities between habitat types, included Red Wattlebird (2.6%), Superb Fairy-wren (2.0%) and Rufous



Whistler (1.4%) (Table 2-3).

An MDS ordination of sites based on the species composition of their bird assemblages clearly displayed the contrast between riparian and non-riparian sites (Figure 2-1) and provided a good fit to the data (stress = 0.1) (Clarke and Gorley 2001). There was a distinguishable clustering of sites, based on bird species composition, which corresponded with ecological vegetation classes (Figure 2-1). Riparian sites (i.e. Riparian Forest) were strongly correlated at the positive end of MDS dimension 1 (MDS1) (Figure 2-1). There was greater variation among non-riparian sites in the composition of bird assemblages, with sites spread in ordination space in a pattern reflecting their vegetation type (Figure 2-1).



**Figure 2-1 Ordination of bird assemblages occurring at sites in the Victorian Highlands (stress = 0.1).**

The ecological vegetation class for the site at which each assemblage occurs is displayed: Riparian Forest (■), Wet Forest (▲), Damp Forest (○), Shrubby Foothill Forest (△), Herb-rich Foothill Forest (+), Lowland Forest (◇), Heathy Dry Forest (x) and Heathy Woodland (□).

Correlation analyses (Spearman rank correlation) showed that many habitat variables were significantly correlated with MDS1. This ordination dimension generally represents a gradient from wet to drier forest types. Variables positively correlated with MDS1 were characteristic of riparian habitats (Figure 2-1), including foliage cover of mid-storey trees ( $r_s = 0.825$ ,  $p < 0.01$ ), cover of tree ferns ( $r_s = 0.750$ ,  $p < 0.01$ ), ground ferns ( $r_s = 0.438$ ,  $p < 0.01$ ), creepers ( $r_s = 0.485$ ,  $p < 0.01$ ), sedges ( $r_s = 0.409$ ,  $p < 0.01$ ) and canopy height ( $r_s = 0.446$ ,  $p < 0.01$ ). Variables negatively correlated with MDS1 were indicative of non-riparian habitats (Figure 2-1). These included high densities of trees in the  $\leq 10$  cm dbh ( $r_s = -0.631$ ,  $p < 0.01$ ), 11–20 cm ( $r_s = -0.724$ ,  $p < 0.01$ ) and 21–40 cm dbh ( $r_s = -0.724$ ,  $p < 0.01$ ) size-classes, shrub richness ( $r_s = -0.666$ ,  $p < 0.01$ ), cover of low shrubs  $< 1$  m ( $r_s = -0.606$ ,  $p < 0.01$ ) and cover of grasses ( $r_s = -0.599$ ,  $p < 0.01$ ).

The second MDS dimension (MDS2) was not as readily interpretable as MDS1. It represents a gradient from sites with a high density of trees of smaller diameter and a dense low shrub layer, to sites with larger trees, of increased height, and a dense ground fern layer (Figure 2-1).

## 2.4 Discussion

### 2.4.1 Landscape pattern and bird assemblages

The value of riparian habitats for birds in mesic forests of the Victorian Highlands is disproportionately high compared with the extent of riparian vegetation in the forest landscape ( $< 10\%$  of the area). The ecological value of these habitats is evidenced by the higher richness, diversity and abundance of bird species that they support, and by the distinctive composition of the avifauna which complements that occurring in adjacent habitats. These observations from continuous forest are consistent with the findings from studies of riparian zones in arid and semi-arid environments (Shurcliff 1980; Szaro and Jakle 1985; Saab 1999; Aumann 2001), and of remnant riparian vegetation in developed landscapes (Warkentin *et al.* 1995; Fisher and Goldney 1997; Rottenborn 1999; Miller *et al.* 2003), and amongst plantation and production forests (Friend 1982; Armstrong and van Hensbergen 1994; Lindenmayer *et al.* 2002; Conner *et al.* 2004). The high value of riparian habitats for wildlife has been linked to a number

of factors associated with the riparian zone, including greater availability of water (Gregory *et al.* 1991), increased habitat complexity (Bull and Skovlin 1982; Douglas *et al.* 1992), greater levels of food resources (Gray 1993; Murakami and Nakano 2002), and the benefits associated with multiple edge-effects (Gates and Giffen 1991).

The influence of riparian habitats in shaping bird assemblages in mesic forest landscapes in this study is emphasised by several factors. First, riparian assemblages might have been expected to be less distinct given the relatively small distances between paired riparian and non-riparian sites (<1 km). Second, the mobility of birds, coupled with the continuity of forest habitat between riparian and non-riparian sites, also contributes to an expectation of greater similarity between habitat types. Third, in temperate and mesic forests the more-subtle gradient in vegetation structure away from streams (cf. dry environments) can be expected to have less impact on the structure of bird assemblages (McGarigal and McComb 1992; Catterall *et al.* 2001). However, despite the relatively narrow width and limited extent of riparian vegetation in the forest mosaic, marked differences in the structure and composition of bird communities between riparian and non-riparian sites clearly show that riparian habitats have a strong influence on the distributional patterns of birds in this forest landscape.

Five broad groups of species can be distinguished in this study area, based on their distributional patterns (Table 2-3). Forest generalists (36% of all species) are species that are widespread throughout the forested landscape; riparian and non-riparian sites each supported between 25–75% of all individuals recorded (e.g. Brown Thornbill, Striated Thornbill, Spotted Pardalote, Grey Shrike-thrush, Crimson Rosella, Grey Fantail and White-throated Treecreeper) (Table 2-3). Overall, much of the avifauna of this study area is composed of species with widespread distributions throughout southeast Australia (Blakers *et al.* 1984; Loyn 1985b; Emison *et al.* 1987; Brown *et al.* 1989; Barrett *et al.* 2003) and predictably these were found throughout the landscape mosaic. Many of these species, although widespread, were more abundant in riparian than non-riparian habitats.

Riparian habitats were characterised by a suite of species more typical of wetter forest types in south-east Australia. Many of these species typically had a restricted distribution in the forest mosaic. Riparian selective species (7%) are those that occurred exclusively in riparian habitats (e.g. Yellow-tufted Honeyeater, Pink Robin,

Satin Bowerbird and the introduced Common Blackbird), while riparian associated species (43%) were strongly linked to riparian habitats (i.e. >75% of all individuals were from riparian sites), although they also occurred in non-riparian habitats, particularly wetter vegetation types (e.g. Red-browed Treecreeper, Large-billed Scrubwren, Lewin's Honeyeater, Rose Robin, Eastern Whipbird, Olive Whistler, Rufous Fantail and Beautiful Firetail) (Table 2-3). Several such species have core ranges centred on rainforests and closed forests of coastal central and northern Australia, and are uncommon in Victoria (e.g. Large-billed Scrubwren and Lewin's Honeyeater) (Loyn *et al.* 1980; Emison *et al.* 1987; Barrett *et al.* 2003).

In contrast, several species recorded at non-riparian sites were conspicuously absent from, or seldom occurred in, riparian habitats. Notably, many of these species were most prominent in the low, open heathy woodland communities, which were the most distinct from riparian habitats in structure, floristic composition and bird composition. Non-riparian selective species (2%) are those birds that occurred exclusively in non-riparian habitats (e.g. Buff-rumped Thornbill and Yellow Thornbill) while non-riparian associated species (10%) are those strongly linked to non-riparian habitats (i.e. supporting >75% of all individuals), although they also occurred in riparian habitats (e.g. Scarlet Robin, Southern Emu-wren, Rufous Whistler and Olive-backed Oriole) (Table 2-3).

Any classification of birds in relation to riparian habitats is likely to be scale-specific (Kinley and Newhouse 1997; Woinarski *et al.* 2000), or responsive to other factors such as landscape position (Knopf 1985; Finch 1989), such that the specific composition of groups can not necessarily be generalised between regions. For example, in the dry box-ironbark forests of central Victoria, Mac Nally *et al.* (2000) recorded distributional patterns for a range of species occurring at 'gully' (intermittent stream channels) and ridge sites, including a number of species common to this study. There, the Red Wattlebird and Eastern Rosella were among species which were more abundant in gullies and which contributed strongly to compositional differences between gully and ridge sites. In this study, both species were more abundant in non-riparian habitats (Table 2-3). Thus, while the underlying principle is the same, that riparian zones support high bird species richness and abundance and distinct assemblages, species affinities may differ across large spatial scales.

### 2.4.2 *Habitat characteristics and bird assemblages*

Structural complexity of habitats has long been known to influence avian species richness and composition (MacArthur and MacArthur 1961; Willson 1974; Cody 1981) and frequently has been cited as a key factor to explain contrasts between bird assemblages of riparian zones and surrounding habitats (Hubbard 1977; Emmerich and Vohs 1982; Finch 1989). In this study, riparian habitats were floristically and structurally distinct from adjacent upland vegetation and consequently their presence promotes habitat diversity across the forest landscape. Riparian habitats have a more complex vegetation structure, including a mid-storey tree layer largely absent from non-riparian habitats. They also support plant species and associations not generally found in non-riparian situations. For example, eucalypts of the sub-genus *Symphyomyrtus* (e.g. Manna Gum *Eucalyptus viminalis*, Mountain Swamp Gum *E. camphora* and Swamp Gum *E. ovata*) are dominant in riparian situations, while species of sub-genus *Monocalyptus* (e.g. Messmate *E. obliqua*, Narrow-leaved Peppermint *E. radiata*, Silvertop Ash *E. sieberi* and Brown Stringybark *E. baxteri*) tend to dominate non-riparian habitats (Austin *et al.* 1996; Catterall *et al.* 2001).

While habitat structural complexity has been associated with greater richness and abundance of bird assemblages in riparian zones (Douglas *et al.* 1992; Sanders and Edge 1998), less emphasis has been given to floristic composition in shaping the avifauna of riparian habitats. In this study, both physiognomic and floristic differences between habitat types influence bird assemblages. For example, the complex mid-storey of riparian vegetation provides favoured foraging habitat for several species characteristic of riparian habitats (e.g. Rose Robin, Lewin's Honeyeater and Golden Whistler). Similarly, the occurrence of a number of bark-foraging species (e.g. Crested Shrike-tit and White-eared Honeyeater) was closely associated with that of bark-decortivating eucalypts (e.g. Manna Gum *Eucalyptus viminalis*, Mountain Swamp Gum *E. camphora* and to a lesser degree Narrow-leaved Peppermint *E. radiata*), which predominate in riparian zones (Austin *et al.* 1996). Birds more typical of non-riparian habitats include several that favour the more-open ground layer for foraging, including Buff-rumped Thornbill and Scarlet Robin. Indeed, consideration of community level measures (e.g. richness, diversity) in isolation may mask the interrelated influences of physiognomic and floristic factors on bird communities. The taxonomic diversity and

the wide range of ecological requirements among species strongly associated with riparian zones (i.e. riparian selective and riparian associated species), suggests that the riparian influence is unlikely to be due to a specific structural feature or floristic characteristic (Woinarski *et al.* 2000).

#### 2.4.3 Implications for conservation

Riparian habitats are important for avifaunal conservation in continuous forest landscapes for at least five reasons. First, the vegetation differs in both floristic composition and structural complexity from that of adjacent non-riparian habitats. Thus, riparian zones add to the diversity of the landscape mosaic and to the diversity of habitats and resources available to forest birds. Second, a suite of bird species is strongly associated with, or predominantly confined to, the riparian zone. These species are likely to occur in relatively lower abundance (or be absent) from the forest landscape if not for the presence of riparian vegetation. Third, most forest bird species use riparian habitats at some stage of their life, and more than a third of all species (36%) attained higher densities in riparian habitats than in other forest types. Fourth, the distinctiveness of riparian vegetation and the prevalence of bird species typical of wet forests, suggest that they may function as seasonal or refuge habitats when conditions become stressful in upland habitats. This includes the potential for these habitats to function as drought and fire refuges (Nix 1993). Last, riparian habitats in this study area are known to be used by several species of threatened conservation status, including the Powerful Owl *Ninox strenua* and Sooty Owl *Tyto tenebricosa* (Loyn *et al.* 2001).

While riparian habitats characteristically support richer and more abundant assemblages, they comprise only a small proportion of the forest landscape (<10% of the total area). Most of the landscape consists of non-riparian forest and it is these forests, by virtue of their greater area, that serve as the major population reservoirs for most species of forest birds. Consequently, the ecological role and value of non-riparian habitats should not be overlooked. Further, riparian habitats are not suitable for all species (McGarigal and McComb 1992; Murray and Stauffer 1995; Mac Nally *et al.* 2000). In this study a number of species clearly were associated with non-riparian habitats, including at least 12% of species classed as non-riparian selective and non-

riparian associated species. Clearly, the maintenance of diverse and sustainable assemblages of birds in forest landscapes depends on complementary management of both riparian and non-riparian vegetation types. This highlights the importance of landscape-level planning and management for avifaunal conservation in forest mosaics.

### 3 Seasonal patterns of variation in the structure of riparian and non-riparian bird assemblages in a forest mosaic

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White-naped Honeyeater *Melithreptus lunatus* (T. Wilson)



### 3.1 Introduction

Riparian habitats are widely considered to be key elements for biodiversity in the landscape (Brooker 1983; Decamps *et al.* 1987; Catterall 1993; Naiman *et al.* 1993; Knopf and Samson 1994; Kelsey and West 1998). The value of riparian habitats is often attributed to their role in supporting an increased richness and abundance of birds, and wildlife in general, than is found in the surrounding non-riparian matrix (Szaro and Jakle 1985; Recher *et al.* 1991; Naiman *et al.* 1993; Chan 1995; Soderquist and Mac Nally 2000; Pearson and Manuwal 2001; Iwata *et al.* 2003). Greater structural complexity of vegetation (Stauffer and Best 1980; Bull and Skovlin 1982), increased availability of food resources (Gray 1993; Lynch *et al.* 2002) and benefits of edge-associated effects (Bull 1978) in riparian zones have been some of the major features associated with such trends. Reduced variation in microclimatic conditions (i.e. temperature and humidity), interacting with higher nutrient concentrations and greater water availability in riparian situations often facilitate increased primary production and stability in plant growth and resource states throughout the year (Gregory *et al.* 1991; Malanson 1993). It has been proposed that riparian habitats provide stable, high-quality habitats for wildlife throughout the year, or importantly at crucial times in the year (Catterall 1993; Lynch and Catterall 1999).

Species richness and abundance is closely tuned to available energy, and areas of greater productivity have been shown to support greater numbers of individuals, and accordingly more species (Hawkins *et al.* 2003; Hurlbert and Haskell 2003). Species-energy theory predicts that seasonal variation in avian richness should reflect underlying variation in available energy, and that it is not overall energy supply that determines species richness, but the seasonal stability in productivity that does so. Less seasonal variation in productivity is believed to permit finer ecological structuring in communities, thus promoting richness (Turner *et al.* 1988). These principles have been examined at large spatial scales (e.g. Hurlbert and Haskell 2003), but they are also likely to operate at the landscape level.

There is evidence that the buffering of riparian habitats from seasonal cycles operating within the landscape, and the associated provision of more predictable and reliable

conditions, benefits wildlife. For example, in Zimbabwe, large mammalian herbivores were found to move on to the expansive floodplain areas of the Zambezi River during the dry season as conditions away from the river deteriorated (Dunham 1994).

Similarly for birds, the distributions of some species in the tropical savannas of northern Australia contract into riparian habitats across the landscape, as resource availability (particularly nectar) declines in the late dry season (Woinarski *et al.* 2000).

Birds present a sound opportunity to evaluate the effects of spatial and temporal change in habitat quality on species richness and abundance, as they are capable of movements that enable them to respond to temporal shifts in habitat suitability at a range of spatial scales. Preferred or high-quality habitats are therefore likely to be identified in the landscape via disproportionate use when compared to other habitat types. Species' preferences for higher quality habitat in the landscape may or may not be registered by a greater abundance of individuals, but are likely to be reflected in less variability in abundance in high-quality than in marginal habitats, at least if habitat occupancy patterns are driven by density (Wiens 1989).

In Chapter 2 it was shown that riparian assemblages supported a greater richness and abundance of birds, and a distinct composition when compared with non-riparian assemblages. This chapter investigates seasonal patterns in these features between riparian and non-riparian assemblages occurring in foothill eucalypt forest in the Victorian Highlands in south-east Australia. While bird-habitat relationships and temporal variation in community parameters are common research interests in community ecology, the focus in this study is the season-by-habitat interaction of riparian and non-riparian bird assemblages. Here the objective is to quantify and compare the variation in bird assemblages between seasons in riparian and non-riparian habitats.

This research was designed to test two hypotheses:

1. The structure (i.e. richness, abundance) of riparian bird assemblages displays less variation through time than non-riparian assemblages.
2. The composition of riparian bird assemblages displays less variation through time than non-riparian assemblages.

## 3.2 Methods

### 3.2.1 *Study area*

The study was conducted in three areas of extensive eucalypt forest in the foothills of the south-west part of the Victorian Highlands, south-east Australia. The study area is described in detail in Chapter 1 and Chapter 2.

### 3.2.2 *Study sites*

A set of 30 paired riparian and non-riparian sites (described in Chapter 2) was used as a basis to compare seasonal patterns of variation in the structure of riparian and non-riparian bird assemblages.

### 3.2.3 *Bird surveys*

Bird assemblages were sampled using a fixed-point count method (Pyke and Recher 1984). Fixed-points were centrally located in two adjoining plots – each 50 m x 50 m – yielding a combined sampling area of 0.5 ha. At each fixed-point the survey time was standardised to 8 min. Upon completion of the survey at the first point, the observer moved to the next point and commenced another 8 min count, a standard 2 min after completion of the first. All birds seen or heard within the two plots were recorded. Occurrence of birds within plots and movements between plots were closely monitored to avoid duplication of individual observations wherever possible. The avian data reported here is limited to that recorded from the 0.5 ha sampling area unless otherwise specified.

During the period of study, each site was visited on 29 occasions, amounting to 3 480 point counts across the 60 sites. Between July 2001 and December 2002, visits to sites were as follows: winter 2001 (n = 2 visits), spring 2001 (n = 5), summer 2001 (n = 5), autumn 2002 (n = 5), winter 2002 (n = 5), spring 2002 (n = 5) and summer 2002 (n = 2). Two ‘familiarisation’ trips to all sites were undertaken prior to beginning surveys. Surveys were conducted throughout the day (between sunrise and sunset) in suitably still and dry conditions. Sympathetic to the constraints posed by geographic separation, sites were grouped by stream units and the order of site-pair censuses was randomised

within these units. Similarly, the sequence in which the paired sites were visited was randomised and the sequence in which fixed-points at a site were surveyed was alternated.

### 3.2.4 *Movement groups*

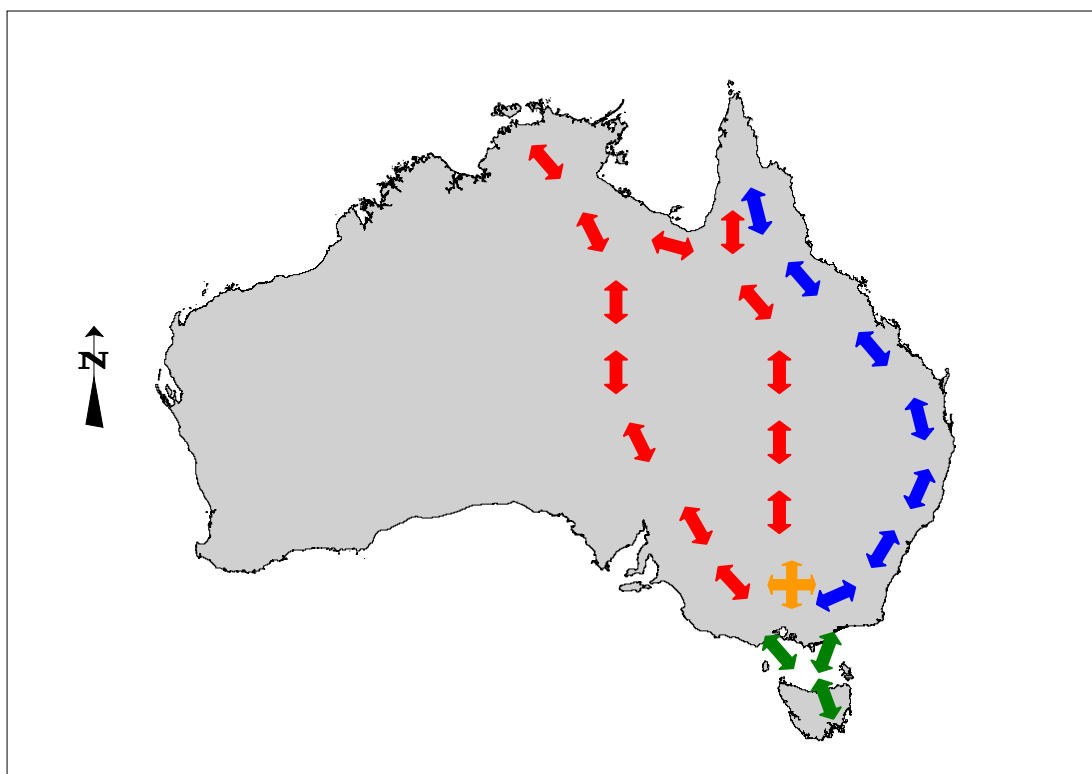
Bird species were categorised into groups based on the large-scale movement patterns (Table 3-1) described by Griffioen and Clarke (2002) from analyses of the Birds Australia Atlas database for south-east Australia (Figure 3-1). These movement groups were defined as follows.

1. Resident – mostly sedentary, no obvious population shifts detected beyond 200 km (e.g. Brown Thornbill, White-throated Treecreeper, Eastern Yellow Robin and Superb Lyrebird).
2. Local – population shifts greater than 200 km evident for populations in some parts of the species range (e.g. Red Wattlebird, Spotted Pardalote, Yellow-tailed Black-Cockatoo and Varied Sittella).
3. Coastal – northward east-coast migration from study area during winter (e.g. Yellow-faced Honeyeater, Golden Whistler, Grey Fantail, Rose Robin and Shining Bronze-Cuckoo).
4. Inland – northward inland migration from south-east Australia during winter (e.g. Striated Pardalote, Sacred Kingfisher, Black-faced Cuckoo-shrike and Olive-backed Oriole).
5. Tasmanian – northward trans-Bass Strait migration from Tasmania to nearby areas on the mainland during winter (e.g. Flame Robin, Pink Robin and Olive Whistler).

### 3.2.5 *Dietary groups*

Each species was placed in one of five diet groups based on their main dietary preference: insectivore, nectarivore/insectivore, nectarivore, vertebrate and seeds/fruit (Table 3-1). Diet information was referenced from Barker and Vestjens (1990), Marchant and Higgins (1990b; 1990a; 1993), Higgins and Davies (1996), Higgins

(1999), Higgins *et al.* (2001), Higgins and Peter (2002) and Higgins *et al.* (2006a; 2006b).



**Figure 3-1** A generalised diagram of the large-scale movement patterns displayed by birds in eastern Australia (adapted from Griffioen and Clarke (2002)) that were used to classify species into large-scale movement groups.

Large-scale movement groups are: coastal (blue arrows), inland (red), Tasmanian (green) and local (orange).

### 3.2.6 Data analysis

The structure of bird assemblages (i.e. species richness and abundance) through time was analysed using a repeated measures ANOVA (rmANOVA) to compare between riparian and non-riparian sites for each pair. In this design, habitat type represented subjects, with riparian and non-riparian being a fixed within-subject factor. Sites within each habitat type were effectively random factors, as they represented a randomly

selected sample of these habitats in the landscape. Seasons represented trials, with seven levels specified (winter 2001, spring 2001, summer 2001, autumn 2002, winter 2002, spring 2002 and summer 2002). In analysing assemblage structure, two response variables were used: mean species richness per visit ( $\sqrt{}$ -transformed to meet homogeneity of variance assumptions for the ANOVA) and individual birds ha<sup>-1</sup> (averaged across all visits in the season). Mean species richness per visit was used to control for variation in the numbers of visits between seasons.

Variation in species richness through time was also analysed by using paired *t*-tests to compare coefficient of variation (CV) values between riparian and non-riparian assemblages. A similar technique was used to examine variation in abundance of individuals through time between habitat types.

Analysis of the species composition of bird assemblages through time was based on a visit-by-species matrix. Observations of each bird species from each of the 30 sites in riparian and non-riparian habitats, respectively, were pooled for each visit (*viz.* a complete survey round of all sites). Multi-dimensional scaling (MDS) ordinations, based on a Bray-Curtis similarity index, were then undertaken to examine the relationship of the bird assemblages for each habitat type (*i.e.* riparian or non-riparian) over time (*i.e.* consecutive visits, seasons).

The similarity in the species composition of assemblages through time was analysed using paired *t*-tests to compare Bray-Curtis similarity values between riparian and non-riparian sites.

The SIMPER procedure (PRIMER package) was used to identify species that contributed most to assemblage dissimilarities between riparian and non-riparian habitats. The 10 species that contributed most to the dissimilarities for each visit were highlighted.

To investigate differences in the patterns of occurrence of movement groups in riparian and non-riparian bird assemblages, chi-squared tests of association were used to compare the proportional contribution of bird species assigned to movement groups between riparian and non-riparian habitats for each season. Residual values were used to indicate where the main differences lay. A similar technique was used to

investigate differences in the pattern of occurrence of dietary groups between habitat types.

Seasonal variation between habitats for species classified as sedentary (i.e. residents, no movement) was tested using a rmANOVA, applying the same design as above, with the response variable being the proportion of resident individuals in the assemblage.

For all analyses, a test statistic was deemed to be significant at the  $p = 0.05$  level.

### **3.3 Results**

#### ***3.3.1 Bird assemblages***

A total of 88 bird species was observed at sites during the study (Table 3-1). Riparian habitats supported a greater species richness and abundance of individuals and a distinctive species composition, when compared to non-riparian habitats (Chapter 2).

**Table 3-1 Relative abundance (individuals ha<sup>-1</sup>) of birds occurring in riparian (R) and non-riparian (NR) habitats (n = 30), each season between July 2001 and December 2002.**

The number of visits to each site in each season was: winter 2001 (n = 2), spring 2001 (5), summer 2001/02 (5), autumn 2002 (5), winter 2002 (5), spring 2002 (5), summer 2002/03 (2). Movement pattern (LSM) and diet classifications for all birds recorded. LSM refers to large-scale movement patterns displayed by species in eastern Australia (adapted from Griffioen and Clarke 2002); R = resident, L = local, C = coastal, In = inland, T = Tasmanian. Diet classifications include: A = aquatic, V = vertebrates, I = invertebrates, NI = nectar/invertebrates, N = Nectar, SF = seeds/fruits. \*Introduced species.

Common name	LSM	Diet	Winter 2001		Spring 2001		Summer 2001		Autumn 2002		Winter 2002		Spring 2002		Summer 2002	
			R	NR	R	NR	R	NR	R	NR	R	NR	R	NR	R	NR
Australian Shelduck	R	A	0.07								0.03					
Australian Wood Duck	In	A									0.03					
Pacific Black Duck	R	A	0.07				0.01						0.01			
Whistling Kite	R	V													0.03	
Brown Goshawk	In	V			0.01	0.01					0.03		0.04	0.01	0.03	
Collared Sparrowhawk	R	V				0.01							0.01			
Wedge-tailed Eagle	R	V						0.03			0.03					
Little Eagle	In	V					0.01						0.04			
Swamp Harrier	In	V			0.03											
Peregrine Falcon	L	V														0.03
Brush Bronzewing	L	SF						0.01								
Yellow-tailed Black-Cockatoo	L	SF	0.17		0.03		0.08	0.13	0.15	0.03			0.09	0.05	0.10	0.40
Gang-gang Cockatoo	R	SF	0.07		0.11		0.25		0.05	0.08		0.07	0.08	0.27	0.13	
Sulphur-crested Cockatoo	R	SF			0.09		0.04		0.07		0.09		0.13		0.03	
Musk Lorikeet	R	N							0.03	0.03						
Little Lorikeet	L	N						0.01	0.04							
Purple-crowned Lorikeet	R	N							0.03							
Australian King Parrot	R	SF	0.03		0.08	0.07	0.13		0.04	0.03	0.05	0.04	0.04	0.09	0.03	
Crimson Rosella	R	SF	0.43	0.03	0.35	0.48	0.48	0.31	0.71	0.44	0.47	0.61	0.60	0.57	0.40	0.77



**Table 3–1** continued.

Common name	LSM	Diet	Winter 2001		Spring 2001		Summer 2001		Autumn 2002		Winter 2002		Spring 2002		Summer 2002	
			R	NR	R	NR	R	NR	R	NR	R	NR	R	NR	R	NR
Eastern Rosella	R	SF			0.03	0.09	0.08		0.04		0.07	0.01	0.23	0.03		
Swift Parrot	R	N							0.01							
Pallid Cuckoo	In	I			0.01	0.01										
Fan-tailed Cuckoo	C	I			0.08	0.09	0.04	0.05	0.04		0.01	0.04	0.04	0.13	0.03	
Shining Bronze-Cuckoo	C	I			0.07	0.07	0.08	0.03				0.17	0.04	0.17	0.03	
Southern Boobook	In	V											0.03			
Australian Owlet-nightjar	R	I							0.01							
White-throated Needletail	C	I					0.36			0.01						
Laughing Kookaburra	R	V	0.17	0.20	0.20	0.05	0.09	0.03	0.01	0.07	0.09	0.08	0.08	0.15	0.20	0.07
Sacred Kingfisher	In	V			0.04		0.11					0.09			0.03	
Superb Lyrebird	R	I	0.03	0.03	0.04		0.09	0.03	0.11	0.05	0.13	0.03	0.09	0.08		
White-throated Treecreeper	R	I	0.73	0.20	0.61	0.53	0.47	0.32	0.41	0.37	0.63	0.57	0.53	0.48	0.47	0.37
Red-browed Treecreeper	R	I	0.43		0.65	0.04	0.44	0.09	0.29	0.05	0.47	0.19	0.65	0.05	0.57	0.07
Superb Fairy-wren	R	I	0.37	0.03	0.49	0.45	0.20	0.40	0.33	0.16	0.57	0.67	0.40	0.71	0.43	0.67
Southern Emu-wren	R	I		0.10		0.13	0.03	0.33	0.01	0.19	0.04	0.33	0.05	0.25	0.07	0.30
Spotted Pardalote	L	I	0.90	0.10	1.00	0.43	0.85	0.36	0.56	0.19	0.64	0.20	1.01	0.73	0.47	0.97
Striated Pardalote	In	I	0.47		2.08	0.28	1.47	0.17	0.28	0.04	0.79	0.05	2.12	0.31	1.67	0.40
White-browed Scrubwren	R	I	3.83	0.17	2.40	0.24	2.37	0.17	2.29	0.37	2.97	0.49	3.19	0.64	3.03	0.43
Large-billed Scrubwren	R	I	0.07		0.40	0.03	0.17		0.12		0.17		0.24		0.43	
White-throated Gerygone	In	I					0.01									
Brown Thornbill	R	I	5.03	1.23	5.81	2.39	4.23	1.79	5.44	2.32	7.24	2.96	5.52	2.33	5.77	2.53
Buff-rumped Thornbill	R	I				0.03		0.07		0.08		0.20		0.11		0.13
Yellow Thornbill	R	I				0.09		0.04		0.04						

**Table 3–1**      **continued.**

Common name	LSM	Diet	Winter 2001		Spring 2001		Summer 2001		Autumn 2002		Winter 2002		Spring 2002		Summer 2002	
			R	NR	R	NR	R	NR	R	NR	R	NR	R	NR	R	NR
Striated Thornbill	R	I	10.9	4.30	4.80	4.08	2.47	2.04	4.49	2.56	5.52	4.25	2.91	2.28	4.17	3.53
Red Wattlebird	L	NI		0.03	0.08	0.16	0.60	1.09	0.93	1.36	1.21	4.27	0.28	0.12	0.13	0.03
Noisy Miner	R	NI														0.03
Lewin's Honeyeater	R	NI	0.13		0.13	0.01	0.09		0.15		0.20		0.20		0.13	
Yellow-faced Honeyeater	C	NI	0.33	0.03	2.11	0.40	3.13	0.45	1.16	0.11	0.44	0.16	3.48	0.32	3.23	0.43
White-eared Honeyeater	R	NI	0.20	0.03	0.24	0.05	0.07	0.01	0.20	0.01	0.27	0.08	0.09		0.07	
Yellow-tufted Honeyeater	R	NI	0.27		0.37		0.19		0.24		0.41		0.29		0.30	
Brown-headed Honeyeater	R	NI	0.37		0.28	0.05	0.08	0.03	0.27	0.05	0.33	0.16	0.13	0.15	0.10	0.27
White-naped Honeyeater	R	NI	3.80		4.59	0.12	4.55	0.05	2.83	0.09	4.07	0.60	5.01	0.03	6.40	
Crescent Honeyeater	R	NI	0.47	0.07	0.29	0.12	0.29	0.07	0.77	0.19	1.57	0.57	0.35	0.01		
New Holland Honeyeater	R	N							0.48		0.03	0.03				
Eastern Spinebill	L	N	0.13	0.37	0.16	0.49	0.15	0.32	0.84	0.57	1.23	1.59	0.36	0.32	0.37	0.57
Scarlet Robin	R	I				0.25		0.16	0.03	0.04	0.01	0.16		0.21		0.20
Flame Robin	T	I												0.07		
Rose Robin	C	I			0.69	0.03	0.32	0.01	0.20	0.01	0.11	0.03	0.79	0.07	0.60	0.13
Pink Robin	T	I					0.03		0.04		0.07					
Eastern Yellow Robin	R	I	0.83	0.07	0.88	0.23	1.19	0.19	0.97	0.24	0.77	0.28	1.24	0.35	0.77	0.37
Eastern Whipbird	R	I	0.03		0.32		0.19		0.11	0.01	0.13		0.20		0.33	
Varied Sittella	L	I	0.50		0.11	0.09	0.16	0.03	0.25	0.20	0.09	0.21	0.35	0.29	0.20	0.60
Crested Shrike-tit	R	I	0.03		0.04		0.08	0.01	0.04		0.07		0.21		0.07	
Olive Whistler	T	I	0.17		0.19		0.05		0.08	0.01	0.09	0.01	0.09	0.01	0.20	
Golden Whistler	C	I	0.47	0.13	1.32	0.17	0.84	0.12	0.52	0.17	0.59	0.43	1.31	0.16	1.20	0.20

**Table 3–1** continued.

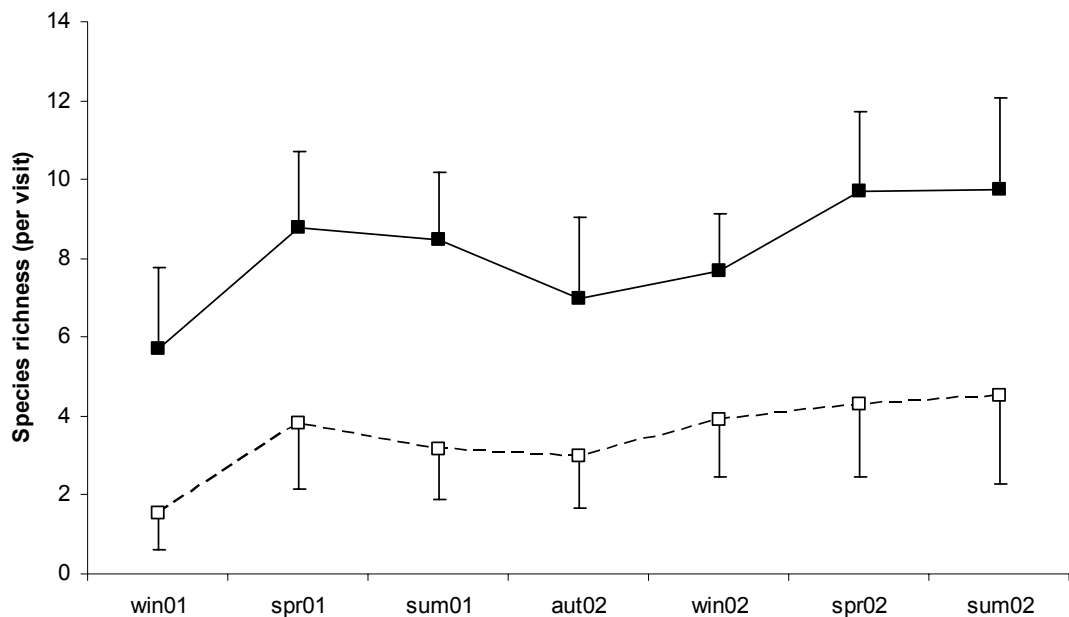
Common name	LSM	Diet	Winter 2001		Spring 2001		Summer 2001		Autumn 2002		Winter 2002		Spring 2002		Summer 2002	
			R	NR	R	NR	R	NR	R	NR	R	NR	R	NR	R	NR
Rufous Whistler	In	I			0.09	0.25	0.07	0.39	0.01	0.09			0.20	0.35	0.20	0.73
Grey Shrike-thrush	R	I	0.13	0.10	0.25	0.33	0.11	0.11	0.19	0.32	0.20	0.20	0.20	0.47	0.50	0.20
Leaden Flycatcher	In	I				0.01										
Satin Flycatcher	C	I			0.28	0.08	0.33	0.04					0.25	0.03	0.57	
Rufous Fantail	C	I			0.19	0.01	1.17	0.07	0.15				0.31		0.80	0.03
Grey Fantail	C	I	0.97		2.36	0.96	1.36	0.87	1.88	0.35	1.81	0.07	2.08	1.03	2.03	1.00
Black-faced Cuckoo-shrike	In	I			0.04	0.27	0.09	0.08	0.01	0.01			0.04	0.08	0.10	0.07
Olive-backed Oriole	In	I				0.07	0.03	0.04		0.01			0.01	0.12	0.13	0.20
Dusky Woodswallow	C	I											0.53	0.04		
Grey Butcherbird	R	V				0.11		0.04		0.03	0.01			0.01		
Australian Magpie	R	I											0.03			
Pied Currawong	R	V		0.07	0.05	0.03	0.11	0.01	0.01	0.07	0.09	0.27	0.01	0.08	0.03	0.03
Grey Currawong	R	V	0.03		0.01	0.03	0.04	0.01	0.01	0.05		0.04	0.09	0.03	0.10	0.07
Australian Raven	R	V					0.05		0.05		0.05	0.01		0.03	0.07	
White-winged Chough	R	I														0.27
Satin Bowerbird	R	SF							0.19		0.21					
Red-browed Finch	L	SF					0.05						0.03			
Beautiful Firetail	R	SF			0.11		0.13		0.17		0.16		0.29	0.04	0.27	
Mistletoebird	L	SF				0.01	0.01		0.09	0.03		0.03	0.01	0.07		0.07
Welcome Swallow	In	I			0.03				0.21	0.09						
Tree Martin	In	I	0.13		1.28	0.11	1.00	0.08	0.03	0.03	0.13		0.92	0.01	1.70	
Silvereye	C	NI	0.03		1.16	0.23	3.16	0.23	1.92	0.16	0.61	0.07	1.35	0.23	2.37	0.43

**Table 3–1      continued.**

Common name	LSM	Diet	Winter 2001		Spring 2001		Summer 2001		Autumn 2002		Winter 2002		Spring 2002		Summer 2002	
			R	NR	R	NR	R	NR	R	NR	R	NR	R	NR	R	NR
Bassian Thrush	R	I			0.09		0.07		0.09		0.21	0.07	0.24	0.01	0.07	
*Common Blackbird	R	I			0.03		0.01		0.11				0.05		0.17	

### 3.3.2 Seasonal changes in the structure of bird assemblages

RmANOVA showed a significant effect of habitat type on species richness of bird assemblages ( $F_{1,58} = 200.001$ ,  $p < 0.001$ ) (Figure 3-2). The species richness of riparian bird assemblages was greater at all times (Figure 3-2). There was a significant effect of season on species richness in riparian and non-riparian assemblages ( $F_{6,348} = 50.584$ ,  $p < 0.001$ ) (Table 3-2). There was also a significant interaction between season and habitat type ( $F_{6,348} = 4.073$ ,  $p = 0.001$ ) (Table 3-2). This shows that the richness of riparian and non-riparian assemblages followed different trends through time. Riparian assemblages display a pronounced spring/summer peak in richness, followed by a decline in richness through autumn/winter (Figure 3-2). Non-riparian assemblages did not display this pattern, and there were no clear peaks or troughs in species richness evident during the annual cycle (Figure 3-2).



**Figure 3-2** Mean values ( $\pm$  standard deviation) of species richness (species/visit) among riparian (■) and non-riparian sites (□) through time.

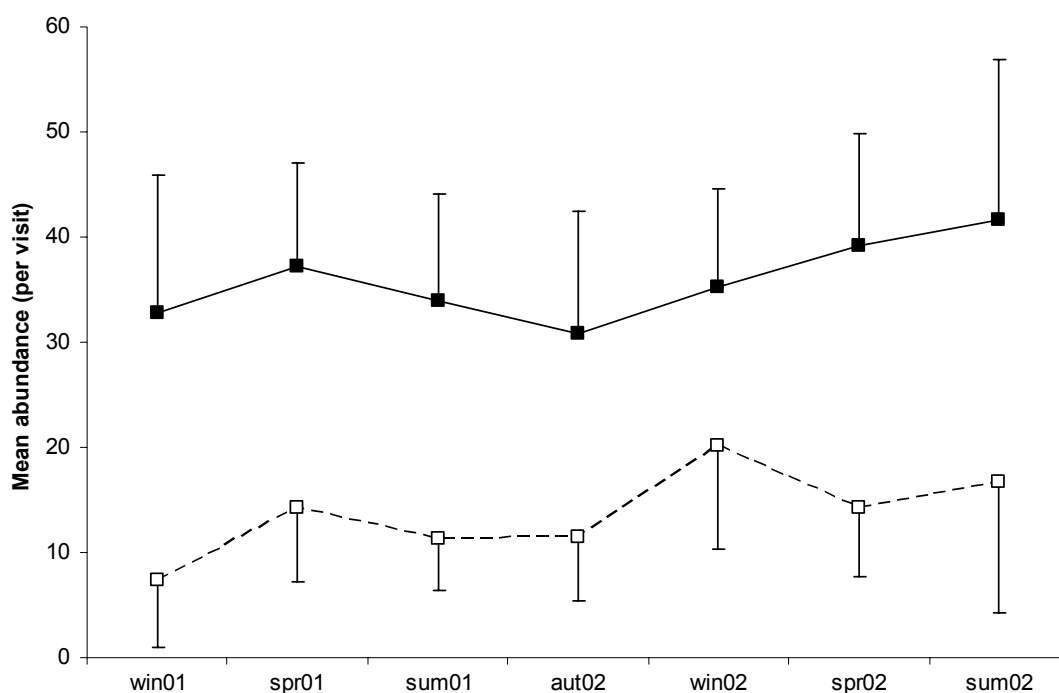
**Table 3-2** Repeated measures ANOVA comparing the mean species richness per survey of bird assemblages at riparian and non-riparian habitats among seasons.

Source	SS	d.f.	MS	F ratio	p	HF p
<i>Between subjects</i>						
Habitat types	2313.81	1	2313.81	200.01	<0.001	
Residual	670.97	58	11.57			
<i>Within subjects</i>						
Season	535.81	6	89.30	50.58	<0.001	<0.001
Habitat type x season	43.14	6	7.19	4.07	0.001	0.001
Residual	614.37	348	1.77			

Huynh-Feldt (HF $\epsilon$  = 0.898) adjustments are presented as a more conservative test reducing the risk of Type I error due to non-sphericity.

Changes in species richness of the overall assemblage ( $n = 30$  sites) through time differed significantly between habitat types (paired  $t = -8.197$ , d.f. = 29,  $p < 0.001$ ), with variation through time being least for riparian assemblages (mean CV = 43.2,  $\pm 9.2$  SD) compared with that for non-riparian assemblages (mean CV = 88.8,  $\pm 32.02$  SD).

Habitat type had a significant effect on the abundance of birds ( $F_{1,58} = 175.72$ ,  $p < 0.001$ ) (Table 3-3). Abundance was greater in riparian bird assemblages at all times when compared to non-riparian assemblages. There was a significant effect of season on the abundance of birds within assemblages ( $F_{6,348} = 15.9$ ,  $p < 0.001$ ) (Table 3-3). A significant interaction between habitat type and season was also found ( $F_{6,348} = 5.83$ ,  $p < 0.001$ ), indicating that the effect of season on the abundance of birds was different between riparian and non-riparian assemblages (Table 3-3). Riparian assemblages displayed a clear trend of peaks in bird abundance during spring and summer, and lower abundance during winter and autumn (Figure 3-3). There was no clear trend in the abundance of birds in non-riparian assemblages through time (Figure 3-3).



**Figure 3-3** Mean values ( $\pm$  standard deviation) of bird abundance (birds ha<sup>-1</sup>) among riparian (■) and non-riparian sites (□), winter 2001 to summer 2002.

**Table 3-3** Repeated measures ANOVA comparing the mean abundance of birds occurring between riparian and non-riparian habitats among seasons.

Source	SS	d.f.	MS	F ratio	p	GG p
<i>Between subjects</i>						
Habitat types	604.9	1	604.9	175.72	<0.001	
Residual	199.66	58	3.44			
<i>Within subjects</i>						
Season	61.85	6	10.31	15.9	<0.001	<0.001
Habitat type x season	22.67	6	3.78	5.83	<0.001	<0.001
Residual	225.62	348	0.65			

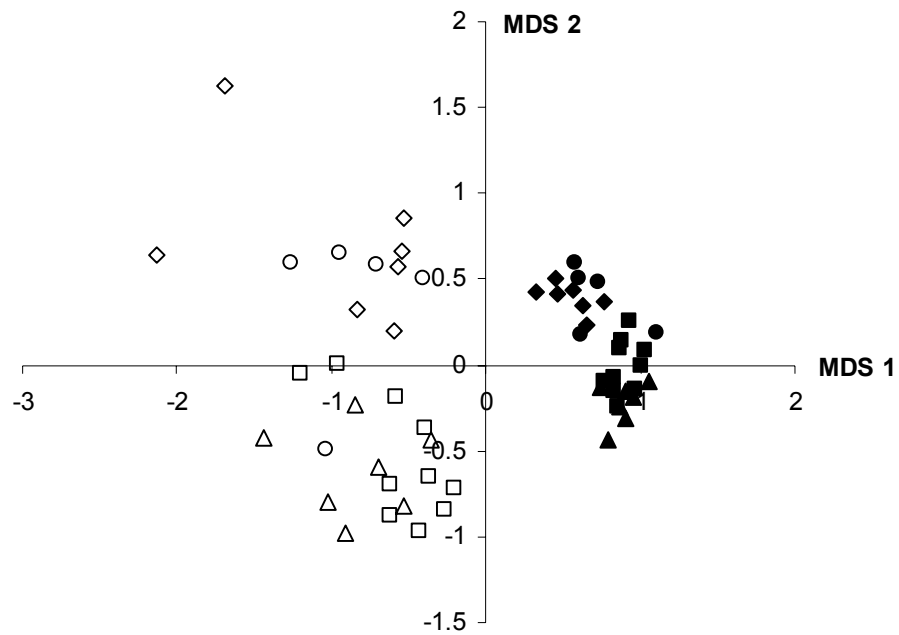
Greenhouse Geisser (GG) adjustments are presented as a more conservative test reducing the risk of Type I error due to non-sphericity.

Variations in the abundance of bird assemblages through time (i.e. pooled data from  $n = 30$  sites) were significantly different for riparian and non-riparian habitats (paired  $t = 9.621$ , d.f. = 29,  $p < 0.001$ ). Riparian assemblages displayed least variation through time (mean CV = 39.8,  $\pm 9.47$  SD; non-riparian mean CV = 77.7,  $\pm 18.55$  SD). In riparian habitats, mean seasonal abundance of birds ranged from 41.6 (summer 2002) to 30.8 individuals  $\text{ha}^{-1}$  (autumn 2002). Non-riparian habitats supported a range in mean abundance of 20.2 (winter 2002) to 7.3 individuals  $\text{ha}^{-1}$  (winter 2001) (Figure 3-3).

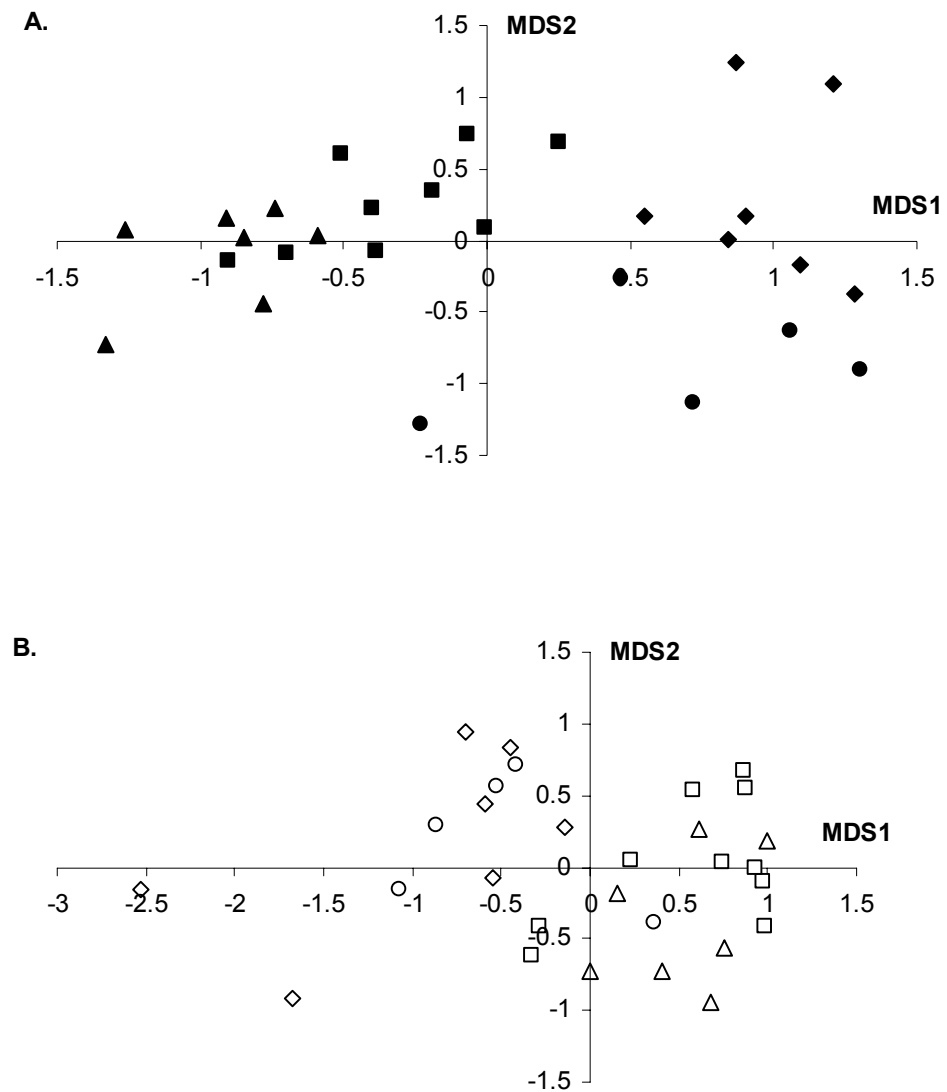
### 3.3.3 *Seasonal changes in the species composition of bird assemblages*

The species composition of bird assemblages in riparian and non-riparian habitats differed through time. Ordination of data from each survey round (i.e. visit) for the set of riparian and non-riparian sites, respectively, displayed two clear trends. First, there was a clear separation of assemblages based on habitat types (stress 0.13) (Figure 3-4). In all seasons, riparian bird assemblages were distinct from non-riparian assemblages (Figure 3-4). Second, for each habitat type there was seasonal variation in the composition of the bird assemblage. An MDS ordination of riparian assemblages alone displays a distinct segregation of assemblages from each survey round based on season (Figure 3-5A). A similar ordination based on non-riparian assemblages for each survey round shows less segregation based on season (Figure 3-5B), although a distinction between spring/summer and autumn/winter assemblages is evident.



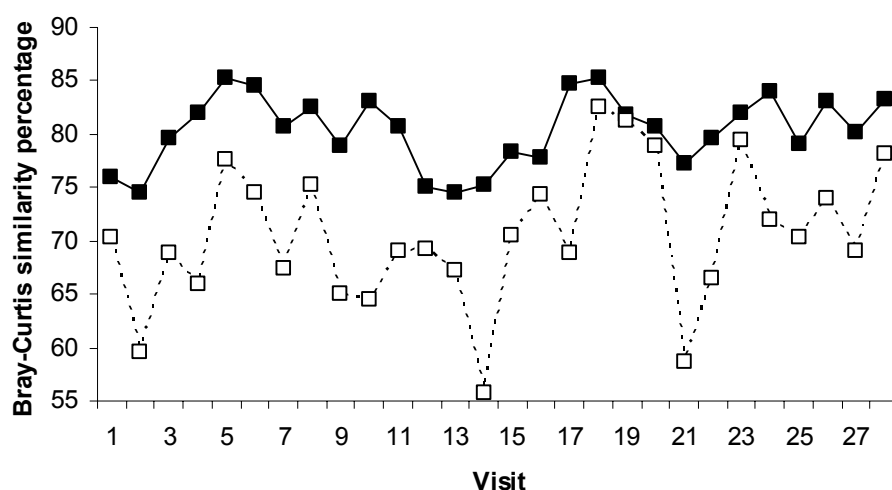


**Figure 3-4** Ordination of seasonal bird assemblages occurring at riparian (solid) and non-riparian sites (open) in the Victorian Highlands. Seasons represented are winter (○), spring (■), summer (▲) and autumn (●).



**Figure 3-5** Ordination of seasonal bird assemblages occurring at riparian (A) and non-riparian sites (B). Seasons are winter (◊), spring (■), summer (▲) and autumn (●).

The similarity of bird assemblages among riparian sites was greater than that for non-riparian sites throughout the sampling period (Figure 3-6). Assemblage composition through time was significantly different between riparian and non-riparian habitats (Bray-Curtis similarity values; paired  $t = 8.372$ , d.f. = 27,  $p < 0.001$ ). Similarities in the species composition of riparian bird assemblages displayed less variability through time, than non-riparian assemblages (Figure 3-6). There were few abrupt changes in the species composition of riparian assemblages between seasons; rather, a gradual change of assemblages is evident, whereby each is closely related to those closest in time (Figure 3-5A; Figure 3-6).



**Figure 3-6** Similarity of bird assemblages in riparian (■) and non-riparian habitats (□) in the Victorian Highlands through time, July 2001 to December 2002. Based on Bray-Curtis similarity index.

In contrast, there were sharp peaks and troughs in the compositional similarity of non-riparian bird assemblages (Figure 3-6), indicating that these assemblages are more variable through time. This is evident in the MDS ordination which shows disparate relationships often exist for assemblages closest in time (Figure 3-5B).

### 3.3.4 Seasonal variation in movement groups

Resident (i.e. sedentary) species dominated the avifauna of both riparian and non-riparian habitats throughout the study period. Overall, residents accounted for 66% of all records of birds and 56% of species. Season had a significant effect on the proportion of resident birds occurring within riparian or non-riparian assemblages ( $F_{6,348} = 23.35$ ,  $p < 0.001$ ) (Table 3-4; Figure 3-7). There was a significant interaction between season and habitat type – i.e. the effect of season was not the same for riparian and non-riparian habitats ( $F_{6,348} = 2.48$ ,  $p = 0.041$ ) (Table 3-4; Figure 3-7). In riparian assemblages the proportion of resident birds peaked in winter in both years (Figure 3-7), when species richness and abundance was lowest (Figure 3-2 and Figure 3-3). This trend coincided with the absence of migrants in the area. Resident species contribute least to differences between riparian and non-riparian habitats between seasons (Table 3-5).

**Table 3-4 Summary of repeated measures ANOVA comparing seasonal differences in the proportion of resident birds within riparian and non-riparian bird assemblages.**

Source	SS	d.f.	MS	F ratio	p	GG p
<i>Between habitat types</i>						
Habitat types	10.76	1	10.76	0.03	0.862	
Residual	20,388.11	58	351.52			
<i>Within habitat types</i>						
Season	33,841.2	6	5,640.2	23.35	<0.001	<0.001
Habitat type x season	3,600.57	6	600.1	2.48	0.023	0.041
Residual	84068.95	348	241.58			

Greenhouse Geisser (GG) adjustments are presented as a more conservative test reducing the risk of Type I error due to non-sphericity.

The occurrence of migrants (coastal, inland and Tasmanian groups) clearly changes between seasons, although different responses occur between riparian and non-riparian habitats (Figure 3-7). The proportion of the bird assemblage comprised of local movement species also changes between seasons (Figure 3-7). In each of the seasons (winter 2001 to summer 2002) there was a significant difference in the

association of movement groups between habitat types (Table 3-5).

One major difference between riparian and non-riparian assemblages was the contribution of locally nomadic (i.e. local) species. Local nomads (e.g. Red Wattlebird, Eastern Spinebill and Yellow-tailed Black-Cockatoo) were recorded at higher frequencies in non-riparian habitats across all seasons (Table 3-5). In winter 2002, large departures in the observed frequencies of local nomads from expected frequencies coincided with a massive influx of Red Wattlebirds into non-riparian habitats in the landscape (Table 3-1).

**Table 3-5 Bird movement groups association with riparian and non-riparian habitats between seasons. Values in the table are residuals, which indicate the extent of differences between expected and observed frequencies. Significance level of  $\chi^2$  are \*  $p < 0.05$ , \*\*  $p < 0.01$ .**

Movement Group	Winter 2001		Spring 2001		Summer 2001		Autumn 2002		Winter 2002		Spring 2002		Summer 2002	
	Rip	NR	Rip	NR	Rip	NR	Rip	NR	Rip	NR	Rip	NR	Rip	NR
Resident	-0.2	0.5	-1.2	1.9	-0.1	0.3	0	0	2.8	-3.7	-1.6	2.6	-0.1	0.2
Local	-0.4	0.9	-3	4.9	-5.1	8.8	-4.2	6.9	-10	13.3	-3.1	5.2	-5	7.9
Coastal	0.8	-1.8	2.6	-4.2	2.6	-4.5	3.9	-6.5	4.3	-5.6	3.8	-6.3	2.7	-4.3
Inland	0.9	-1.8	1.3	-2.1	0.7	-1.1	-0.6	1	3.4	-4.5	1.1	-1.7	0.2	-0.3
Tasmanian	0.5	-1	1.2	-2	0.7	-1.2	0.6	-1	1.3	-1.7	-0.8	1.4	0.8	-1.3
$\chi^2$ (d.f. = 4)	10.08*		73.61**		134.15**		126.58**		385.61**		107.15**		117.03**	

**Table 3-6 Bird diet groups association with riparian and non-riparian habitats between seasons. Residuals indicate extent of differences between expected and observed frequencies. \* Significance level of  $\chi^2 = p < 0.01$ .**

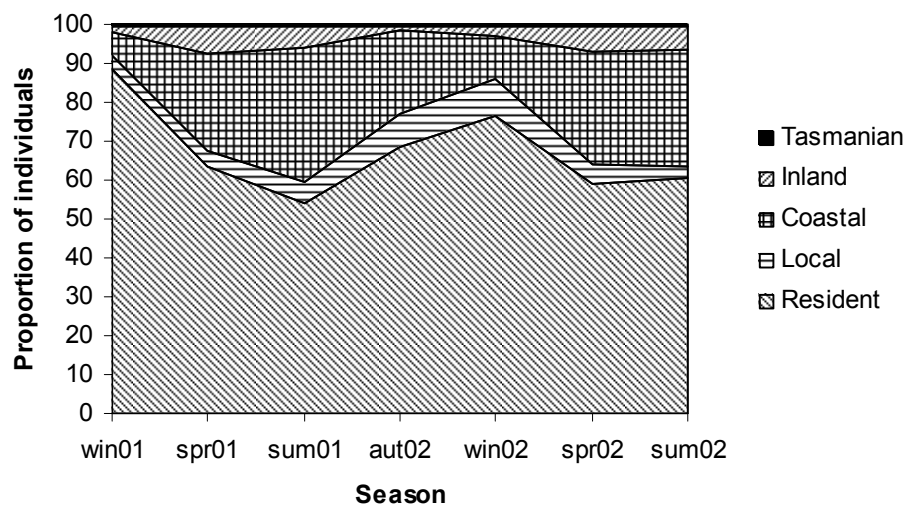
Dietary Group	Winter 2001		Spring 2001		Summer 2001		Autumn 2002		Winter 2002		Spring 2002		Summer 2002	
	Rip	NR	Rip	NR	Rip	NR	Rip	NR	Rip	NR	Rip	NR	Rip	NR
Invertebrate	-0.6	1.2	-1.8	2.9	-2.5	4.4	-1.2	2	2.4	-3.2	-2.3	3.9	-1.9	3
Nectar	-2.4	5	-3.9	6.3	-3.1	5.4	-0.4	0.6	-3.6	4.8	-1.7	2.8	-2	3.2
Nectar/invertebrate	2.2	-4.7	5.5	-8.9	4.2	-7.3	2.7	-4.4	-1.2	1.6	6.9	-11.4	4.9	-7.7
Seeds/fruit	0.7	-1.5	-2.2	3.5	-0.2	0.3	-0.2	0.3	-1.3	1.7	-3.9	6.5	-2.6	4.1
Vertebrate	-1.6	3.4	-1	1.7	0.2	-0.3	-2.4	3.9	-2.2	2.9	-2.2	3.7	-0.3	0.4
$\chi^2$ (d.f. = 4)	76.55*		196.9*		134.99*		53.81*		73.79*		283.52*		132.25*	

Coastal migrants were closely associated with riparian habitats throughout the year (Table 3-5). In all seasons, the observed frequencies of coastal migrants (e.g. Yellow-faced Honeyeater, Golden Whistler, Rufous Fantail) were higher than expected in riparian habitats (Table 3-5). Eight of 11 observed coastal migrants were considered to be riparian associated species (Chapter 2). Two of the remaining species were commonly recorded throughout the forest landscape (Grey Fantail, Fan-tailed Cuckoo). Most coastal migrants departed the study area during winter; however half of the species (e.g. Yellow-faced Honeyeater, Rose Robin, Golden Whistler, Grey Fantail and Silvereye) maintained low populations in the study area during this time and mostly in riparian habitats.

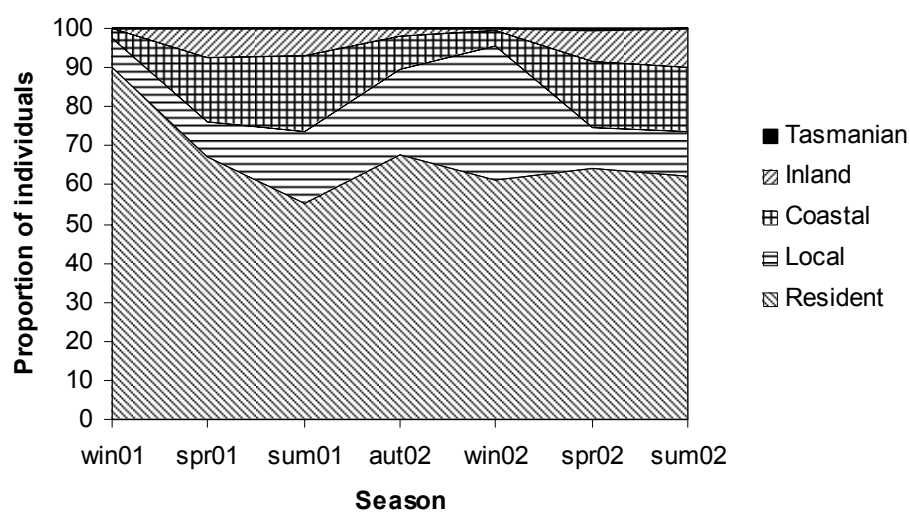
Differences between habitats in the observed frequencies of inland migrants were greatest during winter and spring of both 2001 and 2002, suggesting a seasonal effect; this coincided with times of low proportions of inland migrants in the landscape (Figure 3-7). As a group, the observed frequencies of inland migrants were consistently higher than expected at riparian sites. This trend was mostly driven by two species, the Striated Pardalote and Tree Martin, which showed a distinct preference for riparian sites (Chapter 2). Most other inland migrants were non-riparian associated species including Rufous Whistler, Olive-backed Oriole and Black-faced Cuckoo-shrike (Chapter 2).

Collectively species that migrate between Tasmania and the mainland (i.e. Tasmanian group) were most closely associated with riparian sites, but species-specific trends were evident. The Pink Robin was only observed at riparian sites, while the Olive Whistler was closely associated with these sites (Table 3-1). The Flame Robin, a spring migrant in the study area in 2002, was only recorded from non-riparian sites.

**a) Riparian bird assemblages**



**b) Non-riparian bird assemblages**



**Figure 3-7** Proportion of individuals in movement groups contributing to bird assemblages at riparian (a) and non-riparian (b) sites between seasons, winter 2001 to summer 2002.



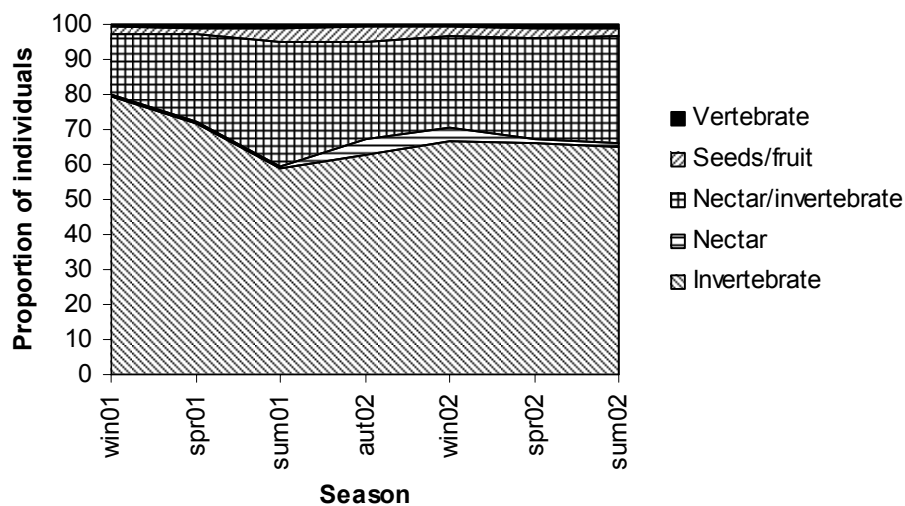
### 3.3.5 *Seasonal variation in dietary groups*

In all seasons there was a significant difference between habitats in the composition of dietary groups making up bird assemblages (Table 3-6). In terms of dietary preference, assemblages were dominated by invertebrate feeding species throughout the landscape (Figure 3-8).

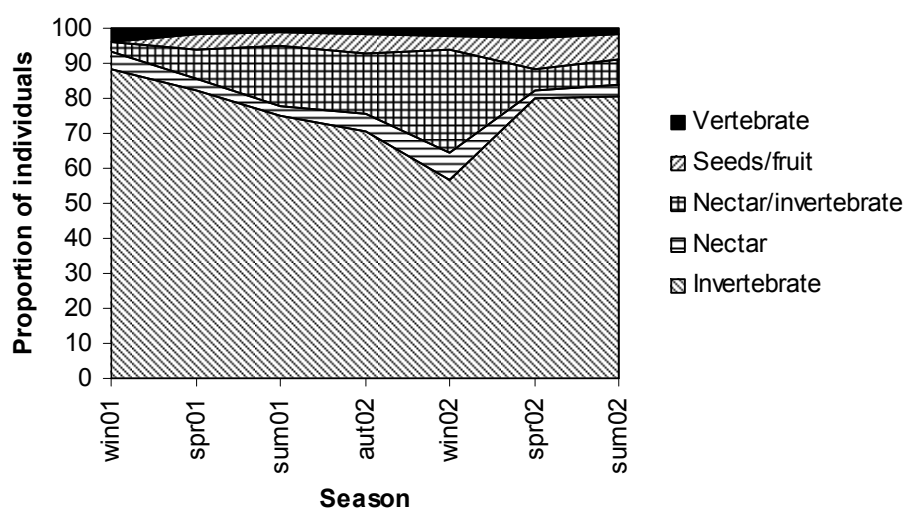
The groups showing most seasonal variation were birds feeding on nectar and nectar/invertebrate groups. There were high numbers of nectar/invertebrate feeders in the landscape during spring/summer in both years (Table 3-1). This group (e.g. White-naped Honeyeater, Yellow-faced Honeyeater and Silvereye) was strongly associated with riparian habitats (Table 3-6). Nectar feeders (e.g. Eastern Spinebill and New Holland Honeyeater) were prominent in all seasons in non-riparian assemblages (Figure 3-8b), and occurred sporadically in riparian assemblages (Figure 3-8a).

Vertebrate-feeding species, which tend to be sedentary species with large home ranges (e.g. currawongs, Laughing Kookaburra, Grey Butcherbird and Australian Magpie) occurred consistently across seasons (Figure 3-8). For all dietary groups, lower residual values from  $\chi^2$  analysis for riparian bird assemblages showed that more consistent and stable assemblages are maintained through time (Table 3-6).

**a) Riparian assemblages**



**b) Non-riparian assemblages**



**Figure 3-8** Proportion of individuals in dietary groups contributing to bird assemblages at riparian (a) and non-riparian (b) sites between seasons, winter 2001 to summer 2002.

### 3.3.6 *Seasonal variation in individual species*

Birds that consistently contributed to dissimilarities between riparian and non-riparian assemblages were either more widespread, or more commonly, occurred in much greater abundance in one of the habitat types (Table 3-7). Several species that were widespread in the landscape (e.g. resident insectivores such as White-browed Scrubwren, Brown Thornbill, Striated Thornbill and Grey Fantail) contributed strongly to dissimilarities throughout the study (Table 3-7). These species were all more abundant in riparian habitats (Table 3-1). Other species strongly associated with riparian habitats (e.g. White-naped Honeyeater and Eastern Yellow Robin) also consistently contributed to dissimilarities throughout the year.

Migratory species also contributed strongly to assemblage dissimilarities at particular times in the annual cycle. Summer migrants to the study area such as the Rufous Fantail, Yellow-faced Honeyeater and Silvereye were concentrated within riparian habitats (Table 3-1). Likewise, locally nomadic birds, in particular nectarivores such as the Eastern Spinebill and Red Wattlebird, contributed strongly to assemblage dissimilarities during winter (Table 3-7). Large numbers of individuals were recorded coinciding with prolific flowering of banksias, mainly in non-riparian sites (Table 3-1; Chapter 5).

**Table 3-7 Bird species that had the greatest influence on dissimilarities (SIMPER) between riparian and non-riparian assemblages, July 2001 to December 2002. Corresponding seasons for each visit are included in heading: w = winter, sp = spring, su = summer, a = autumn.**

Bird species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
	w	w	sp	sp	sp	sp	sp	su	su	su	su	su	a	a	a	a	a	w	w	w	w	w	sp	sp	sp	sp	sp	su	su
White-browed Sc	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Brown Thornbill	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Striated Thornbill	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Grey Fantail	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
White-naped HE	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•			•	•	•	•	•	•	•	•	•	•	•	•
Yellow-faced HE			•	•	•	•	•	•	•	•	•	•	•	•	•				•					•	•	•	•	•	•
Spotted Pardalote	•		•	•	•	•	•	•			•	•	•	•	•					•		•	•	•	•	•		•	•
Striated Pardalote			•	•	•	•	•	•	•	•											•	•	•	•	•	•	•	•	•
East. Yellow Robin	•	•							•	•	•	•	•	•	•	•	•	•				•	•				•		
Golden Whistler	•	•		•	•	•	•											•		•			•	•	•	•	•	•	•
Silvereye					•	•		•	•	•	•	•	•	•		•									•	•	•	•	•
White-throated TC	•	•	•	•											•	•	•	•		•	•								
Eastern Spinebill	•													•		•	•	•	•	•	•	•							
Crescent HE		•													•	•	•	•	•	•	•	•							
Red Wattlebird								•								•	•	•	•	•	•								
Rufous Fantail									•	•	•	•	•																
Crimson Rosella																						•							
Superb Fairy-wren		•																											
Rose Robin			•																										

Key to Abbreviated species names: Sc = Scrubwren; HE = Honeyeater; East. = Eastern; TC = Treecreeper

### 3.4 Discussion

#### 3.4.1 *Riparian zones and the structure of bird assemblages through time*

In the temperate, forested landscapes of south-east Australia, riparian zones are clearly important for bird communities (Chapter 2). Riparian zones support bird assemblages that have greater species richness and abundance when compared with non-riparian assemblages, with the magnitude of these differences being maintained throughout the year. While the value of riparian zones for birds has been shown in other studies (Loyn *et al.* 1980; Braithwaite *et al.* 1989; Recher *et al.* 1991; Kinley and Newhouse 1997), an understanding of the year-round value of these habitats to birds has been the focus of few studies, or has been masked by the inclusion of seasonal data into a single or yearly summary (e.g. Mac Nally *et al.* 2000).

In general, temperate bird communities are characterised by peak abundance during the spring/summer period (Karr 1976; Avery and van Ripper III 1989), which generally has a positive correlation with peak productivity in the temperate zone (Nix 1976; Hurlbert and Haskell 2003). Australian bird communities commonly display pronounced within-year, seasonal variation in species richness and the number of individuals (Recher *et al.* 1983; Mac Nally 1995; Slater 1995; Mac Nally 1996; French *et al.* 2003). In south-east Australia, communities typically support a lower abundance and species richness of birds during winter due to the exodus of species to northern Australia (Frith 1976; Nix 1976; Osborne and Green 1992). These temporal changes in community structure are driven by the regular movement of birds (i.e. migration) as they cope with change in environmental conditions by moving to a location where conditions are favourable or less limiting. The Australian avifauna is characterised by a high proportion of species that undergo large-scale movements (Nix 1976). This includes regular seasonal movements that have a constant direction (i.e. migration), as well as irregular movements over relatively large scales tracking changing resource availability (i.e. local movements).

At the landscape level there were distinct differences in the pattern of bird assemblages between habitats. Resident species formed the bulk of the assemblage throughout the year in both riparian and non-riparian habitats, but an influx of seasonal migrants

elevated species richness and abundance in the landscape during spring and summer, particularly at riparian sites. Riparian assemblages were more stable through time with less variation in species richness and abundance than non-riparian assemblages. Conditions in the riparian zone are likely to benefit birds by providing stable and predictable environments. For example, riparian zones supported structurally complex habitats in the forest landscape (Chapter 3). More complex vegetation structure in combination with the positioning of riparian zones in valleys would be expected to ameliorate environmental conditions by providing a buffer effect that reduces the impact of seasonal fluctuations such as in temperature and rainfall (Karr 1976; Gregory *et al.* 1991; Tabacchi *et al.* 1998). Biotic components respond to greater stability in environmental conditions by displaying less variation in numbers and diversity between seasons (e.g. Janzen and Schoener 1968; Cody 1974; Karr 1976; Woinarski *et al.* 2000).

While species richness and abundance in riparian assemblages showed a similar trend, there was no clear relationship between richness and abundance in non-riparian assemblages. These assemblages were characterised by relatively low species richness and abundance at most times. Under these circumstances, either small or large influxes of birds caused considerable variation in species richness and abundance through time. For example, the sharp reduction in similarity registered in winter 2002 for non-riparian assemblages (Figure 3-6), coincided with a massive influx of Red Wattlebirds into these habitats in response to mass flowering of banksia and hakea shrubs.

To understand bird communities, knowledge of the spatial and temporal dynamics in habitat use of individual species is essential. While the importance of regional scale dynamics has been discussed (e.g. Mac Nally 1995), the role of local and landscape patterns is also important. The use of riparian or non-riparian habitats by birds comprises a spatial component (use of habitat) and a temporal component (change in habitat use with time). Significant differences in the dynamics of community structure between riparian and non-riparian assemblages registered in this study, shows that there is a disproportionate use of riparian zones across the forest landscape. This indicates that riparian zones provide superior or higher quality habitats for birds throughout the annual cycle.

### 3.4.2 *Riparian zones and the composition of bird assemblages through time*

The composition of bird assemblages in riparian habitats was distinct from non-riparian assemblages in all seasons. Species composition of bird assemblages in both habitats changed during the annual cycle, but riparian assemblages maintained greater similarity through time than did non-riparian assemblages (Figure 3-6). One reason for this may be that the vegetation composition and habitat structure of riparian sites was more similar between sites; in contrast non-riparian sites included a range of different vegetation communities with associated differences in vegetation composition and habitat structure. However, the relatively large fluctuations in similarity through time for non-riparian assemblages when compared to riparian assemblages points to a seasonal effect.

Typical of bird assemblages in temperate regions (e.g. Nix 1976; Avery and van Ripper III 1989), assemblages in this study were comprised of a core of resident species, complemented by seasonal migrant species, which combined to form a varying community composition throughout the year. Resident species characteristically display little variation between seasons and their richness and abundance is likely to be controlled by minimum productivity levels in the environment (Hurlbert and Haskell 2003). Stability in the availability of resources throughout the annual cycle contributes to a higher proportion of resident species in bird assemblages (Karr 1976). The proportion of resident individuals (i.e. individuals of species classified as residents) in the bird assemblage did not differ between riparian and non-riparian habitats. However, several residents (e.g. White-browed Scrubwren, Brown Thornbill, Striated Thornbill, White-naped Honeyeater, Eastern Yellow Robin, White-throated Treecreeper, Crescent Honeyeater and Crimson Rosella) were among the birds most commonly contributing to dissimilarities between riparian and non-riparian bird assemblages, and all were more abundant in riparian zones.

The species composition of bird assemblages in both habitat types were strongly influenced by migrating and locally nomadic species (Figure 3-4). Migrants visit south-east Australia from the north of the continent (including New Guinea) during spring and summer: there are few winter immigrants in the avifauna (Nix 1976; Emison *et al.* 1987; Griffioen and Clarke 2002). Of the suite of summer migrants to south-east Australia, some species are partial migrants, with a proportion of the population remaining

during the winter exodus (e.g. Grey Fantail, Golden Whistler and Yellow-faced Honeyeater) (Emison *et al.* 1987; Griffioen and Clarke 2002). Individuals that remained during winter mostly occurred in riparian habitats.

The large-scale movement patterns adopted by migrating species were linked to their habitat preferences. Species which migrate along the east coast do not occupy inland regions of Australia (Griffioen and Clarke 2002; Barrett *et al.* 2003). These species (e.g. Rufous Fantail, Rose Robin and Satin Flycatcher) typically displayed a preference for riparian zones in the study area. Those species that migrate through inland Australia (e.g. Striated Pardalote, Rufous Whistler and Black-faced Cuckoo-shrike) typically have broad distributions in a wide range of wooded environments (Barrett *et al.* 2003), and in this study area were mostly associated with non-riparian habitats.

Riparian habitats were particularly important for coastal migrants; eight of the eleven species observed in this study were riparian associated species (Chapter 2). Coastal migrants comprised up to 30% of individuals in riparian assemblages during the spring/summer period. All were classified in the invertebrate dietary group, apart from Yellow-faced Honeyeater and Silvereye (nectarivore/invertebrate dietary group), which also extensively feed on invertebrates. These species are breeding migrants to the study area. The close association of coastal migrants with riparian habitats indicates a preference for those areas containing structurally complex, lush vegetation (Chapter 2), which potentially provides a greater range of nest sites (Cody 1981; Bub *et al.* 2004), and foraging opportunities (Chapter 4), and contributes to more abundant and consistent food resources (Chapter 5). Other features of riparian vegetation are also likely to be attractive to migrating species. The lush, structurally complex vegetation in riparian zones resembles the warm tropical forests that migrants (e.g. Rufous Fantail and Satin Flycatcher) inhabit in northern Australia and New Guinea. A similar pattern of use was found in tropical savannas in northern Australia (Woinarski *et al.* 2000), where riparian areas had more significant increases in wet season migrants, which typically inhabit wet monsoon forests. In North America, neotropical migrants prefer areas of lush, structurally complex vegetation, particularly that found in riparian zones (Wiebe and Martin 1998).

Over 90% of spring/summer migrants were insectivorous, a proportion greater than expected based on the overall proportion of these groups in the avifauna (50% of total).



The migration of species in eucalypt forest in south-east Australia is tied to seasonal changes in invertebrate numbers (Recher *et al.* 1983). Invertebrate abundance is typically highest during spring and summer in temperate regions and is linked to pulses in plant growth (Nix 1976). The abundance of invertebrates is generally high in riparian environments (Gray 1993; Lynch *et al.* 2002; Murakami and Nakano 2002; Iwata *et al.* 2003), which would contribute to the greater use of these habitats by migrating species when compared to adjacent non-riparian habitats.

Another function of riparian zones is their importance for birds on passage during migration (Stevens *et al.* 1977; Winker *et al.* 1992; Machtans *et al.* 1996; Skagen *et al.* 1998; Wiebe and Martin 1998). The geographical location of the study area in southern Australia is near the southern limit of migration for many species observed in this study (some continue on to Tasmania), so their value for passage migrants could not be assessed. However, the features that makes these a high quality habitat for birds in the study area are likely to be common to riparian zones throughout eastern Australia. This includes riparian zones forming interconnected networks of linear habitat across landscapes (Malanson 1993; Bren 1995; Forman 1995; Bennett 1999); and, providing structurally diverse vegetation that supports rich and abundant resources (Chapter 5).

The composition of non-riparian assemblages showed greater variation through time. While this may, in part, be a function of low species richness and abundance, less predictable environmental conditions in non-riparian habitats may also be a factor (Recher *et al.* 1983; Woinarski *et al.* 2000; Kingston 2005). Resources such as eucalypt flowering and loose bark are less abundant and predictable in non-riparian habitats (Chapter 5), and therefore the associated bird assemblages are likely to show greater variation through time. In this study much of the variation evident in non-riparian bird assemblages was driven by locally nomadic birds, such as the nectarivores, Red Wattlebird and Eastern Spinebill, which moved into non-riparian habitats from outside the study area in response to irregular flowering events. Unpredictable, but periodic abundance of resources is likely to promote variation in habitat quality over time, which may contribute to fluctuating densities or be a trigger for temporal changes in habitat preferences of species within the landscape. In deciduous blue-oak woodland in North America, for example, seasonal patterns of leaf and acorn production resulted in periodic resource abundance that was exploited by an array of

species, which caused greater turnover of species and less predictability in the bird assemblage from season to season (Avery and van Ripper III 1989). Seasonal variation in primary production is a factor in determining the number of species that are able to co-exist in an area during a given season. Migratory and itinerant species respond to the rate and timing of such production and influence the species composition of bird communities (Hurlbert and Haskell 2003).

Non-riparian assemblages have sometimes been considered to be depauperate representations of assemblages associated with moister forests, particularly those in riparian situations (e.g. Recher *et al.* 1991). While these assemblages had fewer species and lower abundance of individuals, non-riparian habitats are important areas for species that undergo large-scale movements through inland Australia (e.g. Rufous Whistler, Black-faced Cuckoo-shrike, Olive-backed Oriole) and provide key resources, particularly nectar, for locally nomadic birds (e.g. Red Wattlebird, Eastern Spinebill) at particular times during the year (Chapter 5). These habitats are also likely to be entwined in the annual cycle of many species closely associated with riparian habitats, but which depend on adjacent non-riparian habitats for resources at particular times of the year.

### 3.4.3 *Implications for conservation*

Seasonal variation in bird assemblages reflects both the dynamism of individuals and species, and the differences within and between habitats in the landscape. Riparian habitats are important to the seasonal dynamics of the avifauna for at least three reasons. First, riparian zones supported a greater richness and abundance of birds throughout the annual cycle. Species may regularly use riparian habitats within their seasonal life cycles, as winter or summer habitat, for breeding, or as part of migratory movements. Second, riparian zones were particularly important for species that migrate along the east coast of Australia. This group concentrated their activities, including breeding, in riparian habitats when in the forest landscape. Third, riparian zones provided important habitat for some birds at particular times during the year, such as over-wintering migrants. For example, the Grey Fantail was widespread during summer, but that part of the population that remained during winter was largely concentrated in riparian zones.

Temporal variation in habitat relationships shown here may further complicate our ability to apply effective conservation programs at the local level for many species. At the landscape scale, few species were found exclusively in riparian or non-riparian habitats (Chapter 2): many species used both riparian and non-riparian habitats, and may depend on either habitat at particular times in the annual cycle. At a broader scale, many migratory species move across extensive areas, well beyond the size of traditional conservation reserves, to complete their annual cycle. It is important to recognise temporal variation in the requirement of birds for forest habitats across the range of spatial scales when planning conservation programs.

#### 4 Structure and ecological characteristics of bird assemblages: differences between riparian and non-riparian habitats in eucalypt forest

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Beautiful Firetail *Stagonopleura bella* at its breeding nest

## 4.1 Introduction

The availability of different types of resources and the ways in which animals use resources have important implications for the structure of communities. Bird assemblages provide a good indication of niche availability in forests as they use most habitat features within the forest environment (Recher *et al.* 1985; Decamps *et al.* 1987; Recher 1991; Mac Nally 1994). The subdivision of assemblages into ecological groupings, based on similarities in the use of habitat features, has been commonly used to investigate community structure. In particular, the use of guilds, groups of species that exploit the same class of environmental resources in a similar way (Root 1967), has been widely employed in analyses of community structure (Sabo and Holmes 1983; Holmes and Recher 1986). The foraging locations and prey types exploited by species are parameters typically used to define guilds within bird assemblages (Recher *et al.* 1985; Ford *et al.* 1986; Knopf *et al.* 1988b; Mac Nally 1994; Pearman 2002). Bird assemblages have also been subdivided into groups based on life-history features such as nest type (e.g. Lindenmayer *et al.* 2002) and migratory patterns (e.g. Wiebe and Martin 1998). Such groupings represent ecological building blocks within assemblages (Mac Nally 1994), and by assessing and comparing these components a better understanding can be achieved of the relationship between the availability of exploitable niches and their potential use by birds. If each group exploits a different subset of resources, then group structure and composition of assemblages should reflect the availability of resource types (Hawkins and MacMahon 1989).

Significant differences in the structure of riparian and non-riparian bird assemblages were shown in Chapter 2. Riparian bird assemblages have greater species richness and higher bird abundance when compared to non-riparian assemblages. The objective of this chapter is to examine the ecological mechanisms by which riparian bird assemblages are richer and support more individual birds. Two hypotheses to account for greater richness in riparian zones were investigated:

1. Riparian habitats are more structurally complex and diverse and therefore there are more opportunities (i.e. niches) available. This hypothesis predicts that assemblages in riparian sites will be composed of species representing a greater number of ecological groups than are

present in assemblages in non-riparian sites.

2. Riparian habitats support a similar number of niches to non-riparian habitats but there is greater species packing within ecological groups. This hypothesis predicts that there is no difference between riparian and non-riparian sites in the number of ecological groups present, but that on average there will be more species per group in riparian sites.

## **4.2 Methods**

### *4.2.1 Study area*

This study was conducted in foothill eucalypt forests of the south-west part of the Victorian Highlands, approximately 75 km east of Melbourne, Victoria, Australia. It utilised the same study area discussed in detail in Chapter 1 and Chapter 2.

### *4.2.2 Study sites*

A set of 30 paired riparian and non-riparian sites (described in Chapter 2) was used for this investigation of the structure and ecological characteristics of bird assemblages.

### *4.2.3 Bird surveys*

Bird surveys were conducted using a fixed-point count method (Pyke and Recher 1984) between July 2001 and December 2002 as described in Chapter 2.

### *4.2.4 Foraging observations*

Observations of the foraging behaviour of birds were gathered throughout the survey period. For each individual observed foraging, the height, structural feature, substrate and foraging method were recorded for the initial foraging attempt. Structural features included air, trees (tall, medium, small or sapling), dead standing trees (DST), shrubs, ground vegetation, tree ferns, low ferns, ground and coarse woody debris (CWD). Substrates included gaps in the vertical profile (above canopy, canopy, mid or low), plant foliage (inner = plant foliage within the outer perimeter; outer = plant foliage on the outer perimeter), flowers, mistletoe, fruits/nuts, branches (major, minor or dead), trunk,

decorticating bark, grasses/sedges, litter (open or sheltered), bare ground (open or sheltered), fallen tree/branch and water. The height of foraging attempts was recorded as the proportional height within the vertical profile of the forest (0 = ground surface to 1 = maximum canopy height). Observations of aerial foraging above the canopy were not considered in this chapter. The species of plant was also recorded when foraging took place on or within a plant. Foraging observations were pooled for the 18 months of the study. It was assumed that the detectability of birds was similar for riparian and non-riparian habitats, but the greater vegetation complexity at riparian sites may have some influence on the detectability of foraging.

#### 4.2.5 Foraging groups

Classification of foraging groups was based on the location of foraging activity and the food items consumed by individuals. The set of foraging groups was established with reference to the literature for assemblages in comparable habitats (e.g. Recher *et al.* 1985; Ford *et al.* 1986; Mac Nally 1994,1996; Loyn 1998; Recher and Holmes 2000). Dominant prey items were also determined from the literature (Barker and Vestjens 1990; Marchant and Higgins 1993; Higgins and Davies 1996; Higgins 1999; Higgins *et al.* 2001; Higgins and Peter 2002; Higgins *et al.* 2006a, 2006b). Species occurring in the study area were assigned to foraging groups based on a combination of previous assessments and published information on their foraging ecology (Recher and Holmes 1985; Ford *et al.* 1986; Mac Nally 1994,1996; Loyn 1998; Tzaros 2001), and these classifications were corroborated by observations (see above) made during the study.

**Table 4-1 Foraging group definitions for bird assemblages in the Victorian Highlands, south-east Australia.**

Foraging group	Code	Definition	Example species
Aquatic	Aq	Birds that forage in aquatic situations	Pacific Black Duck, Australian Wood Duck
Aerial – invertebrates	A-I	Birds that forage aerially above or below the canopy and take invertebrates as the main part of their diet	Tree Martin, Welcome Swallow, Dusky Woodswallow
Arboreal – seeds/fruits	A-S/F	Birds that forage from shrubs and trees and take seeds or fruits as the main part of their diet	Crimson Rosella, Gang-gang Cockatoo, Mistletoebird
Bark – invertebrates	B-I	Birds that forage from bark surfaces and take invertebrates as the main part of their diet	White-throated Treecreeper, Crested Shrike-tit, White-eared Honeyeater
Generalist carnivore	GC	Birds that take vertebrate prey or large insects as the main part of their diet and forage from a range of substrates	Laughing Kookaburra, Grey Currawong, Australian Raven, Brown Goshawk
Ground layer – seeds/fruits	G-S/F	Birds that forage from the ground or ground layer vegetation and take seeds or fruits as the main part of their diet	Beautiful Firetail, Brush Bronzewing
Nectar/Flowers	N/F	Birds that forage from shrub and tree flowers and take nectar as the main part of their diet	Little Lorikeet, Swift Parrot, Red Wattlebird, Eastern Spinebill
Open ground – invertebrates	OG-I	Birds that forage from open ground and take invertebrates as the main part of their diet	Scarlet Robin, Superb Fairy-wren, Buff-rumped Thornbill, White-winged Chough
Sheltered ground – invertebrates	SG-I	Birds that forage from ground below cover amongst dense understorey and take invertebrates as the main part of their diet	Superb Lyrebird, Eastern Yellow Robin, Bassian Thrush, Southern Emu-wren, Olive Whistler, Eastern Whipbird
Shrub/small tree – invertebrates	S/ST-I	Birds that forage from shrubs and small trees and take invertebrates as the main part of their diet	Brown Thornbill, Rufous Fantail, Silvereye, Large-billed Scrubwren
Sub-canopy – invertebrates	S-c-I	Birds that forage above ground at all levels below the canopy and take invertebrates as the main part of their diet	Yellow-faced Honeyeater, Rose Robin, Golden Whistler, Grey Fantail, Shining Bronze-Cuckoo
Tree layer – invertebrates	TL-I	Birds that forage amongst canopy trees and take invertebrates as the main part of their diet	Spotted Pardalote, Striated Thornbill, White-naped Honeyeater, Rufous Whistler, Olive-backed Oriole, Satin Flycatcher

#### 4.2.6 Nest type

Species were classified into nest-type groups based on the literature (Campbell 1900; North 1984; Beruldsen 2003). Observations of nests made during the study were used to support classifications. Groups were identified by the type of nest used and its



location. Nest types were of four basic forms.

- Open top nests - nest structures often referred to as cups or platforms that do not have enclosed tops (e.g. Australian Magpie, robins and whistlers).
- Domed nests - nest structures tend to be globular and mostly enclosed, with a side entrance (e.g. Superb Fairy-wren, thornbills and finches).
- Hollow nests - those nests located in cavities in trees, including fallen trees (e.g. parrots, kingfishers and treecreepers).
- Burrow nest - those nests located within cavities in the ground (e.g. Spotted Pardalote)

The locations of nests were broadly classified as being in tall trees, shrubs and small trees, ground layer vegetation (e.g. sedges, grasses, ferns and low shrubs), or burrows (e.g. Spotted Pardalote). The eight nest-type groups identified were: hollow (H), open top – tall tree (O-TT), open top – shrub/small tree (O-S/ST), open top – dense understorey (O-DU), domed nest – tall tree (D-TT), domed – shrub/small tree (D-S/ST), domed – dense understorey (D-DU) and burrow (B).

#### 4.2.7 *Body mass*

Data on the body mass of birds was collated from the literature (Rogers *et al.* 1986; Marchant and Higgins 1990b; Rogers *et al.* 1990; Marchant and Higgins 1993; Higgins and Davies 1996; Strahan 1996; Higgins 1999; Higgins *et al.* 2001; Higgins and Peter 2002; Higgins *et al.* 2006a, 2006b). The mass of an adult male was used as the standard measure across all species. Species were categorised into one of six groups: <10 g, 11–30 g, 31–60 g, 61–100 g, 101–300 g and >301 g.

#### 4.2.8 *Data analysis*

To test hypotheses concerning the processes underlying differences in richness between riparian and non-riparian assemblages, bird species observations were compiled and pooled for all 29 visits to each site. Two types of comparisons were made between pairs of riparian and non-riparian sites, by using paired *t*-tests:

- a) the number of foraging, nest-type and body mass groups represented in the assemblage at each site;
- b) the species richness and abundance of birds in each ecological group at each site.

An ordination of the foraging profile of bird species was constructed by using multidimensional scaling (MDS), based on a Bray-Curtis similarity matrix. The similarity matrix represented the proportional use of combinations of structural feature of habitat and substrate by each species while foraging. Species included in the analysis were restricted to those with  $\geq 30$  foraging observations, as recommended by Morrison (1984). This procedure was conducted using PRIMER software (Clarke and Gorley 2001).

To test whether there were differences in the foraging profiles of species between riparian and non-riparian sites, foraging observations were compiled and pooled for the 18 months of bird surveys. Differences in the proportional use of structural features of habitats, substrates and foraging heights were compared between riparian and non-riparian sites by using chi-squared tests.

Differences in the niche breadth of species were compared between habitat types, for species with sufficient foraging observations (i.e. 30 observations) in each habitat, by using paired *t*-tests. The plasticity of an individual species' foraging profile was assessed as the diversity of use of the available resource states. Niche breadth is widely used as a measure of the degree of specialisation of a species' foraging ecology (Krebs 1999). The Shannon-Wiener diversity index has been widely used in studies measuring the foraging profile of species (e.g. Willson 1974; Ford *et al.* 1986; Antos and Bennett 2006). To standardise this index (scale of 0–1) the evenness measure of this index,  $J'$ , was used as suggested by Krebs (1998).  $J'$  measures the evenness of the use of the available resource states (i.e. structural features of habitats, substrates and proportional heights).

For all analyses, a test statistic was deemed to be significant at the  $p = 0.05$  level.

## 4.3 Results

### 4.3.1 *Bird assemblages*

A total of 88 bird species was recorded across the set of 30 paired riparian and non-riparian sites during the study. Riparian assemblages were significantly richer in species and supported a greater relative abundance of individuals than non-riparian assemblages (Chapter 2).

The forest bird assemblage included species that mostly consume invertebrates (59% of all species), seeds/fruits (13%), nectar/flowers (9%) or vertebrates (16%). In terms of abundance, the forest bird assemblage is dominated by invertebrate feeders (68% of individuals observed) and nectar/invertebrate feeders (24%).

**Table 4-2 Foraging group, nest-type classification and body mass of bird species (n = 88) recorded at riparian (Rip) and non-riparian (NR) sites during the field survey.**

Name	Common name	Code	Site records (n = 30)		Forage observations (n)		Forage group	Nest type	Body mass (g) <sup>#</sup>
			Rip	NR	Rip	NR			
Australian Shelduck	<i>Tadorna tadornoides</i>		2	-	-	-	Aq	H	1559
Australian Wood Duck	<i>Chenonetta jubata</i>		1	-	-	-	Aq	H	815
Pacific Black Duck	<i>Anas superciliosa</i>		1	-	-	-	Aq	H	1059
Whistling Kite	<i>Haliastur sphenurus</i>		1	-	-	-	GC	O-TT	792
Brown Goshawk	<i>Accipiter fasciatus</i>		6	2	1	1	GC	O-TT	353
Collared Sparrowhawk	<i>Accipiter cirrihocephalus</i>		1	1	-	-	GC	O-TT	126
Wedge-tailed Eagle	<i>Aquila audax</i>		-	2	-	-	GC	O-TT	3140
Little Eagle	<i>Hieraaetus morphnoides</i>		1	2	-	-	GC	O-TT	633
Swamp Harrier	<i>Circus approximans</i>		2		-	-	GC	O-DU	617
Peregrine Falcon	<i>Falco peregrinus</i>		-	1	-	-	GC	O-TT	537
Brush Bronzewing	<i>Phaps elegans</i>		-	1	-	-	GL-S/F	O-S/ST	219
Yellow-tailed Black-Cockatoo	<i>Calyptorhynchus funereus</i>		8	8	6	3	A-S/F	H	731
Gang-gang Cockatoo	<i>Callocephalon fimbriatum</i>		14	8	8	4	A-S/F	H	255
Sulphur-crested Cockatoo	<i>Cacatua galerita</i>		8	-	1	-	A-S/F	H	815
Musk Lorikeet	<i>Glossopsitta concinna</i>		2	1	-	2	N/F	H	79
Little Lorikeet	<i>Glossopsitta pusilla</i>		2	1	1	-	N/F	H	39
Purple-crowned Lorikeet	<i>G. porphyrocephala</i>		1	-	-	-	N/F	H	44
Australian King Parrot	<i>Alisterus scapularis</i>		12	10	2	3	A-S/F	H	222
Crimson Rosella	<i>Platycercus elegans</i>	crro	30	28	49	49	A-S/F	H	140
Eastern Rosella	<i>Platycercus eximius</i>		8	9	-	6	A-S/F	H	109
Swift Parrot	<i>Lathamus discolor</i>		1	-	-	-	N/F	X	65
Pallid Cuckoo	<i>Cuculus pallidus</i>		1	1	-	-	S-c-I	O-S/ST	90

**Table 4–2** continued.

Name	Common name	Code	Site records (n = 30)		Forage observations (n)		Forage group	Nest type	Body mass (g) <sup>#</sup>
			Rip	NR	Rip	NR			
Fan-tailed Cuckoo	<i>Cacomantis flabeliformis</i>		13	11	-	-	S-c-I	D-DU	50
Shining Bronze-Cuckoo	<i>Chrysococcyx lucidus</i>		20	10	2	1	S-c-I	D-S/ST	26
Southern Boobook	<i>Ninox novaeseelandiae</i>		1	-	-	-	GC	H	254
Australian Owlet-nightjar	<i>Aegotheles cristatus</i>		-	1	-	-	S-c-I	H	44
White-throated Needletail	<i>Hirundapus caudacutus</i>		1	5	1	-	A-I	X	98
Laughing Kookaburra	<i>Dacelo novaeguineae</i>		19	15	-	5	GC	H	325
Sacred Kingfisher	<i>Todiramphus sanctus</i>		10	1	-	-	GC	H	43
Superb Lyrebird	<i>Menura novaehollandiae</i>		15	6	-	4	SG-I	D-DU	1100
White-throated Treecreeper	<i>Corombates leucophaeus</i>	wtrr	30	26	86	85	B-I	H	22
Red-browed Treecreeper	<i>Climacteris erythrops</i>	rbtr	27	9	97	15	B-I	H	24
Superb Fairy-wren	<i>Malurus cyaneus</i>		23	23	3	6	OG-I	D-DU	10
Southern Emu-wren	<i>Stipituris malachurus</i>		4	15	1	7	SG-I	D-DU	8
Spotted Pardalote	<i>Pardalotus punctatus</i>	sppa	30	29	18	12	TL-I	B	9
Striated Pardalote	<i>Pardalotus striatus</i>	stpa	30	23	24	6	TL-I	H	13
White-browed Scrubwren	<i>Sericornis frontalis</i>	wbsc	30	17	33	8	SG-I	D-DU	13
Large-billed Scrubwren	<i>Sericornis magnirostris</i>	lpsc	22	1	41	-	S/ST-I	D-S/ST	11
White-throated Gerygone	<i>Gerygone olivacea</i>		1	-	-	-	TL-I	D-S/ST	8
Brown Thornbill	<i>Acanthiza pusilla</i>	brth	30	30	254	110	S/ST-I	D-DU	7
Buff-rumped Thornbill	<i>Acanthiza reguloides</i>		-	4	-	7	OG-I	D-S/ST	8
Yellow Thornbill	<i>Acanthiza nana</i>		-	5	-	3	TL-I	D-S/ST	7
Striated Thornbill	<i>Acanthiza lineata</i>	stth	30	30	127	122	TL-I	D-TT	8
Red Wattlebird	<i>Anthochaera carunculata</i>	rewa	28	27	27	78	N/F	O-TT	120
Noisy Miner	<i>Manorina melanocephala</i>		-	1	-	-	TL-I	O-TT	63

**Table 4–2**      **continued**

Name	Common name	Code	Site records (n = 30)		Forage observations (n)		Forage group	Nest type	Body mass (g) <sup>#</sup>
			Rip	NR	Rip	NR			
Lewin's Honeyeater	<i>Meliphaga lewinii</i>		15	1	19	-	S-c-I	O-S/ST	40
Yellow-faced Honeyeater	<i>Lichenostomus chrysops</i>	yfho	30	29	89	16	S-c-I	O-S/ST	18
White-eared Honeyeater	<i>Lichenostomus leucotis</i>	weho	22	7	25	8	B-I	O-DU	27
Yellow-tufted Honeyeater	<i>Lichenostomus melanops</i>	ytho	5	-	32	-	S-c-I	D-S/ST	24
Brown-headed Honeyeater	<i>Melithreptus brevirostris</i>		21	12	11	4	TL-I	O-TT	14
White-naped Honeyeater	<i>Melithreptus lunatus</i>	wnho	29	15	168	4	TL-I	O-TT	15
Crescent Honeyeater	<i>Phylidonyris pyrrhoptera</i>	crho	28	15	25	23	N/F	O-DU	17
New Holland Honeyeater	<i>P. novaehollandiae</i>		7	1	11	-	N/F	O-S/ST	20
Eastern Spinebill	<i>Acanthorhynchus tenuirostris</i>	easp	28	29	30	52	N/F	O-S/ST	12
Scarlet Robin	<i>Petroica multicolor</i>		2	19	-	14	OG-I	O-S/ST	13
Flame Robin	<i>Petroica phoenicea</i>		-	3	-	4	OG-I	X	13
Rose Robin	<i>Petroica rosea</i>	roro	30	5	48	3	S-c-I	O-S/ST	8
Pink Robin	<i>Petroica rodinogaster</i>		6	-	4	-	SG-I	O-S/ST	9
Eastern Yellow Robin	<i>Eopsaltria australis</i>	eayr	30	21	30	18	SG-I	O-S/ST	22
Eastern Whipbird	<i>Psophodes olivaceus</i>		19	1	11	1	SG-I	O-DU	68
Varied Sittella	<i>Daphoenositta chrysoptera</i>	vasi	21	17	11	22	B-I	D-TT	12
Crested Shrike-tit	<i>Falcunculus frontatus</i>		16	1	14	-	B-I	O-TT	30
Olive Whistler	<i>Pachycephala olivacea</i>		21	3	8	1	SG-I	O-DU	41
Golden Whistler	<i>Pachycephala pectoralis</i>	gowh	30	28	31	28	S-c-I	O-S/ST	27
Rufous Whistler	<i>Pachycephala rufiventris</i>	ruwh	15	26	1	29	TL-I	O-S/ST	26
Grey Shrike-thrush	<i>Colluricincla harmonica</i>	gyst	28	28	12	23	B-I	O-S/ST	69
Leaden Flycatcher	<i>Myiagra rubecula</i>		-	1	-	-	TL-I	O-TT	15
Satin Flycatcher	<i>Myiagra cyanoleuca</i>		22	6	5	4	TL-I	O-TT	18

**Table 4–2 continued**

Name	Common name	Code	Site records (n = 30)		Forage observations (n)		Forage group	Nest type	Body mass (g) <sup>#</sup>
			Rip	NR	Rip	NR			
Rufous Fantail	<i>Rhipidura rufifrons</i>	gyfa	28	5	16	4	S/ST-I	O-S/ST	9
Grey Fantail	<i>Rhipidura fuliginosa</i>		30	29	159	53	S-c-I	O-S/ST	8
Black-faced Cuckoo-shrike	<i>Coracina novaehollandiae</i>		11	13	-	12	TL-I	O-TT	112
Olive-backed Oriole	<i>Oriolus sagittatus</i>		4	13	-	6	TL-I	O-TT	98
Dusky Woodswallow	<i>Artamus cyanopterus</i>	silv	2	2	-	-	A-I	O-S/ST	39
Grey Butcherbird	<i>Cracticus torquatus</i>		1	3	-	2	GC	O-TT	92
Australian Magpie	<i>Gymnorhina tibicen</i>		1	-	1	-	OG-I	O-TT	306
Pied Currawong	<i>Strepera graculina</i>		7	9	1	4	GC	O-TT	350
Grey Currawong	<i>Strepera versicolor</i>		9	8	2	6	GC	O-TT	348
Australian Raven	<i>Corvus coronoides</i>		6	2	-	-	GC	O-TT	680
White-winged Chough	<i>Corcorax melanorhamphos</i>		-	1	-	-	OG-I	O-TT	372
Satin Bowerbird	<i>Ptilonorhynchus violaceus</i>		4	-	10	-	A-S/F	O-S/ST	201
Red-browed Finch	<i>Neochmia temporalis</i>		3	-	2	-	GL-S/F	D-S/ST	12
Beautiful Firetail	<i>Stagonopleura bella</i>		16	2	5	-	GL-S/F	D-S/ST	14
Mistletoebird	<i>Dicaeum hirundinaceum</i>		8	9	-	2	A-S/F	D-TT	9
Welcome Swallow	<i>Hirundo neoxena</i>		4	3	-	1	A-I	O-TT	15
Tree Martin	<i>Hirundo nigricans</i>		22	5	17	-	A-I	H	15
Silvereye	<i>Zosterops lateralis</i>		30	23	28	6	S/ST-I	O-S/ST	9
Bassian Thrush	<i>Zoothera lunulata</i>		19	4	5	1	SG-I	O-S/ST	113
*Common Blackbird	<i>Turdus merula</i>		12	-	1	-	SG-I	O-S/ST	90

Abbreviations for foraging groups and nest types are as follows. Forage groups: Aquatic (Aq); Aerial – invertebrates (A-I); Arboreal – seeds/fruits (A-S/F); Bark – invertebrates (B-I); Generalist carnivore (GC); Ground layer – seeds/fruits (GL-S/F); Nectar/flowers (N/F); Open ground – invertebrates (OG-I); Sheltered ground – invertebrates (SG-I); Shrub/small tree – invertebrates (S/ST –I); Sub-canopy – invertebrates (S-c-I); Tree layer – invertebrates (TL-I). Nest-type: Burrow (B); Hollow (H); Domed – dense understorey (D-DU); Domed – shrub/small tree (D-S/ST); Domed – tall tree (D-TT); Open top – dense understorey (O-DU); Open top – shrub/small tree (O-S/ST); Open top – tall tree (O-TT); Non-breeding in study area (X). <sup>#</sup>Body weight is for an adult male. \* Introduced species.

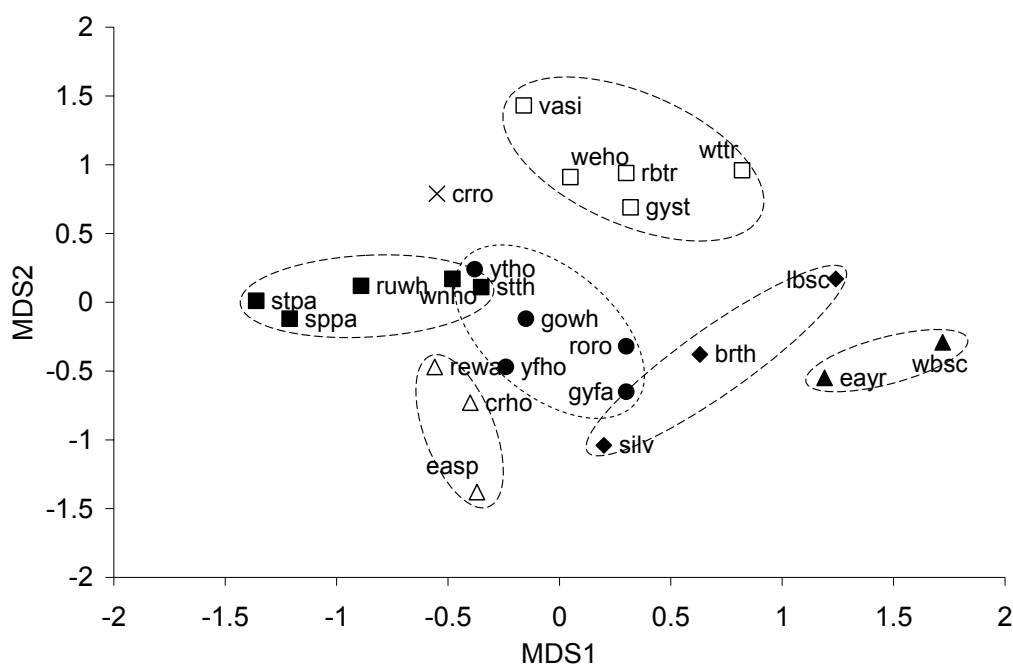
#### 4.3.2 *Foraging groups*

The bird assemblage was classified into 12 foraging groups based on a qualitative assessment of structural features of habitat and substrate used while foraging, and diet (Table 4-2).

A total of 2 501 foraging observations was gathered for 65 species during the field survey and these were used to corroborate the accuracy of the qualitative assessment. The largest numbers of observations were for Brown Thornbill, Striated Thornbill, Grey Fantail, White-throated Treecreeper and White-naped Honeyeater (Table 4-2). Thirty or more observations were gathered for 24 species, which include members of seven of the 12 foraging groups. For some species, many foraging observations were gathered in both riparian and non-riparian habitats (e.g. Brown Thornbill, Striated Thornbill and White-throated Treecreeper). For other species, most observations were from either riparian (e.g. Red-browed Treecreeper, Rose Robin and White-naped Honeyeater) or non-riparian habitats (e.g. Red Wattlebird and Eastern Spinebill). Foraging observations of Large-billed Scrubwren and Yellow-tufted Honeyeater were only gathered from riparian sites.

An ordination of the combination of structural features of habitat and substrates used by these common species displays the similarity between species in their foraging profile (Figure 4-1). There is a distinct clustering of species (Figure 4-1) and the seven foraging groups represented in the sample of species are readily distinguished (Figure 4-1). This gives confidence that the qualitative assignment of species into foraging groups (Table 4-2) is supported by empirical data from this study area.





**Figure 4-1** Ordination of species based on empirical data on structural features of habitats and substrates used during foraging attempts (stress = 0.19). Dashed lines enclose species assigned to foraging groups as qualitatively defined from the literature.

Symbols as follows: arboreal – seeds/fruits (x), bark – invertebrates ( $\square$ ), nectar/flowers ( $\Delta$ ), sheltered ground – invertebrates ( $\blacktriangle$ ), shrubs/small tree – invertebrates ( $\blacklozenge$ ), sub-canopy – invertebrates ( $\bullet$ ) and tree layer – invertebrates ( $\blacksquare$ ). See Table 4-2 for full bird names.

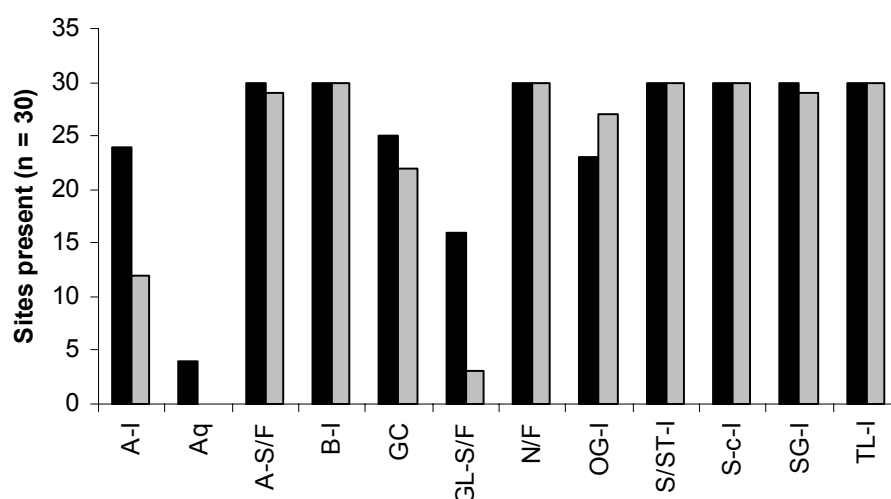
### 4.3.3 Comparison of foraging groups between riparian and non-riparian sites

#### 4.3.3.1 Number of foraging groups

Excluding the aquatic group, species from all foraging groups were represented in both riparian and non-riparian assemblages. However, the number of foraging groups represented at a site differed significantly between habitat types (paired  $t = 3.218$ , d.f. = 29,  $p = 0.003$ ). The mean number of foraging groups was greater in riparian assemblages ( $10.07$ ,  $\pm 1.26$  SD) than non-riparian assemblages ( $9.07$ ,  $\pm 0.94$  SD).

Representatives of most foraging groups were observed at the majority of sites throughout the forest mosaic (Figure 4-2). Members of five groups, the bark – invertebrates, nectar/flower, shrub/small tree – invertebrates, sub-canopy –

invertebrates and tree layer – invertebrates foraging groups were observed at all sites (Figure 4-2). Birds in the arboreal – seeds/fruits and sheltered ground – invertebrates foraging groups were observed at all riparian sites and almost all non-riparian sites (Figure 4-2). Ground layer – seeds/fruits foragers were not widely distributed in the forest mosaic, being recorded at 53% of riparian sites and just 10% of non-riparian sites (Figure 4-2). Open ground – invertebrates foragers were the only group that occurred at more non-riparian sites than riparian sites.



**Figure 4-2** Number of riparian (black) and non-riparian sites (grey) at which representatives of foraging groups were recorded.

Forage groups: Aerial – invertebrates (A-I); Aquatic (Aq); Arboreal – seeds/fruits (A-S/F); Bark – invertebrates (B-I); Generalist carnivore (GC); Ground layer – seeds/fruits (GL-S/F); Nectar/flowers (N/F); Open ground – invertebrates (OG-I); Sheltered ground – invertebrates (SG-I); Shrub/small tree – invertebrates (S/ST-I); Sub-canopy – invertebrates (S-c-I); Tree layer – invertebrates (TL-I).

#### 4.3.3.2 *Richness within foraging groups*

The most species-rich foraging groups in eucalypt foothill forests in the Victorian Highlands were generalist carnivores (14 species observed), tree layer – invertebrates (13), sub-canopy – invertebrates (10) and sheltered ground – invertebrates (9) (Table 4-3).

Riparian bird assemblages supported a significantly greater richness of species in seven of the 12 foraging groups: arboreal-seeds/fruits, aerial – invertebrates, bark – invertebrates, ground layer – seeds/fruits, nectar/flowers, sheltered ground – invertebrates, shrub/small tree – invertebrates and sub-canopy – invertebrates foraging groups (Table 4-3). Non-riparian assemblages supported a significantly greater richness of species in one group, the open ground – invertebrates foraging group (Table 4-3). The richness of the generalist carnivores and tree layer – invertebrates foraging groups did not differ between habitat types (Table 4-3).

#### 4.3.3.3 *Relative abundance of birds in foraging groups*

In terms of abundance, the forest bird assemblage was dominated by birds in the tree layer – invertebrates, shrub/small tree – invertebrates, sub-canopy – invertebrates and sheltered ground – invertebrates foraging groups. The generalist carnivore and ground layer – seeds/fruits foraging groups supported low numbers of individuals across all sites. The aquatic group was only observed within riparian habitats and in very low abundance (Table 4-3).

Riparian assemblages supported a significantly higher abundance of individuals in most foraging groups, including aerial – invertebrates, bark – invertebrates, ground layer – seeds/fruits, sheltered ground – invertebrates, shrub/small tree – invertebrates, sub-canopy – invertebrates and tree layer – invertebrates (Table 4-3). There was a significantly greater abundance of individuals in the open ground – invertebrates foraging group at non-riparian sites (Table 4-3). The abundance of generalist carnivores and nectar/flower foragers was similar between habitat types.

**Table 4-3 Species richness and relative abundance of birds (individuals ha<sup>-1</sup>) for each foraging group occurring in riparian and non-riparian assemblages.**

Foraging group	Measure	Total	Riparian			Non-riparian			<i>t</i>	<i>p</i>
			N	Mean	SD	N	Mean	SD		
Aquatic	Richness	3	3	0.13	0.35		–	–		
	Abundance			0.02	0.06		–	–		
Aerial – invertebrates	Richness	4	4	0.97	0.67	4	0.50	0.68	2.626	0.014
	Abundance			0.84	1.31		0.12	0.22	2.905	<0.01
Arboreal – seeds/fruits	Richness	8	8	3.07	1.31	6	2.40	0.97	2.484	0.019
	Abundance			0.94	0.71		0.74	0.68	1.947	0.061
Bark – invertebrates	Richness	6	6	4.80	1.03	6	2.93	1.08	5.956	<0.01
	Abundance			1.71	0.83		0.99	0.69	3.339	<0.01
Generalist carnivore	Richness	14	11	2.10	1.35	12	1.57	1.22	1.562	0.129
	Abundance			0.30	0.28		0.27	0.31	0.349	0.730
Ground layer – seeds/fruits	Richness	3	2	0.63	0.67	2	0.10	0.31	4.287	<0.01
	Abundance			0.18	0.26		0.01	0.03	3.662	<0.01
Nectar/flowers	Richness	8	8	3.23	1.10	6	2.47	0.82	2.841	<0.01
	Abundance			1.75	1.17		2.03	1.57	-0.673	0.506
Open ground – invert.	Richness	6	3	0.87	0.57	5	1.67	0.84	-3.890	<0.01
	Abundance			0.41	0.38		0.74	0.54	-2.591	0.015
Sheltered ground – invert.	Richness	9	9	5.20	1.30	7	2.23	1.07	9.493	<0.01
	Abundance			4.34	1.03		0.92	0.71	16.760	<0.01
Shrub/small tree – invert.	Richness	4	4	3.67	0.55	4	1.97	0.67	9.778	<0.01
	Abundance			7.79	1.97		2.50	1.58	14.380	<0.01
Sub-canopy – invertebrates	Richness	10	9	5.80	0.96	9	3.83	0.99	8.125	<0.01
	Abundance			5.74	1.51		1.22	0.67	15.173	<0.01
Tree layer – invertebrates	Richness	13	10	6.43	1.14	12	5.80	1.65	1.959	0.060
	Abundance			11.50	5.10		4.42	2.07	7.852	<0.01

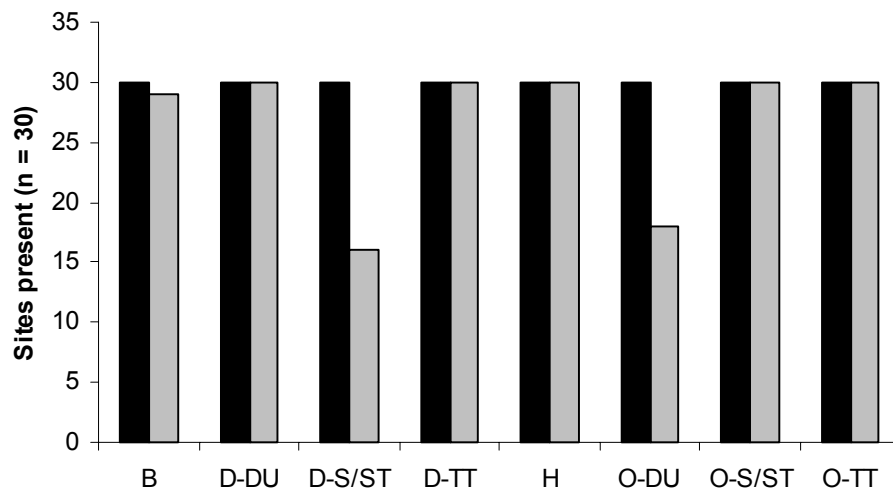
#### 4.3.4 Comparison of nest-type groups between riparian and non-riparian sites

The bird assemblage was classified into eight groups based on the types of nests used (Table 4-4). Species which were observed, but do not breed in the study area (i.e. Swift Parrot and White-throated Needletail) were not included in the analyses.

##### 4.3.4.1 Number of nest-type groups

Representatives of all nest-type groups occurred in both riparian and non-riparian bird

assemblages. The number of nest-type groups represented at a site was significantly greater (paired  $t = 6.496$ , d.f. = 29,  $p < 0.001$ ) in riparian bird assemblages (8) compared with non-riparian assemblages (7.1,  $\pm 0.14$  SD). Representatives of all nest-type groups were recorded at all riparian sites. Some groups were not as widely represented in non-riparian assemblages, with domed – shrub/small tree nesters and open top – dense understorey nesters being observed at 53% and 60% sites, respectively (Figure 4-3).



**Figure 4-3** Number of riparian (black) and non-riparian sites (grey) at which representatives of nest-type groups were recorded.

Nest-type: Burrow (B); Hollow (H); Domed – dense understorey (D-DU); Domed – shrub/small tree (D-S/ST); Domed – tall tree (D-TT); Open top – dense understorey (O-DU); Open top – shrub/small tree (O-S/ST); Open top – tall tree (O-TT)

#### 4.3.4.2 Richness of species within nest-type groups

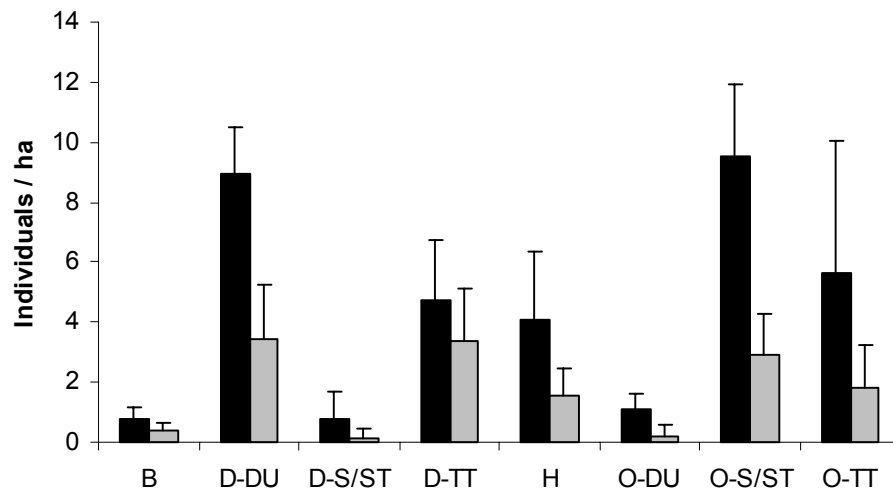
The most species-rich nest-type groups in the study area were open top – tall tree (22 species observed), open top – shrub/small tree (20) and hollow ( $n = 20$ ), which included approximately 70% of all species observed.

**Table 4-4 Species richness and relative abundance of birds (individuals ha<sup>-1</sup>) for each nest-type group occurring in riparian and non-riparian assemblages.**

Nest type	Measure	Total	Riparian			Non-riparian			<i>t</i>	<i>p</i>
			N	Mean	SD	N	Mean	SD		
Burrow	Richness	1	1	1.00	–	1	0.97	0.18	1.000	0.326
	Abundance			0.80	0.37		0.40	0.26	6.130	<0.01
Hollow	Richness	20	18	7.57	2.10	15	4.87	1.48	6.630	<0.01
	Abundance			4.10	2.27		1.53	0.91	6.989	<0.01
Domed – dense u'storey	Richness	6	6	3.83	0.99	6	3.40	1.00	1.557	0.130
	Abundance			8.92	1.60		3.44	1.78	13.458	<0.01
Domed – shrub/small tree	Richness	8	6	2.23	0.57	5	0.73	0.83	7.426	<0.01
	Abundance			0.77	0.89		0.16	0.31	3.392	<0.01
Domed – tall tree	Richness	3	3	1.97	0.77	3	1.87	0.63	0.516	0.610
	Abundance			4.75	2.02		3.37	1.75	2.870	<0.01
Open top – dense u'storey	Richness	5	5	3.07	0.98	4	0.87	0.86	8.061	<0.01
	Abundance			1.07	0.55		0.21	0.35	6.500	<0.01
Open top – shrub/small tree	Richness	20	19	11.57	1.52	17	8.40	1.30	10.846	<0.01
	Abundance			9.50	2.40		2.93	1.38	12.348	<0.01
Open top – tall tree	Richness	22	17	5.60	1.52	20	4.10	1.81	4.082	<0.01
	Abundance			5.61	4.42		1.84	1.37	4.356	<0.01

#### 4.3.4.3 Abundance of birds within nest-type groups

The relative abundance of birds in all eight nest-type groups was significantly greater in riparian habitats (Table 4-4). The open top – shrub/small tree and domed – dense understorey groups had the highest relative abundance of birds in riparian assemblages. In non-riparian assemblages, the groups supporting the highest abundance of birds were the domed – dense understorey group, followed by the domed – tall tree group (Figure 4-4).



**Figure 4-4** Relative abundance of individuals within nest-type groups for riparian (black) and non-riparian (grey) bird assemblages. Error bars represent standard deviation.

Nest-type: Burrow (B); Hollow (H); Domed – dense understorey (D-DU); Domed – shrub/small tree (D-S/ST); Domed – tall tree (D-TT); Open top – dense understorey (O-DU); Open top – shrub/small tree (O-S/ST); Open top – tall tree (O-TT)

#### 4.3.5 Comparison of body mass groups between riparian and non-riparian sites

Almost half (45%) of the species recorded have a body mass less than 60 g. The body mass of birds observed during this study ranged from 6.5 g (Yellow Thornbill) to 3 140 g (Wedge-tailed Eagle) (Table 4-2).

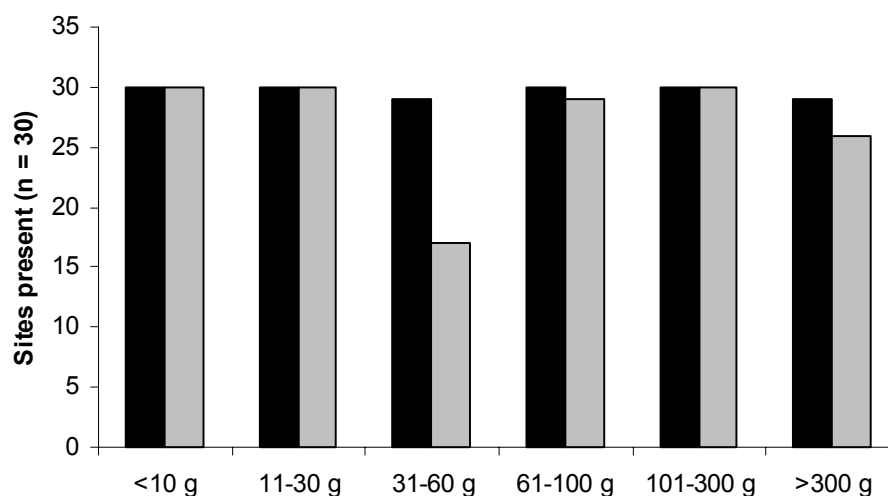
**Table 4-5 Species richness and relative abundance of body mass groups occurring in riparian and non-riparian bird assemblages.**

Body mass	Measure	Total	Riparian			Non-riparian			<i>t</i>	<i>p</i>
			N	Mean	SD	N	Mean	SD		
<10 g	Richness	14	10	6.40	0.89	10	5.97	1.10	1.750	0.091
	Abundance			13.65	2.72		7.38	3.18	8.301	<0.01
11-30 g	Richness	27	26	18.40	1.98	26	11.77	2.71	9.675	<0.01
	Abundance			18.88	6.58		3.79	2.04	11.698	<0.01
31-60 g	Richness	8	8	2.67	1.40	8	0.70	0.70	6.220	<0.01
	Abundance			0.54	0.43		0.06	0.07	5.991	<0.01
61-100 g	Richness	10	9	2.30	1.09	8	1.77	0.94	2.719	0.01
	Abundance			0.47	0.38		0.43	0.31	0.725	0.474
101-300 g	Richness	11	9	4.23	1.41	10	3.40	1.38	2.481	0.02
	Abundance			1.48	0.92		1.96	1.50	-1.533	0.136
>301 g	Richness	18	15	2.90	1.35	11	1.87	1.38	2.920	0.01
	Abundance			0.52	0.35		0.35	0.35	1.919	0.065

#### 4.3.5.1 Number of body mass groups

Representatives spanning all body mass groups occurred in both riparian and non-riparian assemblages. The number of body mass groups represented at a site was significantly greater (paired  $t = 4.877$ , d.f. = 29,  $p < 0.001$ ) in riparian bird assemblages (5.17,  $\pm 0.75$  SD) compared with non-riparian assemblages (4.23,  $\pm 0.86$  SD).





**Figure 4-5** Number of riparian (black) and non-riparian sites (grey) at which representatives of body mass groups were recorded.

Members of three of the six body mass groups, the <10 g, 11-30 g and 101-300 g, were observed at all sites (Figure 4-5). Species representing other body mass groups were observed at all (61-100 g group) or nearly all (29 sites; 31-60 g and >301 g groups) riparian sites (Figure 4-5). For non-riparian sites representatives of the 61-100 g (observed at 29 sites) and >301 g body mass groups (26) were observed at most sites. The 31-60 g group was not widely distributed at non-riparian sites, being recorded at just 57% of sites.

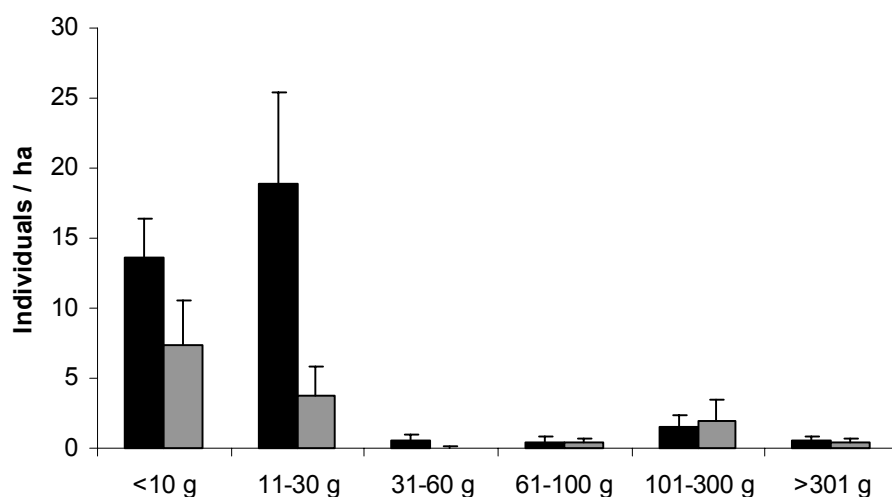
#### 4.3.5.2 *Richness of species within body mass groups*

The most species-rich groups for body mass in the study area were the 11-30 g (27 species observed), >301 g (18) and <10 g (14) groups (Table 4-5). There was a greater species richness at riparian sites in all body mass groups, except the <10 g group, when compared to non-riparian sites (Table 4-5). The richness of the <10 g group did not differ between riparian and non-riparian sites.

#### 4.3.5.3 *Abundance of birds within body mass groups*

Riparian assemblages supported a significantly greater abundance of birds in the

smaller body mass groups (<10 g, 11-30 g and 31-60 g) (Table 4-5), but there was no difference in the relative abundance of birds for body masses >61 g (Table 4-5). There was a sharp decrease in the abundance of species >30 g in the forest bird assemblage (Figure 4-6). One obvious difference between habitat types was the poor representation of species in the size-class 31-60 g in non-riparian assemblages (e.g. Sacred Kingfisher, Lewin's Honeyeater, Crested Shrike-tit and Olive Whistler). Species in this size-class were observed at only 57% of non-riparian sites.

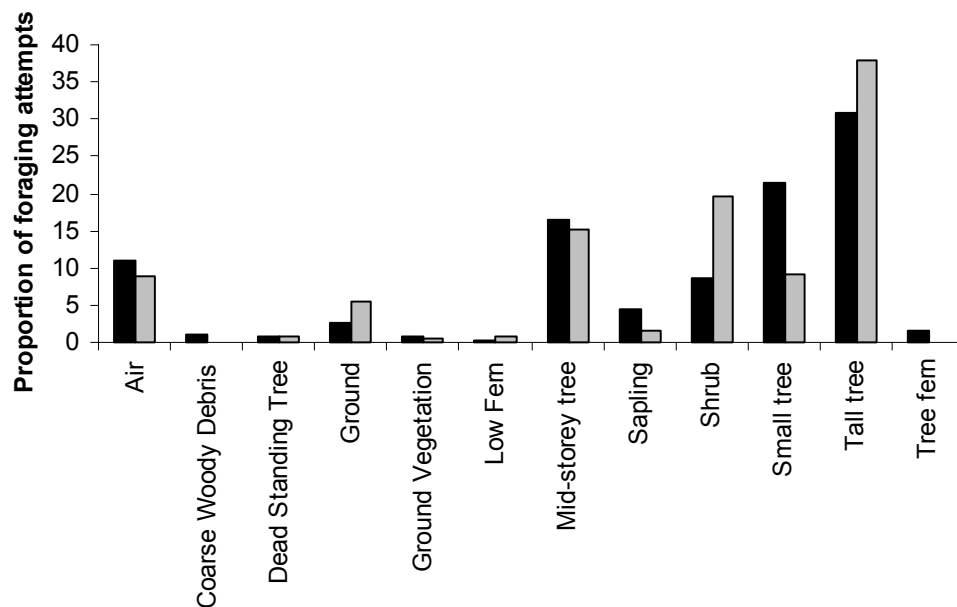


**Figure 4-6** Relative abundance of individuals in body mass groups for riparian (black) and non-riparian bird assemblages (grey). Error bars represent standard deviation.

#### 4.3.6 *Are there differences in foraging patterns between riparian and non-riparian sites?*

The most commonly used structural features of the vegetation during foraging, pooled across all species and all sites, were tall trees (33% of foraging observations), small trees (17%), mid-storey trees (16%), shrubs (12%) and air (10%). Ground-foraging accounted for 4% of all foraging observations.

The proportional use of structural features of the habitats showed significant variation between habitat types ( $\chi^2 = 161.8$ , d.f. = 11,  $p < 0.001$ ). Structural features used more frequently than expected in riparian habitats included small trees (26% more than expected), saplings (37%) and coarse woody debris (47%) (Figure 4-7). Tree ferns were observed to be used 55% more often than expected in riparian habitats, but there were no observations of foraging on tree ferns in non-riparian habitats where they occurred much more sparsely (Chapter 2). Structural features of habitats used more frequently in non-riparian habitats included shrubs (55% more than expected), ground (48%) and tall trees (14%).

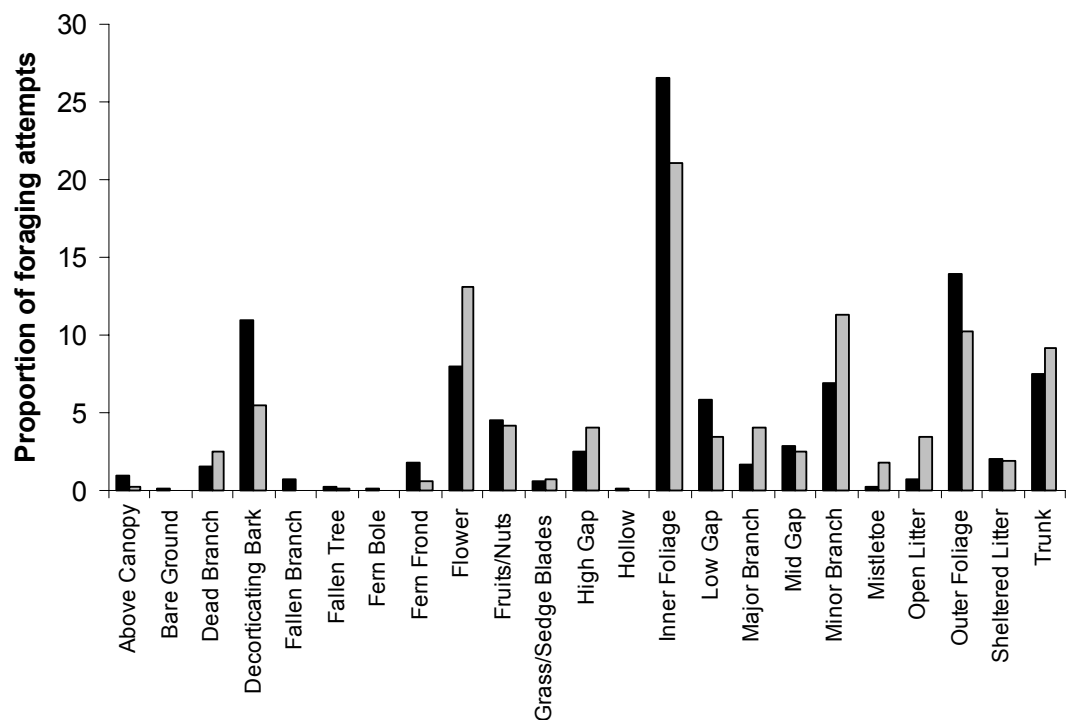


**Figure 4-7** Use of structural features of habitats (% of observations) by birds during foraging attempts in riparian (black) and non-riparian (grey) habitats in foothill eucalypt forest. Data are pooled for all species of birds.

The most commonly used foraging substrates pooled for all foraging observations across all sites, were inner foliage (25% of observations), outer foliage (12%), flowers

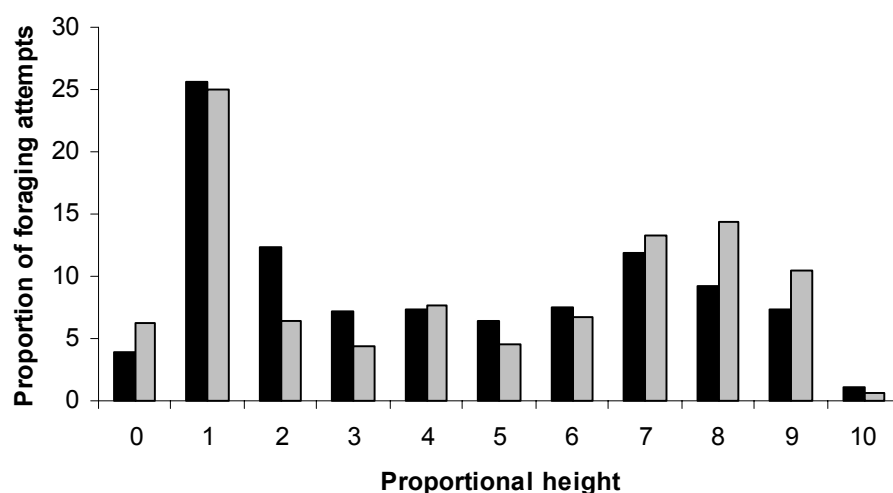
(10%), decortivating bark (9%), trunks (8%) and minor branches (8%).

The proportional use of substrates varied significantly between habitat types ( $\chi^2 = 154.8$ , d.f. = 22,  $p < 0.001$ ). Substrates used more frequently than expected in riparian habitats included decortivating bark (21% more than expected), inner foliage of plants (16%) and fern fronds (32%) (Figure 4-8). Fallen branches were observed to be used 56% more often than expected in riparian habitats, but there were no observations of foraging from fallen branches in non-riparian habitats. Substrates used more frequently than expected in non-riparian habitats included mistletoe (139% more than expected), open litter (108%), major branch (64%) and flowers (34%).



**Figure 4-8** Use of substrates (% of observations) by birds during foraging attempts in riparian (black) and non-riparian (grey) habitats in foothill eucalypt forest. Data are pooled for all species of birds.

The proportional use of different heights by foraging birds showed significant differences between riparian and non-riparian habitats ( $\chi^2 = 69.9$ , d.f. = 10,  $p < 0.001$ ). There was a greater concentration of foraging in low to mid-storey strata in riparian habitats (0.2-0.3 proportional height), whereas in non-riparian habitats there was a greater concentration of foraging on the ground (31% more than expected). There was also a greater proportion of foraging in the upper stratum (0.7-0.9 proportional height) in non-riparian compared with riparian sites (Figure 4-9).



**Figure 4-9** Proportional height of foraging attempts (% of observations) by birds in riparian (black) and non-riparian (grey) habitats in foothill eucalypt forest. Data are pooled for all species of birds.

#### *4.3.7 Do foraging patterns of species differ between riparian and non-riparian sites?*

Six species had sufficient foraging observations (i.e.  $\geq 30$  observations) in each habitat type to enable comparisons. These species were Brown Thornbill, Crimson Rosella, Eastern Spinebill, Grey Fantail, Striated Thornbill and White-throated Treecreeper. Foraging observations for these species comprised 47% of the total foraging observations recorded.

All six species showed significant differences in their frequency of use of structural features of habitat between riparian and non-riparian habitats (Table 4-6). Overall, these species displayed a broad use of the structural features present (Table 4-6), but foraging on the ground, or amongst coarse woody debris or low vegetation was not common for this suite of species. Some species displayed greater specialisation in the use of particular structural features in one or other of the habitat types. For example, the Eastern Spinebill foraged extensively amongst shrubs in non-riparian habitats (83% of observations), but largely foraged in trees (small, medium and tall) in riparian habitats (83% of observations).

Five of the six species showed significant differences in their frequency of use of substrates between habitat types: Brown Thornbill, Crimson Rosella, Eastern Spinebill, Striated Thornbill and White-throated Treecreeper (Table 4-7). The Grey Fantail did not differ in its frequency of use of different substrates between habitat types. Brown Thornbills foraging in riparian habitats exhibited the greatest degree of substrate specialisation amongst these species, largely concentrating their foraging amongst foliage (i.e. inner foliage, outer foliage and fern fronds). In non-riparian habitats Brown Thornbills were more general in their use of substrates, displaying greater use of trunks and branches.

**Table 4-6 Comparison of the proportional use (% of observations) of structural features of habitat in riparian (Rip) and non-riparian (NR) sites for six commonly recorded birds. Significance level of  $\chi^2$  are \*  $p < 0.05$ , \*\*  $p < 0.01$ .**

Structural feature	Brown Thornbill		Crimson Rosella		Eastern Spinebill		Grey Fantail		Striated Thornbill		White-throated Treecreeper	
	Rip	NR	Rip	NR	Rip	NR	Rip	NR	Rip	NR	Rip	NR
Ground	0	1	0	0	0	0	0	0	0	0	0	0
CWD	0	0	0	0	0	0	1	0	0	0	2	0
Ground vegetation	1	1	0	0	0	0	0	0	0	0	0	0
Low fern	0	4	0	0	0	0	1	0	1	0	0	0
Tree fern	4	0	0	0	0	0	3	0	0	0	0	0
Shrub	19	38	6	18	10	83	1	4	2	9	1	0
Sapling	14	9	4	0	0	0	2	2	2	2	1	0
Small tree	51	21	18	10	23	4	12	4	17	8	34	14
Mid-storey tree	7	9	27	6	20	6	3	9	29	20	31	28
Tall tree	2	12	43	65	40	2	8	19	49	60	24	55
DST	0	4	0	0	0	0	0	0	1	0	6	2
Air	1	2	2	0	7	6	70	62	0	0	0	0
<b>Niche breadth</b>	<b>0.62</b>	<b>0.77</b>	<b>0.79</b>	<b>0.72</b>	<b>0.89</b>	<b>0.43</b>	<b>0.48</b>	<b>0.64</b>	<b>0.54</b>	<b>0.71</b>	<b>0.74</b>	<b>0.76</b>
$\chi^2$ d.f.	<b>66.08<sub>11</sub>**</b>		<b>15.67<sub>5</sub>*</b>		<b>45.44<sub>4</sub>**</b>		<b>16.13<sub>8</sub>*</b>		<b>15.26<sub>6</sub>*</b>		<b>22.45<sub>6</sub>*</b>	

**Table 4-7 Comparison of the proportional use (% of observations) of foraging substrates in riparian (Rip) and non-riparian (NR) sites for six commonly recorded birds. Significance level of  $\chi^2$  are \*  $p < 0.05$ , \*\*  $p < 0.01$ .**

Substrate	Brown Thornbill		Crimson Rosella		Eastern Spinebill		Grey Fantail		Striated Thornbill		White-throated Treecreeper	
	Rip	NR	Rip	NR	Rip	NR	Rip	NR	Rip	NR	Rip	NR
Sheltered litter	0	1	0	0	0	0	0	0	0	0	0	0
Fallen branch	0	0	0	0	0	0	1	0	0	0	2	0
Grass / sedge / rush	1	1	0	0	0	0	0	0	0	0	0	0
Fern frond	4	4	0	0	0	0	3	0	1	0	0	0
Trunk	2	13	0	0	0	0	1	4	1	1	62	52
Major branch	0	1	0	0	0	0	0	2	1	2	10	26
Minor branch	2	7	8	29	0	0	2	8	6	11	14	18
Dead branch	0	3	0	0	0	0	1	0	2	2	6	2
Decorticated bark	2	2	0	6	0	0	1	0	16	2	6	2
Inner foliage	57	38	12	4	10	0	8	9	34	47	0	0
Outer foliage	26	25	0	0	3	0	9	8	39	26	0	0
Flower	3	4	8	8	67	83	0	0	2	8	0	0
Fruit / nut	0	0	67	51	0	0	0	0	0	0	0	0
Mistletoe	0	0	0	0	3	10	0	0	0	0	0	0
Low gap	1	2	0	0	10	4	37	34	0	0	0	0
Mid gap	0	0	2	2	7	0	20	19	0	0	0	0
High gap	0	0	2	0	0	4	17	17	0	0	0	0
<b>Niche breadth</b>	<b>0.37</b>	<b>0.60</b>	<b>0.67</b>	<b>0.74</b>	<b>0.70</b>	<b>0.62</b>	<b>0.53</b>	<b>0.81</b>	<b>0.56</b>	<b>0.60</b>	<b>0.66</b>	<b>0.70</b>
$\chi^2$ d.f.	<b>36.11<sub>12</sub>**</b>		<b>12.66<sub>5</sub>*</b>		<b>14.40<sub>6</sub>*</b>		<b>13.01<sub>11</sub></b>		<b>25.64<sub>6</sub>*</b>		<b>11.19<sub>5</sub>*</b>	



**Table 4-8** Comparison of the proportional height of foraging attempts in riparian (Rip) and non-riparian (NR) sites for six commonly recorded birds. Significance level of  $\chi^2$  are \*  $p < 0.05$ , \*\*  $p < 0.01$ .

Height	Brown Thornbill		Crimson Rosella		Eastern Spinebill		Grey Fantail		Striated Thornbill		White-throated Treecreeper	
	Rip	NR	Rip	NR	Rip	NR	Rip	NR	Rip	NR	Rip	NR
0	1	1	0	0	0	4	0	0	1	0	1	0
1	59	55	16	14	23	79	26	30	5	13	26	11
2	23	16	8	12	7	4	17	4	7	3	28	11
3	8	8	4	2	7	2	12	8	8	6	9	7
4	4	11	2	2	13	2	11	11	16	8	16	19
5	2	3	4	0	17	2	5	6	15	6	5	8
6	2	2	8	4	10	0	6	8	14	20	5	8
7	1	3	29	12	17	4	7	7	17	12	5	20
8	0	0	4	16	3	4	12	15	11	17	6	14
9	0	0	24	37	3	0	3	6	7	15	0	5
10	0	0	0	0	0	0	1	2	0	0	0	0
<b>Niche breadth</b>	<b>0.56</b>	<b>0.66</b>	<b>0.83</b>	<b>0.82</b>	<b>0.89</b>	<b>0.45</b>	<b>0.90</b>	<b>0.88</b>	<b>0.95</b>	<b>0.92</b>	<b>0.83</b>	<b>0.93</b>
$\chi^2$ d.f.	<b>13.41<sub>8</sub></b>		<b>11.47<sub>8</sub></b>		<b>32.97<sub>9</sub>**</b>		<b>8.85<sub>9</sub></b>		<b>23.04<sub>9</sub>*</b>		<b>29.54<sub>9</sub>*</b>	

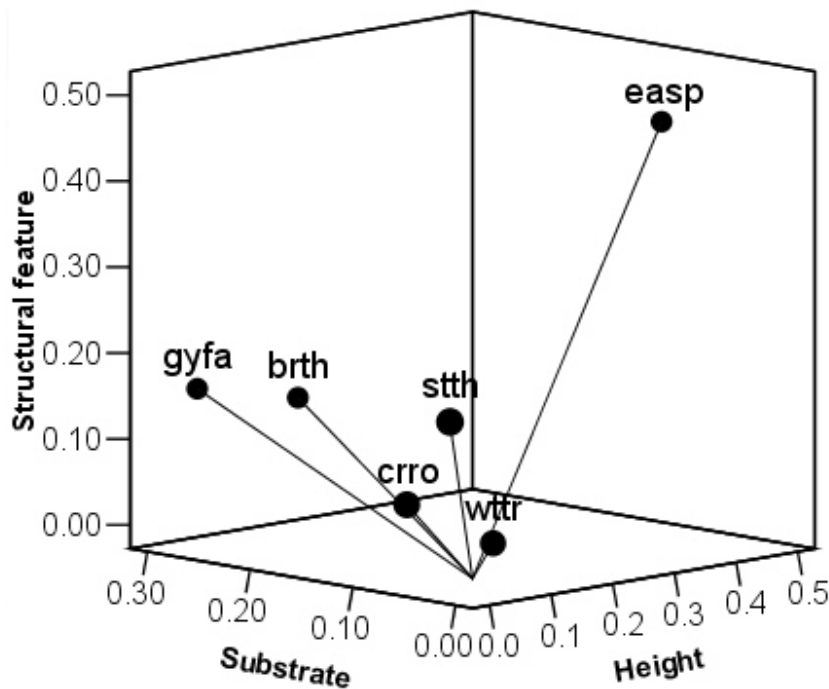
Three of the six species showed significant differences in the height at which they foraged, between riparian and non-riparian sites: Eastern Spinebill, Striated Thornbill and White-throated Treecreeper (Table 4-8). The Eastern Spinebill showed less homogeneity in its foraging height at riparian sites compared with non-riparian sites (Table 4-8), where it generally foraged much lower amongst prolifically flowering shrubs (e.g. banksia). The White-throated Treecreeper showed more homogeneity in its foraging height at riparian sites, generally foraging at lower levels than at non-riparian sites, where it foraged more extensively in the upper stratum (Table 4-8).

Figure 4-10 shows the magnitude of difference in niche breadth for foraging parameters (i.e. structural feature, substrate and height) between riparian and non-riparian habitats for each species. A number of patterns are evident in the way species' foraging patterns differ between site types.

First, some species displayed similar patterns between riparian and non-riparian habitats (e.g. Crimson Rosella and White-throated Treecreeper).

Second, the foraging pattern of some species differed due to disparity in a single parameter (e.g. Eastern Spinebill and Striated Thornbill). The Eastern Spinebill foraged extensively from flowers at both riparian (67% of foraging observations) and non-riparian sites (83%). However, at riparian sites it foraged mostly from trees (83% of observations), while at non-riparian sites it foraged mostly from shrubs (83%).

Third, some species showed marked changes in their foraging pattern between site types due to disparities for two or more foraging parameters (e.g. Brown Thornbill and Grey Fantail). The Brown Thornbill and Grey Fantail displayed greater foraging specialisation at riparian sites. The greatest disparity in niche breadth between site types for these species was associated with the use of substrates, with related changes evident for foraging heights and structural features. The Brown Thornbill foraged from a wide-range of plant surfaces in non-riparian habitats including trunks, branches, and inner foliage of both trees and shrubs. At riparian sites, it foraged almost entirely from inner foliage and outer foliage of predominantly small trees, as well as shrubs. The Grey Fantail mostly foraged aerially in gaps in both site types; however, at non-riparian sites it also foraged extensively from plant surfaces including branches and trunks.



**Figure 4-10** Magnitude of difference in niche breadth between riparian and non-riparian sites for structural features of habitat, substrates and heights used by species. Species are: Brown Thornbill (brth), Crimson Rosella (crro), Eastern Spinebill (easp), Grey Fantail (gyfa), Striated Thornbill (stth) and White-throated Treecreeper (wtrr).

## 4.4 Discussion

In this chapter, I have investigated two mechanisms that may contribute to riparian habitats supporting rich and abundant bird assemblages compared with those in adjacent non-riparian zones. First, to determine whether riparian zones provided distinct habitats and resources for birds in the forest landscape the number of ecological groups represented in riparian and non-riparian bird assemblages was

compared. Second, to determine whether additional species are accommodated in riparian assemblages (i.e. species packing) because of biotic processes (i.e. resource partitioning, niche breadth), the richness of ecological groups in riparian and non-riparian sites was compared.

#### *4.4.1 A greater number of ecological groups are represented in riparian assemblages.*

Riparian assemblages supported a greater number of ecological groups. These groups involved how birds obtain food resources (i.e. foraging groups), where birds nest (i.e. nest-type groups) and their morphological characteristics (i.e. body mass groups). The consistency of the differences found across the range of ecological attributes indicates that riparian zones offer a wider range of niches that are exploited by birds. This is augmented by the provision of distinct resources for foraging (e.g. decorticated bark, damp litter) and nesting (e.g. mid-storey vegetation) that are closely tied to the riparian zones in the landscape. Riparian habitats had a more complex vegetation structure, including greater percent cover of mid-storey trees, tall shrubs, sedges and tree ferns, than in non-riparian vegetation (Chapter 2).

Vegetation structure is a primary determinant of guild structure for a range of assemblages including invertebrates (Haslett 1997), mammals (August 1983; Williams *et al.* 2002) and birds (Wiens and Rotenberry 1981; Gilmore 1985; Holmes and Recher 1986). Increased structural complexity of habitats in forests provides more diverse foraging opportunities for species (Holmes *et al.* 1979; Beedy 1981; Holmes and Recher 1986). Holmes *et al.* (1979) considered the positive relationship between foliage height diversity and bird species diversity to be due to increased foraging opportunities for birds when foliage occurs in a variety of vertical zones. The addition of structural features of habitats has been shown to result in the addition of guilds to assemblages, and species richness within guilds (Willson 1974; Beedy 1981). Structurally diverse vegetation is also likely to provide more potential nest sites for birds (MacArthur and MacArthur 1961; Bub *et al.* 2004).

Increased understorey vegetation (e.g. mid-storey trees, shrubs and tree ferns) benefits ground and shrub nesting species by providing more nesting substrates (Cody 1981; Nakano and Murakami 2001; Bub *et al.* 2004). Most birds that use domed nests in

shrubs or small trees (e.g. Shining Bronze-Cuckoo, Yellow-tufted Honeyeater and Beautiful Firetail), or use open top nests in dense understorey (e.g. White-eared Honeyeater, Olive Whistler and Eastern Whipbird) were closely associated with riparian habitats. The greater complexity of understorey vegetation may be important not only by providing potential nest sites, but also by providing greater protection from predators (e.g. currawongs, Grey Butcherbird and raptors), particularly for species with open top nests which may be more vulnerable to nest predation. Riparian vegetation may also provide better quality nesting habitat, as slopes and ridges are likely to be more exposed to fluctuations in environmental conditions (e.g. sun exposure and temperature) which may affect breeding success (Stauffer and Best 1980; Rotenberry and Wiens 1991; Danchin *et al.* 1998).

Vegetation structure and environmental conditions (e.g. moisture availability) combined to form key habitat features that had a strong influence on bird assemblages. Fine ground litter was evenly distributed in riparian and non-riparian habitats (Chapter 2), but in riparian sites much of this occurred as damp litter under dense understorey vegetation, an important microhabitat for a particular suite of birds (e.g. sheltered ground – invertebrates foraging group). Eucalypt bird assemblages in south-east Australia are characterised by the high proportion of ground foraging that occurs (Recher *et al.* 1985; Ford *et al.* 1986; Mac Nally 1994; Loyn 1998; Tzaros 2001; Antos and Bennett 2006). Among ground foragers there is a division between those species that forage in open situations and those species that forage under vegetation and in sheltered sites (e.g. Robinson and Holmes 1982; Ford *et al.* 1986; Recher and Holmes 2000). Species that forage on damp, sheltered ground were strongly linked to riparian habitats. Of the nine species that comprised the sheltered ground – invertebrates foraging group, eight occurred either exclusively in riparian habitats (e.g. Pink Robin and the introduced Common Blackbird) or were riparian associated species (e.g. Superb Lyrebird, Olive Whistler and Bassian Thrush) (Chapter 2). Damp litter at riparian sites was rich in annelids and amphipods (G. Palmer, unpublished data), which are important prey items for species such as Superb Lyrebird, Bassian Thrush and Eastern Yellow Robin (Barker and Vestjens 1990). Where damp, sheltered litter occurred at non-riparian sites on protected south-facing slopes (e.g. Wet Forest and Damp Forest sites), some sheltered ground – invertebrate foragers (e.g. Superb Lyrebird, Eastern Whipbird and Eastern Yellow Robin) also occurred in the

assemblage.

The open ground – invertebrates group occurred at more non-riparian than riparian sites, and was the only ecological group to do so. Drier non-riparian vegetation (e.g. Heathy Woodland and Heathy Dry Forest) characteristically had a more open understorey (Chapter 2) and provided distinct foraging habitat for species that forage on the ground in open situations (i.e. open ground – invertebrates group). This group was represented by six species; three occurred exclusively in non-riparian habitats (Buff-rumped Thornbill, Flame Robin, White-winged Chough) and another two were closely associated with non-riparian habitats (e.g. Scarlet Robin, Superb Fairy-wren) (Chapter 2). The greater cover of low strata vegetation in riparian habitats (Chapter 2) provided less suitable habitat for ground foragers that pounce from low perches (e.g. Scarlet Robin and Flame Robin), and these species typically avoid sites with dense ground layer vegetation (Holmes and Recher 1986; Robinson 1992; Antos and Bennett 2006).

Some resources exploited by birds were closely tied to riparian habitats and provided distinct opportunities for groups of species. The aquatic foraging group was linked to water and occurred exclusively in riparian habitats where they used water in the stream channel. Riparian habitats also provided distinct opportunities for bark foragers. Decorticating bark is heavily used by birds foraging in eucalypt forests (Recher *et al.* 1983; Loyn 1985b; Holmes and Recher 1986; Recher 1991), and is a feature of eucalypts in the sub-genus *Symphyomyrtus* (e.g. Mountain Grey Gum *Eucalyptus cypellocarpa* and Manna Gum *E. viminalis*) which undergo extensive annual bark shed (Chapter 5). Eucalypts in this sub-genus were dominant in riparian habitats (Chapter 2). Decorticating bark accounted for approximately 12% of substrate use in riparian habitats compared with 5% in non-riparian habitats. The Crested Shrike-tit and White-eared Honeyeater are two species known to forage preferentially amongst decorticating bark (Loyn 1985b; Recher *et al.* 1985); both were identified as riparian associated species (Chapter 2). Another riparian associated species, the Eastern Whipbird, forages extensively amongst piles of decorticating bark around the base of trees. Riparian zones also supported a high percentage cover of sedges (Chapter 2), which provided an important food source for the ground layer – seeds/fruits foraging group. The Beautiful Firetail was the most common member of this group and was closely linked to riparian habitats in the forest mosaic (Palmer 2005).

By supporting structurally complex vegetation and distinctive habitat features (e.g. aquatic environments, damp sheltered litter and decorticated bark) riparian habitats provided a greater range of opportunities for birds. This resulted in the consistent addition of ecological groups to riparian assemblages (e.g. sheltered ground – invertebrates foraging group) and not non-riparian assemblages. This supports the hypothesis proposed in the introduction that riparian habitats are more structurally complex and diverse and therefore there are more opportunities available. However, this is not the only explanation for increased richness in these habitats.

#### *4.4.2 Species richness within ecological groups is greater in riparian assemblages*

Most foraging groups (arboreal – seeds/fruits, aerial – invertebrates, bark – invertebrates, ground layer – seeds/fruits, nectar/flowers, sheltered ground – invertebrates, shrub/small tree – invertebrates and sub-canopy – invertebrates), most nest-type groups (hollow, domed – shrub/small tree, open top – dense understorey, open top – shrub/small tree and open top – tall tree) and most body mass groups (11-30 g, 31-60 g, 61-100 g, 101-300 g and >301 g) supported more species in riparian than non-riparian assemblages. According to Roth (1976), for additional species to be accommodated (i.e. species packing) either of two circumstances must occur. First, for a given type of resource used by a guild, there must be an increase in the number of different microhabitats it provides, to permit spatial segregation; or second, resource partitioning must occur, that minimises competition between similar species. Within ecological groups, competitive interactions are important in determining how many species can use a common resource, and therefore occur in an area (Wiens 1989). Factors that influence the degree of competitive interaction between sympatric species include resource abundance levels and the number of species competing for the resource (Cody 1974). Typically, in habitats where resource availability is limited, a species' niche expands as the species forages more widely. Alternatively, if resources are abundant, then niche narrowing may occur as individuals specialise in their use of resources to what is best for them (Wiens 1989).

The benefits of complex mid-storey vegetation for promoting the number of guilds were described above; the same conditions can also enhance species richness within guilds.

Complex mid-storey vegetation in riparian habitats increases the number of microhabitats available to birds. This benefits groups that use mid-storey vegetation for foraging (e.g. sub-canopy – invertebrates and shrub/small tree – invertebrates foraging groups) and for nesting (e.g. domed – shrub/small tree, open top – dense understorey and open top – shrub/small tree nest-type groups). The presence of a mid-storey tree layer in riparian habitats enhanced the continuity of vegetation and associated resources (e.g. foliage, nest sites) in the vertical profile of the forest. More layers of vegetation in the riparian zone were expected to provide more efficient ways of survival and as a result chances for more species to occur in an area (e.g. Pearson 1975). In North America, increased foliage density in riparian areas accounted for the greater abundance of foliage-gleaning birds in these habitats than in surrounding vegetation (Bub *et al.* 2004). Greater vegetation layers and foliage density provides an enlarged habitat space that accommodates additional species through vertical segregation (MacArthur *et al.* 1962), or by providing additional foraging substrates or food items (Holmes and Recher 1986), or nest sites (Willson 1974).

Forest stratification is considered to be a major factor associated with the segregation of guilds, and of species within guilds, suggesting that foraging opportunities for birds change with height (Crome 1978; Frith 1984; Holmes and Recher 1986). Greater vertical complexity in riparian habitats (Chapter 2) is likely to promote opportunities for vertical stratification of resources. In this study there was evidence of vertical stratification of ecological groups (i.e. ground vs. foliage foragers), and of species within groups. For example, in riparian habitats the addition of another species, the Red-browed Treecreeper to the bark – invertebrates foraging group, was matched by an adjusted foraging profile for the White-throated Treecreeper, but no change in its abundance. The White-throated Treecreeper was widespread through the forest landscape, while the Red-browed Treecreeper was strongly associated with riparian habitats. In riparian sites where these two species commonly occurred, the White-throated Treecreeper generally foraged at lower heights (mean proportional height = 3.05,  $\pm 2.10$  SD,  $n = 86$ ) than the Red-browed Treecreeper (mean proportional height = 5.51,  $\pm 2.29$  SD,  $n = 95$ ). In non-riparian habitats, where the Red-browed Treecreeper was uncommon, the White-throated Treecreeper foraged at all heights, but generally at a greater height than at riparian sites (mean proportional height = 5.02,  $\pm 2.47$  SD,  $n = 85$ ). By segregating resources based on height, the treecreepers



reduced interspecific competition, increased their ability to co-occur in the same habitat (e.g. Cody 1974) and promoted within-guild richness.

Differences in body size are also important in segregating species within guilds (Ford *et al.* 1986; Holmes and Recher 1986; Loyn 2002). The sheltered ground – invertebrates foraging group was a prominent group (9 species) in riparian assemblages and included birds with a wide range of body sizes. This foraging group contained representatives in all body mass groups; <10 g (Pink Robin), 11-30 g (White-browed Scrubwren and Eastern Yellow Robin), 31-60 g (Olive Whistler), 61-100 g (Eastern Whipbird and Common Blackbird), 101-300 g (Bassian Thrush) and >301 g (Superb Lyrebird). Due to differences in size, these species can subdivide the invertebrate resource in damp litter by consuming different sized prey (e.g. Ashmole 1968; Hespenheide 1975; Wheelwright 1985) and by employing different methods to obtain prey. Differences in size (i.e. body mass) were important in segregating 39 pairs of closely-related species that occur in forests and woodlands in south-east Australia, with different foods and foraging methods used as a result of their differences in size (Loyn 2002). Such mechanisms also apply to ecologically similar species (i.e. species within ecological groups) and promoted within-group richness in riparian assemblages. The smallest (Pink Robin) and largest (Superb Lyrebird) members of the sheltered ground – invertebrates foraging group provide a good example. The Superb Lyrebird (1 100 g) foraged by scraping and turning over large amounts of litter. This species consumes a wide size-range of invertebrates (Lill 1996). The Pink Robin (9 g) on the other hand forages by pouncing for small invertebrates on the litter surface (Loyn 1985a).

As riparian habitats provide abundant resources, and there are more species within ecological groups, then it is expected that examples of niche narrowing would occur. The Brown Thornbill, the most common and widespread species in both habitat types, provides an interesting case in point. This bird was the only shrub/small tree – invertebrates forager that was common in non-riparian habitats, foraging over an extensive range of substrates including foliage, trunks, branches and flowers of both trees and shrubs. In riparian vegetation, it was more specialised in its use of substrates, concentrating foraging attempts on the foliage of shrubs and small trees (Table 4-6 and Table 4-7). While, greater specialisation in the foraging behaviour of the Brown Thornbill occurred where food was scarce in eucalypt woodland in north-east

New South Wales (Bell 1985), the greater specialisation in the use of resources here in riparian habitats is more likely to be due to greater resource abundance, allowing greater optimisation of resource use (Wiens 1989). The niche narrowing of Brown Thornbills at riparian sites coincided with the co-occurrence of three other shrub/small tree – invertebrates foragers in these assemblages (Silvereye, Rufous Fantail and Large-billed Scrubwren). Any potential overlap in the use of invertebrates from the foliage of shrubs and small trees for the Brown Thornbill did not have a negative impact on its population size (more than two-fold increase in abundance at riparian sites).

Another example, the Eastern Spinebill, displayed more specialised foraging behaviour in non-riparian habitats where it foraged extensively on prolifically flowering shrubs, particularly Hairpin Banksia *Banksia spinulosa*. Such shrubs did not occur in riparian habitats and the Eastern Spinebill, which occurred at lower abundance there but was equally widespread, showed greater diversity in its foraging behaviour. It made more use of tree flowers and invertebrates at all heights in riparian sites. Despite significant differences in flowering dynamics between riparian and non-riparian habitats (Chapter 5), plasticity in foraging behaviour allowed this species to be a dominant nectar/flower forager in both habitat types.

Riparian zones provided more types of resources (e.g. potential nest sites) and greater abundance of some resources (e.g. eucalypt flowering and decorticating bark; Chapter 5), which permitted greater avian richness because there were simply more ways to sub-divide the environment (Beedy 1981). Species composition in forest habitats depends largely on the foraging opportunities afforded (Holmes and Recher 1986; Loyn 2002) and the complex vegetation structure, abundant resources and favourable conditions (e.g. damp litter) found in riparian zones supported greater richness of ecological groups, and greater richness within groups.

#### 4.4.3 *Ecological mechanisms promoting richness in riparian assemblages*

This study provides evidence that the greater species richness in riparian assemblages involves two ecological mechanisms: (i) the riparian zone provides a greater range of opportunities to birds that cater for additional components of the avifauna (i.e. more ecological groups), and (ii) riparian zones provide conditions that promote segregation between ecologically similar species (i.e. greater species richness within ecological

groups).

While riparian and non-riparian habitats share a common suite of dominant species, the addition of a suite of species that display a diverse range of ecological requirements was a characteristic feature of riparian assemblages. Riparian assemblages included a range of species, representing almost the whole gamut of ecological groups, which do not regularly utilise surrounding non-riparian habitats. That is, the enhanced richness in riparian zones is not due to a single or few groups, but additional species from most groups. Species that were widespread in riparian habitats, but were more or less absent from non-riparian habitats, included sheltered ground – invertebrates (e.g. Bassian Thrush and Eastern Whipbird), shrub/small tree – invertebrates (e.g. Rufous Fantail and Large-billed Scrubwren), sub-canopy – invertebrates (e.g. Lewin's Honeyeater and Yellow-tufted Honeyeater), bark – invertebrates (e.g. Crested Shrike-tit and Red-browed Treecreeper), aerial – invertebrates (e.g. Tree Martin), nectar/flowers (e.g. New Holland Honeyeater) and ground layer – seeds/fruits foragers (e.g. Beautiful Firetail). These species also represent most nest-type groups and body mass groups. Non-riparian assemblages are not impoverished (*cf.* riparian assemblages) due to the loss of peripheral species, as has been found for other assemblages (e.g. Jaksic and Delibes 1987), but rather they do not provide suitable habitat for a suite of species that commonly occur in riparian habitats.

## 5 Resource dynamics in riparian and non-riparian habitats and the relationship to bird assemblages in a eucalypt forest landscape

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Striated Pardalote *Pardalotus striatus* feeding on lerps (T. Wilson)

## 5.1 Introduction

Riparian zones have been identified as preferred habitats for a wide range of taxa in Australia (Kavanagh 1987; Moore and Foley 2000; Tzaros 2001) and internationally (Emmerich and Vohs 1982; England *et al.* 1984; Knopf 1985; Doyle 1990; Robertson *et al.* 1998). It has been suggested that riparian zones provide stable, high-quality habitats for wildlife throughout the year, or importantly at crucial times in the year (Catterall 1993; Nix 1993; Lynch and Catterall 1999). If this is true, then it would be expected that resources used by species would occur in greater abundance, or more reliably, through the year in riparian zones. However, there have been few studies to document the resources available, or their reliability, and how they differ between riparian and non-riparian habitats.

The ‘proximate stimuli’ for the choice of habitats by birds includes structural features of the landscape, foraging or nesting opportunities, or the presence of other species (Cody 1981). The set of available resources forms the foundation of resource selection by individuals, which is influenced by the availability of alternative food types, spatial arrangement among resources, and attributes of resources, including their temporal reliability (Cody 1985; Wiens 1989). In eucalypt forests in south-east Australia, individual birds largely respond to the availability of particular food resources, the arrangement of vegetation and nest sites, but rarely to the presence or absence of any other species (Recher *et al.* 1991).

The availability of food resources has received considerable attention as an influence on habitat selection by birds in eucalypt forests and woodlands in Australia (e.g. Ford 1983; Recher *et al.* 1983; Ford and Paton 1985; Lynch *et al.* 2002). Food resources available in eucalypt vegetation associations include nectar (Ford 1979; Collins and Briffa 1982; Turner 1991; McGoldrick and Mac Nally 1998; French *et al.* 2003; Timewell and Mac Nally 2004); manna and lerps (Woinarski 1985; Wykes 1985); and invertebrates that occur among a range of substrates such as foliage (Majer *et al.* 2000; Recher and Majer 2006), bark (Recher *et al.* 1983; Dickman 1991; Majer *et al.* 2003), and litter (Dickman 1991; Catterall *et al.* 2001).

Like food resources, the presence of nest sites determines habitat suitability for birds.

All birds have specific nesting requirements, and the presence or absence of suitable nest sites contributes to differences in species composition between habitats (Recher and Holmes 1985). In eucalypt forest, nest sites include tree hollows (Saunders *et al.* 1982; Gibbons and Lindenmayer 2002), dead branches, low vegetation, tree foliage and the ground. Tree hollows are a particularly important nest resource in eucalypt forest. In Australia, 18% of terrestrial birds are known to use tree hollows as nest sites, and 21% of non-passerines are obligate hollow nesters (Saunders *et al.* 1982).

This study is based on explicit contrasts of resource availability at 30 pairs of riparian and non-riparian sites in extensive eucalypt forests in the Victorian Highlands. Riparian sites were found to maintain a greater richness and abundance of birds through time (Chapter 3) and assemblages in riparian sites support more ecological groups (i.e. guilds) and more species within groups (Chapter 4) than non-riparian sites. These assemblage patterns confirm that riparian vegetation in forested landscapes is a high quality habitat for birds. In this chapter, I examine the availability and dynamics of resources in riparian and non-riparian habitats to determine whether there is differential availability of particular resources, or in their temporal availability throughout the annual cycle. Patterns shown within components of the riparian and non-riparian bird assemblages that use the selected resources are presented to provide context for discussing the relationship between resource states and birds.

This research was designed to test three hypotheses:

1. Riparian habitats provide a greater abundance of resources used by birds than non-riparian sites.
2. There is a greater reliability in the seasonal availability of resources in riparian habitats than non-riparian sites.
3. Primary productivity is greater and more reliable at riparian sites than non-riparian sites.

## **5.2 Methods**

### *5.2.1 Study area*

The study was conducted in three areas of extensive eucalypt forest in the foothills of the west part of the Victorian Highlands, south-east Australia. The study area is described in detail in Chapter 1 and Chapter 2.

### *5.2.2 Study sites*

A set of 30 paired riparian and non-riparian sites (described in Chapter 2) was used to compare the availability and dynamics of resources, and patterns within components of the bird assemblage that utilise identified resources.

### *5.2.3 Bird surveys*

Bird assemblages were sampled using a fixed-point count method (Pyke and Recher 1984) between July 2001 and December 2002 as described in Chapter 2.

Observations of foraging behaviour were also collected during bird surveys as described in Chapter 4.

### *5.2.4 Resource availability and dynamics*

To compare the availability and dynamics of resources between riparian and non-riparian sites, a suite of resources commonly used by birds for food and foraging, or for nest sites was selected. Food and foraging resources that were measured through time included eucalypt flowering, eucalypt bark shed, and shrub flowering. The availability of mistletoe at a site was also assessed. The availability of tree hollows, which provide an essential nest site and shelter resource for many birds, was also measured.

#### *5.2.4.1 Food and foraging resources*

To compare measures of tree phenology (i.e. eucalypt flowering and bark shed) between riparian and non-riparian sites over the annual cycle, samples of trees were selected at a subset of 15 paired riparian and non-riparian sites, randomly selected from the pool of 30 paired sites used in the study. At each site all eucalypt and acacia

trees (up to a maximum of 10 individuals per species) within a 25 m x 25 m quadrat were marked. The number of trees, their size-class distribution and the species composition of the sample were therefore determined by the predominance of each species in the plant community at each site.

Observations of tree phenology were undertaken bi-monthly in 2002 (February, April, June, August, October and December). The methods used to collect each of these measures are described below.

#### 5.2.4.1.1 *Tree flowering*

The abundance of flowers is a crude measure of nectar abundance that allows sites to be compared through time (Ford and Paton 1985). The amount of tree flowering was measured as the percentage cover of flowers in the canopy and was scored as an index of flowering intensity: 0 (no flowering) to 10 (complete flower cover throughout the entire canopy). Only flowers that were fully opened at the time of observation were considered. Observations of flowering were made using binoculars.

#### 5.2.4.1.2 *Bark shed*

Bark is a major foraging substrate for birds in eucalypt forest and provides a rich source of invertebrate food (Dickman 1991; Recher 1991). Bark components are dynamic through the year on many eucalypt species because these trees seasonally shed their bark. The availability of loose bark was used as a surrogate measure of invertebrate availability for birds (Lindenmayer *et al.* 1990). To compare loose bark between riparian and non-riparian sites over the annual cycle, two measures of bark shed were collected. Bark “peel” comprised sections of bark that had cracked and lifted from the trunk or branch surface, but remained loosely *in situ*. Bark “hang” comprised sections of bark, mostly ribbons, which were completely or almost completely, detached from the trunk or branch surface but remained anchored at a single point, or caught up in a branch junction. The amount of both bark peel and bark hang was scored by using an index with a scale of 0 (no bark peel or bark hang) to 5 (very high bark peel or bark hang). Scoring was based on a whole-of-tree assessment. Therefore, a tree which was undergoing bark peel over the entire trunk and branch surfaces would score higher than a tree with bark peel only evident on the minor branches.



#### 5.2.4.1.3 Mistletoes

Mistletoe is an important food resource for birds in eucalypt forest, providing fruits and abundant nectar (Reid 1986; Turner 1991; Watson 2001). To compare mistletoe availability between riparian and non-riparian sites, the number of mistletoes observed in trees within a 0.25 ha quadrat (100 m x 25 m) was recorded at each site. The species and diameter of each tree containing mistletoe was recorded. All mistletoes observed were from the genus *Amyema*.

#### 5.2.4.1.4 Shrub flowering

Flowering shrubs often provide an abundant foraging and food resource for birds. The abundance of shrub flowers was used as a surrogate measure of nectar availability. A diverse range of shrubs was present at sites (Chapter 2), and many were recorded flowering. Analyses of shrub flowering were limited to plant species whose flowers were observed being visited by nectar-feeding birds. This included plants from the genera *Banksia* (Hairpin Banksia *B. spinulosa* and Silver Banksia *B. marginata*), *Hakea* (Bushy Needlewood *H. sericea*, Furze Hakea *H. teretifolia* and Dagger Hakea *H. ulicina*), *Melaleuca* (Scented Paperbark *M. squarrosa*), *Leptospermum* (Prickly Tea-tree *L. continentale* and Woolly Tea-tree *L. lanigerum*), *Correa* (Common Correa *C. reflexa*) and *Kunzea* (Burgan *K. ericoides*).

Observations were made of the flowering of shrub species within the 25 m x 25 m quadrat used for the collection of tree phenological data. The total amount of flowering for all plants of each species within the quadrat was scored from 0 (no flowering) to 3 (high amount of flowering). Only fully opened flowers were scored.

#### 5.2.4.2 Shelter and nest site resources

##### 5.2.4.2.1 Tree hollows

Tree hollows provide an essential nesting resource for many breeding birds in south-east Australia (Gibbons and Lindenmayer 2002). To compare tree hollow availability between riparian and non-riparian sites, the number and size of all hollows observed in trees within a 0.25 ha quadrat (100 m x 25 m) was recorded at each site. For each hollow observed, the tree species and its diameter at breast height (dbh), and the hollow entrance diameter were recorded. Hollow size was categorised as small

(entrance diameter <10 cm) or large (entrance diameter >10 cm). The occurrence of multiple hollows in a tree was recorded. Observations of hollows were made from the ground using binoculars. Although ground-based surveys of tree hollows are generally limited in their capacity to adequately detect the frequency of individual hollows, detection of the presence or absence of hollows in trees in eucalypt forest is approximately 90% successful using this method (Harper *et al.* 2004).

### 5.2.5 *Tree productivity*

The amount of new foliage is a simple site-level measure of primary production. To compare the amount of new leaf growth between riparian and non-riparian sites over the annual cycle, the amount of new leaf growth as a proportion of the existing canopy area was scored categorically from 0 (no new growth) to 5 (large amount of new growth) for each tree used for tree phenology measures (see 5.2.4.1). Observations of the canopy foliage were made through binoculars and new leaves were recognised by their size, shape, colour and appearance. Only the newest leaves were scored to gain a more accurate estimate of leaf production at a given time.

### 5.2.6 *Data analysis*

The aim of the data analysis was to compare resource availability and dynamics between riparian and non-riparian sites.

The comparison between eucalypt tree flowering through time at riparian and non-riparian sites was based on a balanced repeated measures ANOVA (rmANOVA). In this design, site type (riparian or non-riparian) represented subjects, with riparian and non-riparian being a fixed within-subject factor. Sites within each site type were effectively random factors, as they represented a randomly selected sample of these habitats in the landscape. Month represented trials, with six levels specified (February, April, June, August, October and December). The response variable (i.e. eucalypt flowering) was the flowering index per tree across all species. The response variable was transformed ( $\log_{10} + 0.5$ ) to meet homogeneity of variance assumptions for the rmANOVA.

A similar design was used to compare variation in the amount of bark peel and bark hang through the annual cycle. The response variables were mean amount of bark

peel per tree (bark peel), and mean amount of bark hang per tree (bark hang). Both response variables were transformed ( $\log_{10} + 0.5$ ) to meet homogeneity of variance assumptions for the rmANOVA. The relationship between the abundance of birds that foraged extensively on decorticating bark and the amount of bark hang was analysed using Spearman rank correlations.

The availability of mistletoes was analysed using a paired *t*-test to compare between the number of mistletoes at riparian and non-riparian sites for each pair.

The abundance of shrub flowering through time was analysed using an rmANOVA to compare riparian and non-riparian sites, as described for eucalypt flowering. Months represented trials, with five levels specified (April, June, August, October and December). The response variable was the abundance of flowering for each species, and was transformed ( $\log_{10} + 0.5$ ) to meet homogeneity of variance assumptions for the rmANOVA. The relationship between the abundance of three birds that foraged extensively on shrub flowers (Red Wattlebird, Eastern Spinebill and Crescent Honeyeater) and the flowering of shrubs was analysed using Spearman rank correlations.

The availability of tree hollows was analysed using a paired *t*-test to compare between riparian and non-riparian sites. The difference in the proportions of trees in each size-class ( $\leq 10$  cm dbh, 11-20 cm, 21-40 cm, 41-60 cm, 61-80 cm and  $\geq 81$  cm) that were hollow-bearing, and that contained small or large hollows, was analysed by using a chi-squared test to compare between site types. Chi-squared tests were also used to compare the frequencies of all hollows, small hollows, and large hollows that were observed amongst size-classes for each tree species between riparian and non-riparian sites. The relationship between richness and abundance of hollow-dependent birds and hollow availability was analysed by using Spearman rank correlations. The richness and abundance of hollow-dependent birds was compared between site types by using paired *t*-tests.

New foliage growth for eucalypt trees, a surrogate measure for site productivity, was also analysed using an rmANOVA design. Eucalypt trees within the 15 site pairs were randomly selected for monitoring and effectively represent a random sample of trees in the forest landscape. The bi-monthly monitoring events (i.e. trials) have 5 levels (April,

June, August, October and December). Three response variables were used: mean foliage growth of eucalypt trees (all trees monitored) at a site, mean foliage growth of Messmate *E. obliqua* trees at a site, and mean foliage growth of Narrow-leaved Peppermint *E. radiata* trees at a site. These two species were chosen because they were widespread at riparian and non-riparian sites throughout the study area (Chapter 2).

For all analyses, a test statistic was deemed to be significant at the  $p = 0.05$  level.

## 5.3 Results

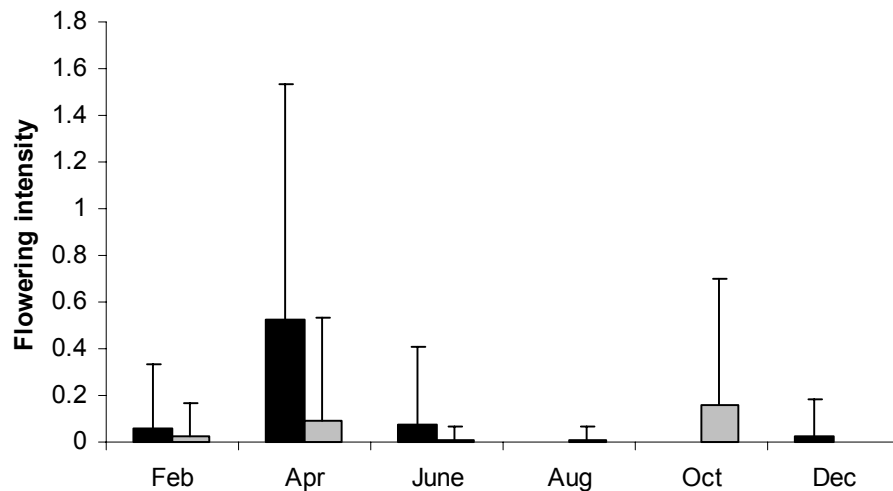
### 5.3.1 Tree flowering

Nine of the 12 eucalypt species were recorded flowering during 2002 (Table 5-1). The three species not recorded flowering were Broad-leaved Peppermint *E. dives*, Yertchuk *E. consideniana* and Red Stringybark *E. macrorhyncha*. All three occurred only in non-riparian sites. All species recorded flowering during the study flowered in at least two of the monitoring periods (Table 5-1). Narrow-leaved Peppermint *E. radiata* was observed flowering during five (February, April, June, August and December) of the six monitoring periods. The peak period of eucalypt flowering in the forest landscape was during April when all nine species that were observed flowering during 2002 flowered (Table 5-1). April was the peak flowering time for Messmate *E. obliqua*, Mountain Swamp Gum *Eucalyptus camphora*, Swamp Gum *E. ovata*, Mountain Grey Gum *E. cypellocarpa*, Manna Gum *E. viminalis* and Mealy Stringybark *E. cephalocarpa* (Table 5-1).

**Table 5-1      Timing and distribution of flowering events observed for tree species in riparian and non-riparian habitats.**

For each tree species the number of trees flowering (n), the proportion of trees flowering (%) and the number of sites at which flowering was observed (s) is shown for each monitoring period. Shaded areas highlight flowering events. Three species that occurred only at non-riparian sites, and that were not observed flowering during the sampling period are excluded: Red Stringybark *E. macroryhyncha*, Yertchuk *E. consideniiana* and Broad-leaved Peppermint *E. dives*

[illegible]



**Figure 5-1** Mean flowering intensity of eucalypt trees (all species) in riparian (black) and non-riparian (grey) habitats. Error bars represent standard deviation.

Repeated measures ANOVA showed significant effects of both sampling period (i.e. season) and site type (i.e. riparian or non-riparian) on eucalypt flowering in the forest landscape (Table 5-2). The intensity of eucalypt flowering in the forest landscape was generally low but differed significantly between sampling periods. This was influenced by the low proportion of individual trees flowering and low flower cover observed (mean index = 1.31, range 1 – 4) for these trees. Flowering intensity was greatest in April, driven by extensive flowering in Mountain Swamp Gum *E. camphora*, Swamp Gum *E. ovata*, Mountain Grey Gum *E. cypellocarpa* and Manna Gum *E. viminalis* in riparian zones.

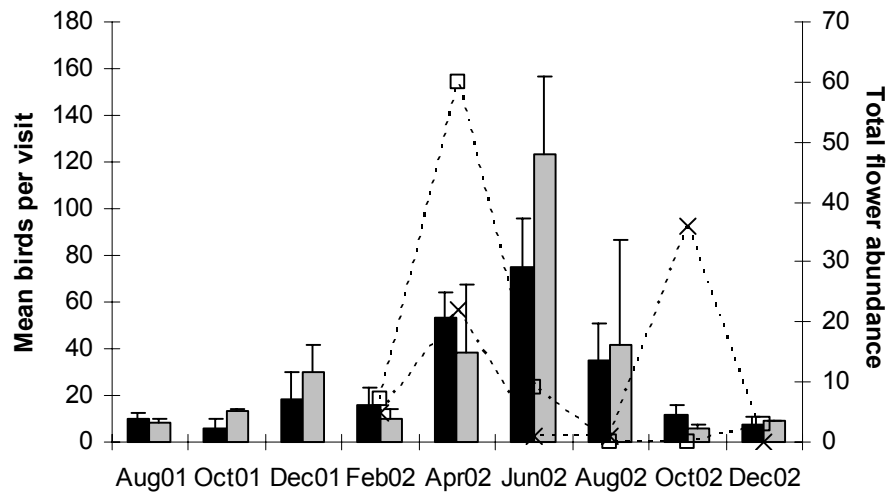
The significant interaction between eucalypt flowering and site type shows that the level of eucalypt flowering differed between riparian and non-riparian sites through time. Eucalypt flowering intensity was greatest in riparian sites in four of the six monitoring periods (Figure 5-1).

**Table 5-2 Results of repeated measures ANOVA comparing eucalypt flowering intensity between riparian and non-riparian sites (site type) over six sampling periods from February 2002 to December 2002.**

Source	SS	d.f.	MS	F ratio	<i>p</i>	GG <i>p</i>
<i>Between subjects</i>						
Site type	0.26	1	0.26	17.27	<0.001	
Residual	5.2	346	0.15			
<i>Within subjects</i>						
Sampling period	2.31	5	0.46	34.03	<0.001	<0.001
Site type X sampling period	1.66	5	0.33	24.42	<0.001	<0.001
Residual	23.49	1730	0.14			

The response variable, eucalypt flowering intensity, was Log<sub>10</sub> transformed to improve variance homogeneity. Greenhouse Geisser (GG) adjustments are presented as a more conservative test reducing the risk of Type I error due to non-sphericity.

Fifteen bird species were observed foraging on flowers of eucalypts. Those observed most often were Yellow-faced Honeyeater (22% of all eucalypt flower foraging observations), White-naped Honeyeater (16%) and Eastern Spinebill (15%). The most visited eucalypt flowers were Mountain Grey Gum *E. cypellocarpa* (27% of observed visits to eucalypt flowers), Mountain Swamp Gum *E. camphora* (23%) and Manna Gum *E. viminalis* (22%).



**Figure 5-2** Number of nectarivores at riparian (black) and non-riparian sites (grey) and relationship to eucalypt flowering events. Total flowering intensity is shown for eucalypts at riparian (□) and non-riparian sites (x) for February-December 2002. Error bars represent standard deviation.

Three species of nectarivores (see Chapter 4), Musk Lorikeet, Little Lorikeet and Swift Parrot, were only observed foraging on eucalypt flowers. Another nectarivore, the New Holland Honeyeater, was observed to mostly forage on eucalypt flowers (90% of foraging observations). These species, and Purple-crowned Lorikeet, were recorded at very low numbers during the study. For other nectarivores, foraging on eucalypt flowers comprised a smaller proportion of total observations; Eastern Spinebill (20% of foraging observations,  $n = 82$ ), Crescent Honeyeater (19%,  $n = 48$ ) and Red Wattlebird (11%,  $n = 105$ ).

Two other honeyeaters, the White-naped Honeyeater and Yellow-faced Honeyeater, are members of the tree layer – invertebrates foraging group (Chapter 4), but also regularly foraged on eucalypt flowers. Visits to eucalypt flowers accounted for 22% of Yellow-faced Honeyeater foraging observations ( $n = 105$ ), and 10% of White-naped Honeyeater observations ( $n = 172$ ).



### 5.3.2 Shrub flowering

The bi-monthly flowering indices for each shrub species are shown in Figure 5-3.

Species recorded flowering in riparian habitats included Scented Paperbark *Melaleuca squarrosa* and Woolly Tea-tree *Leptospermum lanigerum*, but these flowered at low levels in 2002. Riparian habitats did not support profusely flowering shrubs such as Hairpin Banksia *Banksia spinulosa* and Bushy Needlewood *Hakea sericea* which were widespread in non-riparian habitats (see Chapter 2). Non-riparian habitats also supported a range of other flowering shrubs including Silver Banksia *Banksia marginata*, Common Correa *Correa reflexa*, Burgan *Kunzea ericoides*, and Prickly Tea-tree *Leptospermum continentale*.

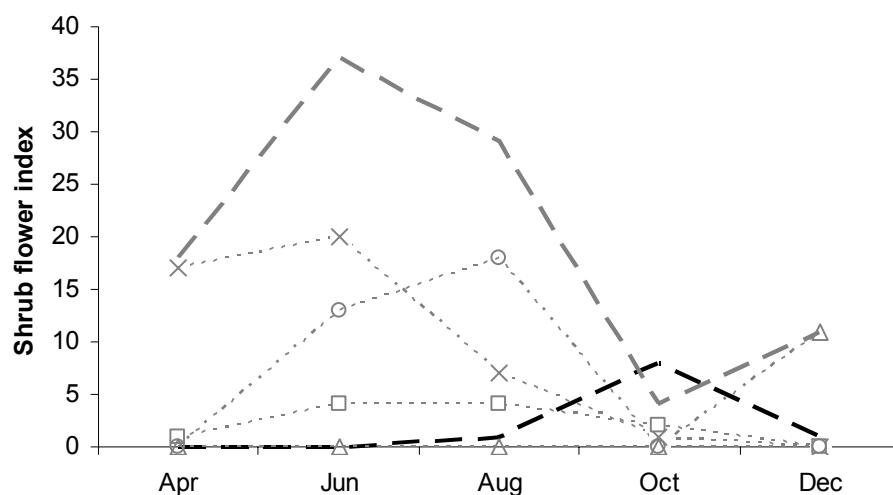
Repeated measures ANOVA showed significant effects of both sampling period (i.e. season) and site type (i.e. riparian or non-riparian) on shrub flowering in the forest landscape (Table 5-3). The significant interaction between shrub flowering and site type shows that the level of shrub flowering differed between riparian and non-riparian sites through time. Shrub flowering intensity was greatest in non-riparian sites in all five monitoring periods (Figure 5-3).

**Table 5-3 Results of repeated measures ANOVA used to compare shrub flowering intensity between riparian and non-riparian sites (site type) over five sampling periods from April 2002 to December 2002.**

Source	SS	d.f.	MS	F ratio	p	GG p
<i>Between subjects</i>						
Site type	2.23	1	2.23	55.84	<0.001	
Residual	1.76	44	0.04			
<i>Within subjects</i>						
Sampling period	0.75	4	0.53	3.08	0.018	0.031
Site type X sampling period	2.1	4	0.33	8.61	<0.001	<0.001
Residual	10.74	176	0.61			

The response variable shrub flowering intensity was Log<sub>10</sub> transformed to improve variance homogeneity. Greenhouse Geisser (GG) adjustments are presented as a more conservative test reducing the risk of Type I error due to non-sphericity.

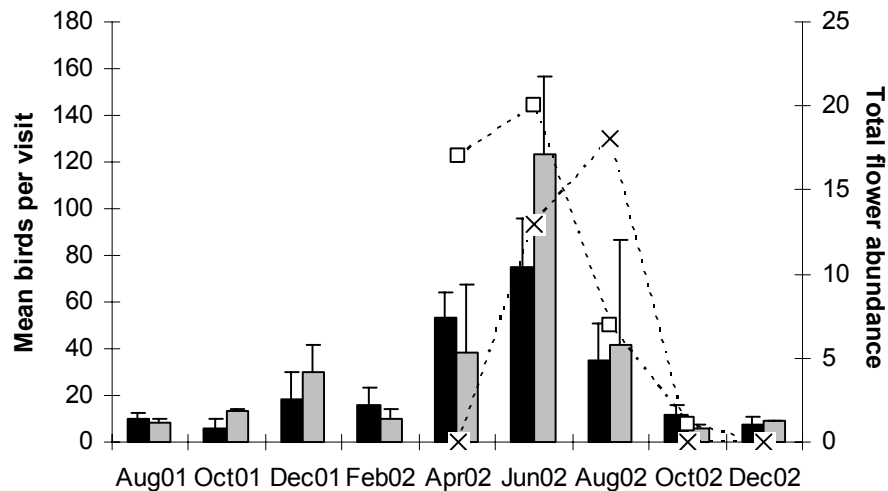
In non-riparian habitats, shrub flowers were available throughout the annual cycle, with peak flowering being between June and October for most species. In December there was very little shrub flowering in the forest landscape. Hairpin Banksia *Banksia spinulosa* had flowers most of the year, except in December, with a flowering peak in June. Bushy Needlewood *Hakea sericea* flowered mainly in winter, with peak flowering in August. Common Correa *Correa reflexa* flowered at low levels throughout the year.



**Figure 5-3 Flowering index of major shrub species at riparian and non-riparian sites. The flowering indices for *Banksia*, *Hakea*, Common Correa *Correa reflexa* and Burchardia *Kunzea ericoides* in non-riparian habitats are displayed.**

The flowering indices displayed are: Riparian habitats – all shrubs combined (— — —); Non-riparian habitats – all shrubs combined (— — —); *Banksia* (x); *Hakea* (o); Common Correa *Correa reflexa* (□) and Burchardia *Kunzea ericoides* (Δ).

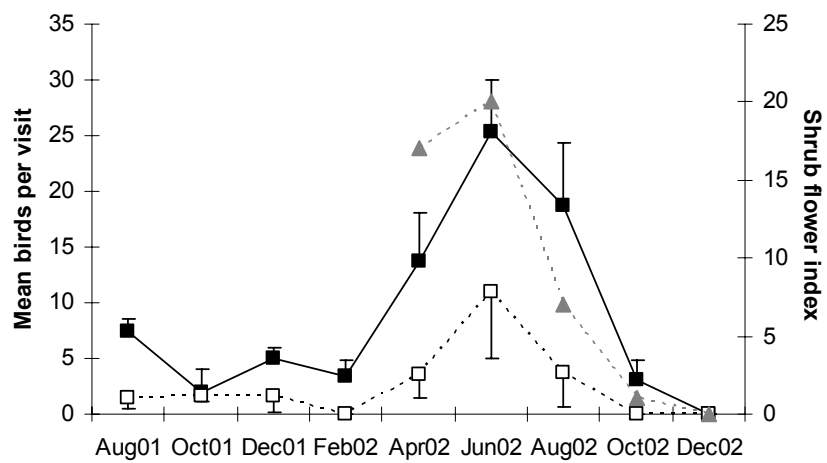
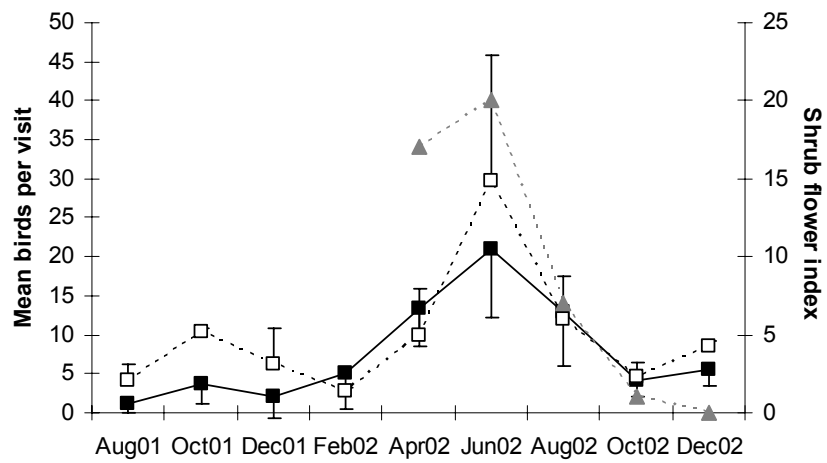
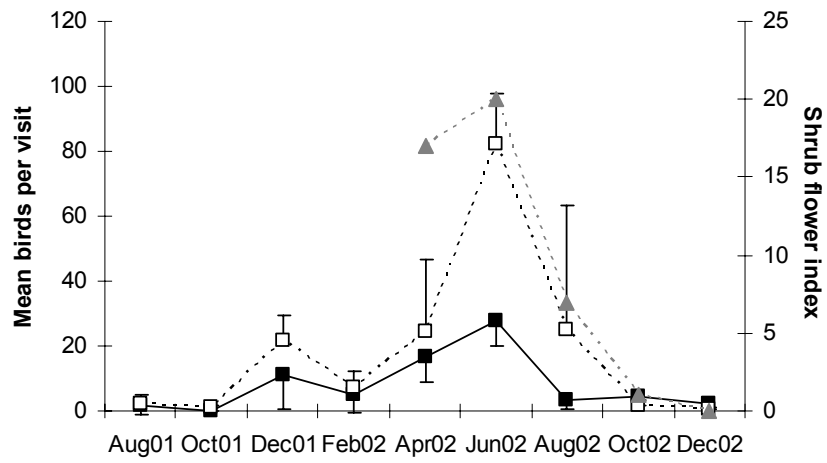
Ten bird species were observed visiting flowers on shrubs. The species observed most often foraging on shrub flowers were Eastern Spinebill (40% of all shrub flower foraging observations), Red Wattlebird (29%) and Crescent Honeyeater (16%). Flowers on Hairpin Banksia *Banksia spinulosa* accounted for 95% of observed foraging attempts on shrub flowers by all birds.



**Figure 5-4** Number of nectarivores at riparian (black) and non-riparian (grey) sites ( $n = 30$ ) and the relationship to shrub flowering events in *Banksia* (□) and *Hakea* (X) at non-riparian sites.

Shrub flowering was only monitored between April and December 2002. Error bars represent standard deviation.

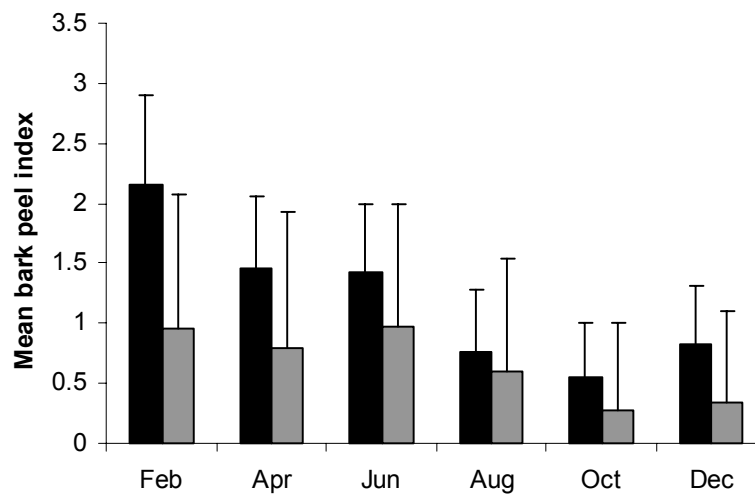
The numbers of Red Wattlebird were positively correlated ( $r_s = 0.900$ , d.f. = 4,  $p = 0.037$ ,  $n = 5$ ) with the flowering of *Banksia* in non-riparian habitats from April to December 2002 (Figure 5-4); Hairpin Banksia *Banksia spinulosa* was the only shrub whose flowers were observed to be visited by this species. There was a massive influx of Red Wattlebird into the forest landscape in winter 2002 coinciding with heavy flowering of Hairpin Banksia *Banksia spinulosa* in non-riparian habitats (Figure 5-5). The number of Eastern Spinebills or Crescent Honeyeaters was not significantly correlated with the flowering of particular shrubs, or shrub flowering when pooled for all shrub taxa, however Figure 5-5 shows that peaks in individual numbers for both species coincided with peaks in *Banksia* flowering at non-riparian sites.



**Figure 5-5** Abundance of Red Wattlebird (top), Eastern Spinebill (middle) and Crescent Honeyeater (bottom) at riparian (■) and non-riparian sites (□) and flowering of *Banksia* (▲) at non-riparian sites. Error bars represent standard deviation.

### 5.3.3 Bark shed

Repeated measures ANOVA showed significant effects of both site type (riparian or non-riparian) and sampling period (month) on the amount of bark peel amongst eucalypts in the forest landscape (Table 5-4). Bark peel occurred throughout the year at both riparian and non-riparian sites. During all sampling periods there was a greater amount of bark peel at riparian than non-riparian sites (Figure 5-6).



**Figure 5-6** Timing and extent of bark peel at riparian (black) and non-riparian sites (grey). Error bars represent standard deviation.

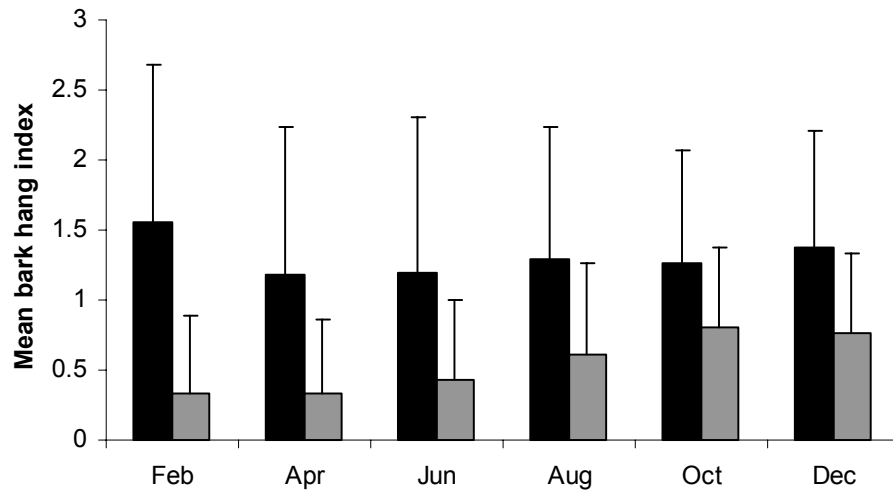
**Table 5-4 Results of repeated measures ANOVA comparing the amount of bark peel between riparian and non-riparian sites (site type) over six sampling periods from February 2002 to December 2002.**

Source	SS	d.f.	MS	F ratio	<i>p</i>	GG <i>p</i>
<i>Between subjects</i>						
Site type	6.97	1	1.94	16.28	<0.001	
Residual	41.29	346	0.12			
<i>Within subjects</i>						
Sampling period	3.35	5	3.35	115.03	<0.001	<0.001
Site type X sampling period	1.13	5	0.23	5.01	<0.001	<0.001
Residual	78.32	1730	0.45			

The response variable, bark peel, was Log<sub>10</sub> transformed to improve variance homogeneity. Greenhouse Geisser (GG) adjustments are presented as a more conservative test reducing the risk of Type I error due to non-sphericity.

The significant interaction between sampling period and site type shows that the trend in the amount of bark peel differed between riparian and non-riparian sites through time. Figure 5-6 shows that the amount of bark peel at riparian sites was greatest in February and declined through the year to its lowest levels in spring (October) and early summer (December). At non-riparian sites, there was a less obvious peak in the amount of bark peel with a relatively constant amount through late summer (February) to early winter (June), before declining through late winter (August) to early summer (December) (Figure 5-6).

Repeated measures ANOVA showed significant effects of both site type (riparian or non-riparian) and sampling period (month) on the amount of bark hang amongst eucalypts in the forest landscape (Table 5-5). Hanging bark was present at riparian and non-riparian sites throughout the year. During all sampling periods there was a greater amount of bark hang at riparian sites (Figure 5-7).



**Figure 5-7** Extent of hanging bark at riparian (black) and non-riparian sites (grey) through the annual cycle. Error bars represent standard deviation.

The significant interaction between sampling period and site type shows that the trend in amount of bark hang differed between site types through time. The amount of bark hang at riparian sites displayed a minor peak in February, but was relatively constant through the year (Figure 5-7). At non-riparian sites, it was lowest in February, and then slowly increased through the remainder of the annual cycle (Figure 5-7).

The canopy trees at sites represent two *Eucalyptus* subgenera, *Monocalyptus*, which have fibrous bark, and *Symphyomyrtus*, the gum-barked eucalypts. Non-riparian sites were dominated by eucalypts in the subgenus *Monocalyptus* (99% of eucalypts).

*Monocalyptus* also accounted for 43% of eucalypt trees at riparian sites.

*Symphyomyrtus* were characteristic of riparian zones, representing 57% of eucalypt trees, compared with just 1% at non-riparian sites. Figure 5-8 displays the different levels of bark shed between the two sub-genera. *Symphyomyrtus* eucalypts undergo annual bark shed over the entire plant surface and accordingly displayed higher levels of bark peel and bark hang through the annual cycle (Figure 5-8).

**Table 5-5 Results of repeated measures ANOVA comparing the amount of bark hang between riparian and non-riparian sites (site type) over six sampling periods from February 2002 to December 2002.**

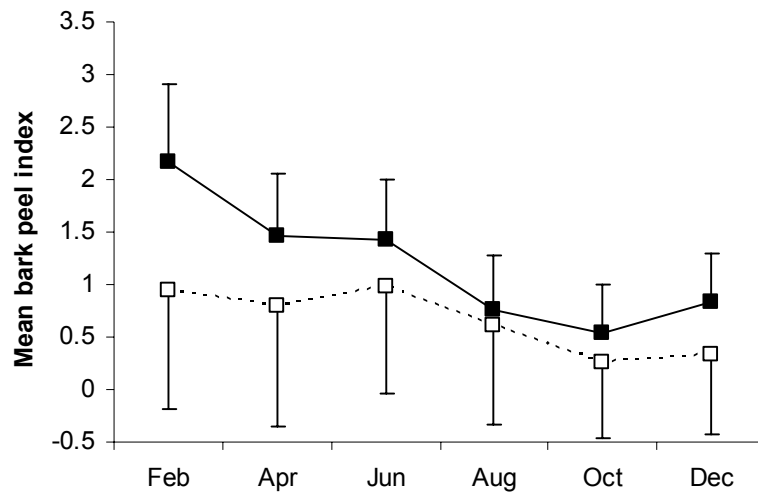
Source	SS	d.f.	MS	F ratio	<i>p</i>	GG <i>p</i>
<i>Between subjects</i>						
Site type	25.94	1	25.94	146.09	<0.001	
Residual	61.44	346	0.18			
<i>Within subjects</i>						
Sampling period	5.77	5	1.15	28.13	<0.001	<0.001
Site type X sampling period	2.91	5	0.58	14.18	<0.001	<0.001
Residual	70.9	1730	0.41			

The response variable, bark hang, was Log<sub>10</sub> transformed to improve variance homogeneity. Greenhouse Geisser (GG) adjustments are presented as a more conservative test reducing the risk of Type I error due to non-sphericity.

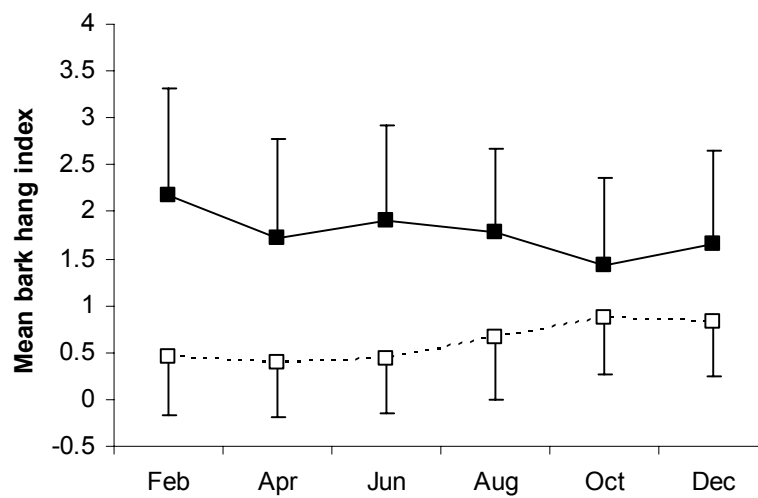
Riparian bird assemblages supported a greater richness and abundance of bark – invertebrates foragers when compared with non-riparian bird assemblages (Chapter 4).

Loose and hanging bark (i.e. decorticated bark) was widely used as a foraging substrate at sites, being used by 26 species and accounting for 9% of all foraging observations. Hanging bark (i.e. decorticated bark) was the most used foraging substrate for four of the six members of the bark – invertebrates foraging group, including Crested Shrike-tit (64% of foraging observations), White-eared Honeyeater (53%), Red-browed Treecreeper (45%) and Grey Shrike-thrush (37%). The abundance of Red-browed Treecreeper ( $r_s = 0.547$ ,  $p < 0.001$ ), White-eared Honeyeater ( $r_s = 0.447$ ,  $p < 0.001$ ) and Crested Shrike-tit ( $r_s = 0.489$ ,  $p < 0.001$ ) all showed significant positive correlations with the number of *Symphomyrtus eucalypt* trees at a site.





#### A) Bark peel



#### B) Bark hang

**Figure 5-8** Patterns of bark shed in *Symphyomyrtus* (■) and *Monocalyptus* (□) eucalypts through the annual cycle, for all sites pooled. A) bark peel index and, B) bark hang index. Error bars represent standard deviation.

### 5.3.4 Mistletoes

Mistletoes were scarce in the forest landscape with <0.4% of trees (n = 29 of 7438 trees) containing mistletoe. Mistletoe was especially rare in riparian vegetation (0.01% of trees contained mistletoe), compared with non-riparian vegetation (0.5% of trees).

Trees with multiple mistletoes were very rare in the forest landscape (0.05% of trees). Mistletoes were recorded in Brown Stringybark *E. baxteri* (30% of all mistletoe), Narrow-leaved Peppermint *E. radiata* (27%), Messmate *E. obliqua* (10%), Broad-leaved Peppermint *E. dives* (10%), Yertchuk *E. considiniana* (10%), Red Stringybark *E. macroryhyncha* (7%) and Mountain Swamp Gum *E. camphora* (7%).

Six birds species were observed visiting mistletoe flowers or fruits, including the Eastern Spinebill, Crescent Honeyeater, Yellow-faced Honeyeater, Red Wattlebird, Australian King Parrot and Mistletoebird.

### 5.3.5 Tree hollows

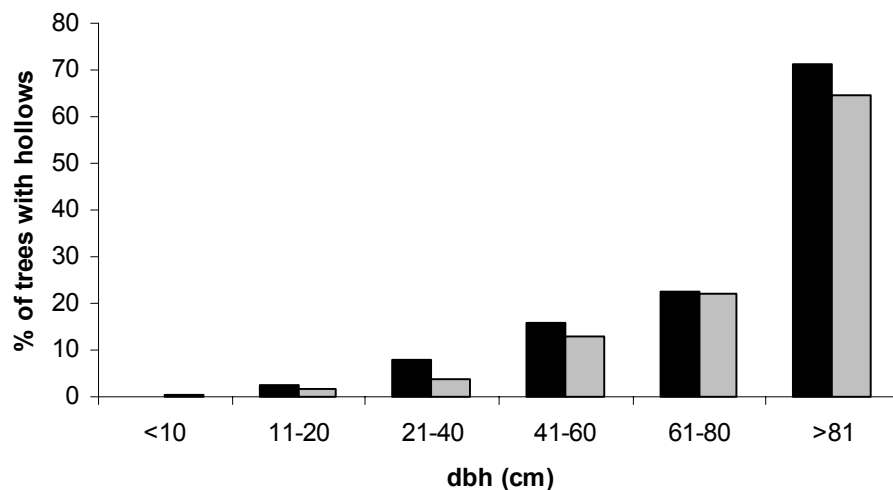
A total of 416 trees with hollows was recorded, representing 6% of trees (n = 7438) assessed at 60 sites in the forest landscape. Hollow-bearing trees were recorded from all sites. At riparian sites, a total of 216 trees with hollows was recorded, representing 7.5% of all trees (n = 2896 trees). At non-riparian sites, a total of 200 trees with hollows was recorded, representing 4.4% of all trees (n = 4562). There was no significant difference (paired  $t = 0.530$ , d.f. = 29,  $p = 0.600$ ) in the density of hollow-bearing trees between riparian (mean = 7.2,  $\pm 4.54$  SD) and non-riparian sites (mean = 6.67,  $\pm 4.60$  SD).

There was marked variation between size-classes of trees in the proportion of trees that were hollow-bearing. Few trees (2.5%) of <40 cm diameter contained hollows. The proportion of trees in the 41-60 cm and 61-80 cm size-classes that contained hollows was 14% and 22.2%, respectively, and for large trees (>81 cm), 68.2% contained hollows. There was no difference ( $\chi^2 = 4.393$ , d.f. = 5,  $p = 0.494$ ) between riparian and non-riparian sites in the frequency of trees with hollows in each tree size-class (Figure 5-9).

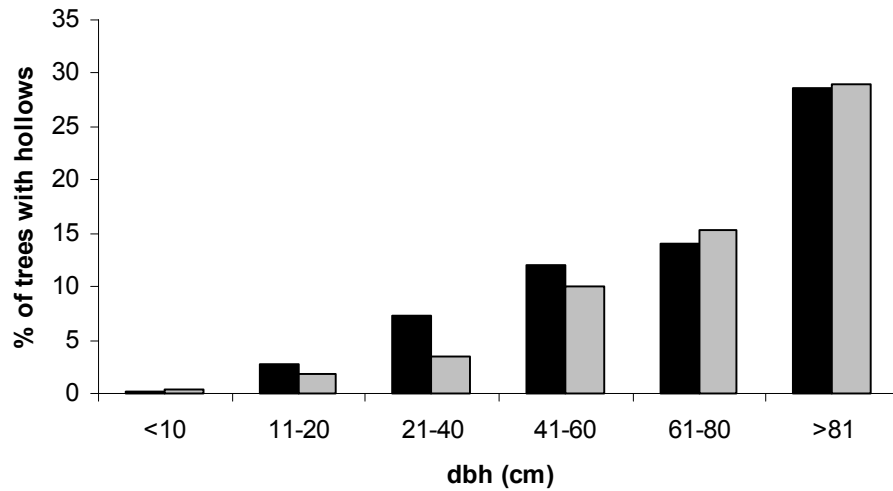
Most trees (72%) with hollows only contained smaller hollows (i.e. <10 cm entrance

diameter). There was no difference ( $\chi^2 = 3.70$ , d.f. = 5,  $p = 0.593$ ) between riparian and non-riparian habitats in the frequency of trees with small hollows for tree size-classes (Figure 5-10).

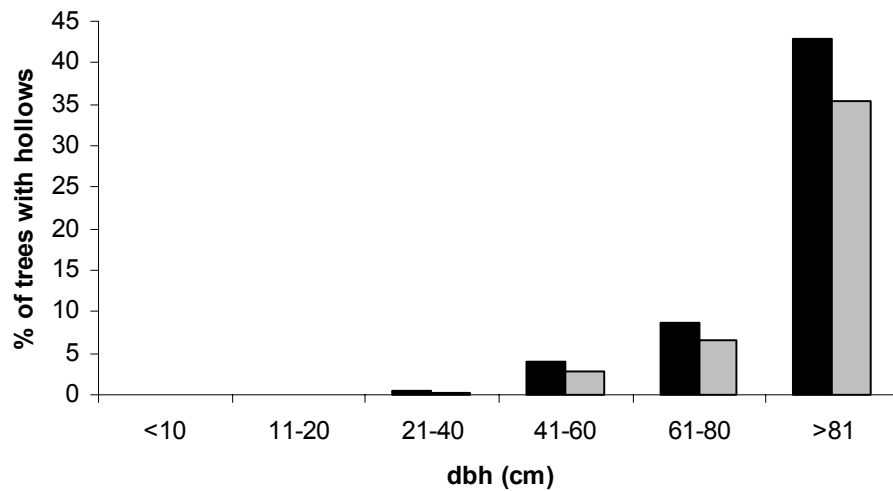
Trees containing large hollows (i.e. >10 cm entrance diameter) represented 28% ( $n = 118$  trees) of all hollow-bearing trees. Large hollows were mostly observed in trees >81 cm (66% of trees with large hollows). There was no difference ( $\chi^2 = 0.40$ , d.f. = 3,  $p = 0.900$ ) between riparian and non-riparian habitats in the frequency of trees with large hollows for tree size-classes (i.e. hollows occur in trees of a given size-class at the same rate, regardless of whether they are in riparian or non-riparian situations) (Figure 5-11).



**Figure 5-9** Proportion of trees containing hollows for tree size-classes in riparian (black) and non-riparian (grey) habitats.



**Figure 5-10** Proportion of trees containing small hollows (entrance <10 cm diameter) for tree size-classes in riparian (black) and non-riparian (grey) habitats.



**Figure 5-11** Proportion of trees containing large hollows (>10 cm entrance diameter) for tree size-classes in riparian (black) and non-riparian (grey) habitats.

Differences between tree species in the proportion of trees that contained hollows was

investigated for two size-classes, 20-80 cm dbh and >81 cm dbh. Non-eucalypts were excluded to reduce the limitations associated with the differing growth form of non-eucalypt understorey tree species such as Blackwood *Acacia melanoxylon*, Silver Wattle *A. dealbata* and Scented Paperbark *Melaleuca squarrosa*. There was a significant difference ( $\chi^2 = 211.47$ , d.f. = 13,  $p < 0.001$ ) between species in the proportion of trees of 20-80 cm dbh that contained hollows. The highest frequencies of trees that contained hollows were for dead standing trees, Swamp Gum *E. ovata* and Narrow-leaved Peppermint *E. radiata* and the lowest was for Manna Gum *E. viminalis*, Mountain Grey Gum *E. cypellocarpa* and Silvertop Ash *E. sieberi* (Table 5-6). The proportion of trees >81 cm that contained hollows was not significantly different ( $\chi^2 = 17.03$ , d.f. = 10,  $p = 0.074$ ) between species. All species with trees greater than >81 cm were represented by specimens that contained hollows, except Brown Stringybark *E. baxteri*. The highest frequencies of trees that contained hollows were for dead standing trees, Mountain Grey Gum *E. cypellocarpa*, Mountain Swamp Gum *E. camphora*, Manna Gum *E. viminalis* and Swamp Gum *E. ovata* (Table 5-6).

Hollow-dependent birds comprised 22.7% ( $n = 20$  species) of the overall assemblage and included, parrots and cockatoos, kingfishers, treecreepers, ducks, Southern Boobook, Australian Owlet-nightjar and Striated Pardalote. Several species identified as being closely associated with riparian habitats (see Chapter 2) are hollow-dependent, including Red-browed Treecreeper, Sacred Kingfisher, Sulphur-crested Cockatoo and Striated Pardalote. Riparian assemblages supported a significantly greater species richness of hollow-dependent birds (paired  $t = 6.630$ , d.f. = 29,  $p < 0.001$ ) (mean = 7.57,  $\pm 2.10$  SD) when compared to non-riparian assemblages (mean = 4.87,  $\pm 1.48$  SD). Riparian assemblages also supported a significantly greater abundance (paired  $t = 6.989$ , d.f. = 29,  $p < 0.001$ ) of hollow-dependent birds (mean = 4.10,  $\pm 2.27$  SD) when compared to non-riparian assemblages (mean = 1.53,  $\pm 0.91$  SD). However, neither species richness of hollow-dependent birds ( $r_s = 0.071$ , d.f. = 59,  $p = 0.590$ ,  $n = 60$ ) nor the abundance of hollow-dependent birds ( $r_s = 0.154$ , d.f. = 59,  $p = 0.241$ ,  $n = 60$ ) showed significant correlation with the number of hollow-bearing trees at a site. There was a weak positive relationship between the number of hollows and the abundance of hollow-dependent birds during the breeding season (Figure 5-12), but the relationship was not significant ( $r = 0.205$ ,  $p = 0.116$ ).

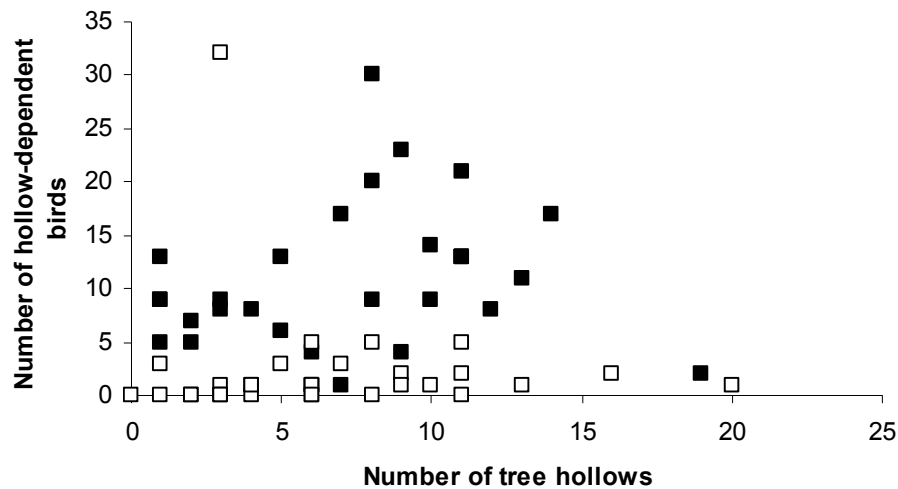
**Table 5-6      Distribution and abundance of tree hollows at riparian and non-riparian sites.**

The proportion of trees in each size-class is shown, and the proportion that contain hollows is indicated in parentheses

Species	Habitat type	Total trees	<10 cm	11-20 cm	21-40 cm	41-60 cm	61-80 cm	>81 cm
<i>Eucalyptus macroryhyncha</i>	NR	52	30.8	30.8	32.7	5.8	-	-
<i>Eucalyptus baxteri</i>	RIP	2	-	-	-	-	-	100
	NR	340	10.3	17.9	45.9	16.5 (1.8)	6.2 (19)	3.2 (63.6)
<i>Eucalyptus obliqua</i>	RIP	160	1.3	8.1	48.1 (1.3)	23.1 (8.1)	9.4 (6.7)	10.0 (56.3)
	NR	648	14.8	16.2	40.9 (0.4)	18.2 (5.9)	4.8 (6.5)	5.1 (60.6)
<i>Eucalyptus consideniana</i>	NR	201	36.3 (1.4)	22.9 (2.2)	34.3 (4.3)	3.5 (14.3)	2.0	1.0 (100)
<i>Eucalyptus sieberi</i>	NR	462	25.5	19.7	31.0	12.8 (1.7)	4.3 (5)	6.7 (58.1)
<i>Eucalyptus radiata</i>	RIP	219	12.8	17.4	39.3 (4.7)	19.6 (25.6)	7.8 (23.5)	3.2 (42.9)
	NR	1642	37.5 (0.5)	29.1 (1.5)	28.6 (6.6)	3.6 (28.8)	0.9 (42.9)	0.3 (80)
<i>Eucalyptus dives</i>	NR	256	34.0	27.3 (2.9)	35.5	2.7 (14.3)	0.4	-
<i>Eucalyptus camphora</i>	RIP	217	1.8	6.5	47.5 (5.8)	31.3 (7.4)	9.7 (28.6)	3.2 (100)
<i>Eucalyptus ovata</i>	RIP	59	23.7	16.9	32.2 (21.1)	15.3 (66.7)	6.8 (75)	5.1 (66.7)
<i>Eucalyptus cypellocarpa</i>	RIP	78	7.7	10.3	29.5	16.7	11.5	24.4 (84.2)
	NR	12	-	25.0	41.7	16.7	-	16.7 (50)
<i>Eucalyptus viminalis</i>	RIP	129	3.1	3.9	23.3	23.3	14.7	31.8 (68.3)
<i>Eucalyptus cephalocarpa</i>	RIP	9	-	33.3	33.3	11.1	22.2 (100)	-
	NR	42	16.7	35.7	40.5 (5.9)	2.4	4.8 (50)	-
<i>Eucalyptus aromaphloia</i>	RIP	4	-	-	50.0	25.0	-	25.0 (100)

**Table 5–6**      **continued.**

Species	Habitat type	Total trees	<10 cm	11-20 cm	21-40 cm	41-60 cm	61-80 cm	>81 cm
<i>Acacia melanoxylon</i>	RIP	302	19.2	29.5	48.0 (4.8)	3.3 (20)	-	-
	NR	3	100.0	-	-	-	-	-
<i>Acacia dealbata</i>	RIP	252	38.9	29.4	31.7 (2.5)	-	-	-
	NR	13	30.8	30.8	38.5	-	-	-
<i>Melaleuca squarrosa</i>	RIP	996	61.4 (0.3)	28.8 (4.9)	9.7 (21.6)	-	-	-
Dead standing tree (all species)	RIP	469	35.0	26.9 (3.2)	32.0 (12.7)	3.0 (64.3)	1.3 (83.3)	1.9 (100)
	NR	871	59.5 (0.2)	22.3 (4.6)	13.8 (12.5)	2.1 (77.8)	1.4 (75)	1.0 (88.9)



**Figure 5-12 Relationship between the number of tree hollows and the total number of hollow-dependent birds at riparian (■) and non-riparian sites (□) during the breeding season**

(Breeding season is months October, November and December; 2001 and 2002 breeding seasons combined).

### 5.3.6 Productivity trends in riparian and non-riparian habitats

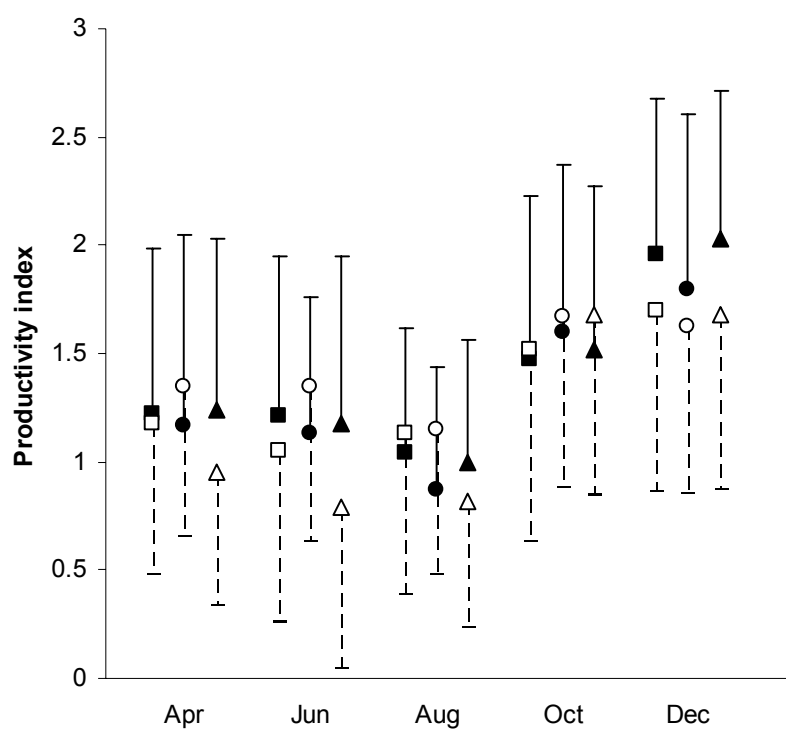
Repeated measures ANOVA showed a significant effect of sampling period on the productivity of eucalypts among riparian and non-riparian habitats (Table 5-7). A significant effect of sampling period was also shown for productivity of Messmate *E. obliqua* and Narrow-leaved Peppermint *E. radiata* (Table 5-7). Across the study area eucalypt growth was seasonal, with a trough evident during autumn/winter and peaks in spring/summer (Figure 5-13). There was a significant interaction between habitat type and month for eucalypt growth (Table 5-7), with higher growth in early winter and summer at riparian sites (Figure 5-13). Growth of Narrow-leaved Peppermint *E. radiata* was significantly different between habitat types (Table 5-7), being greater at riparian sites at most times (Figure 5-13).



**Table 5-7** Site type and sampling period differences in productivity of all eucalypts, and of Messmate *E. obliqua* and Narrow-leaved Peppermint *E. radiata*, showing *F*-values for a repeated measures ANOVA of site type (riparian or non-riparian) X sampling period (April, June, August, October, December).

	Habitat type	Month	Habitat type X Month
Eucalypts	1.555 (1,350)	67.594** (4,1400)	3.605** (4,1400)
<i>E. obliqua</i>	1.359 (1,80)	15.746** (4,320)	1.388 (4,320)
<i>E. radiata</i>	11.347** (1,108)	31.999** (4,432)	0.418 (4,432)

$p < 0.05$ ; \*\*  $p < 0.01$



**Figure 5-13** Productivity index scores for riparian (closed symbols; upwards, solid error bars = s.d.) and non-riparian habitats (open symbols; downwards, dashed error bars = s.d.) for all eucalypts (■), Messmate *E. obliqua* (●) and Narrow-leaved Peppermint *E. radiata* (▲) during 2002.

## 5.4 Discussion

Riparian zones are widely recognised as important habitats for wildlife because they often support rich and abundant fauna communities. A positive relationship between structural diversity of vegetation and the richness and diversity of assemblages (e.g. MacArthur and MacArthur 1961) has been widely used to explain this trend. However, while the structural diversity of vegetation may reflect the spatial distribution of habitat features that provide resources, it does not quantify the availability of these resources. In this chapter, explicit contrasts of resource availability between riparian and non-riparian sites provide quantitative evidence that identifies riparian sites as high quality habitats for birds in the forest landscape. The ecological value of these habitats is evidenced by the provision of key food and foraging resources such as nectar (i.e. eucalypt flowers) and bark substrates; and nest sites, including a higher proportion of trees that are hollow-bearing. Greater production of new leaf growth in eucalypts at riparian sites compared with non-riparian sites, suggests that primary production is also greater at riparian sites.

Abiotic conditions characteristically differ in riparian zones compared with surrounding non-riparian habitats (Gregory *et al.* 1991; Malanson 1993). Less variation in microclimatic conditions (i.e. temperature and humidity), together with higher soil nutrient levels and greater water availability in riparian zones may facilitate increased production and stability in plant growth and resource states throughout the year (Janzen and Schoener 1968; Gregory *et al.* 1991; Malanson 1993).

### 5.4.1 *Comparison of resource availability between riparian and non-riparian sites*

Eucalypt flowers provide a key food resource (nectar) for many birds in south-east Australia (Ford 1983; Paton 1986; McGoldrick and Mac Nally 1998). Flowering in eucalypts is often variable; some may fail to flower every year or show large variations in the number of flowers produced in a season (Ashton 1975; Ford 1979; Wilson and Bennett 1999). In moist, coastal eucalypt forests of south-east Australia, there is often

a continuous cycle of nectar-producing flowers (Paton 1986). Eucalypt flowers were more abundant at riparian sites in four of the six sampling periods when compared with non-riparian sites. It is likely that riparian sites provide conditions that promote flowering in eucalypts, such as higher moisture availability and more fertile soils (Gregory *et al.* 1991; Malanson 1993). Observations from this study support such a scenario. First, trees flowering at riparian sites bore more flowers (Figure 5-1). Second, at most times during the annual cycle, there were more trees bearing flowers at riparian sites (Table 5-1). Third, during the annual cycle, more species of eucalypt flowered at riparian sites than at non-riparian sites (Table 5-1). Last, flowering occurred at more riparian sites than non-riparian sites (Table 5-1).

Riparian sites provided an extensive 'loose' bark resource, an important microhabitat for invertebrates (Dickman 1991; Majer *et al.* 2003). Riparian sites contained significantly more peeling bark and hanging bark throughout the year than non-riparian sites. Invertebrates are more abundant under the loose bark of eucalypts than on the foliage (Recher *et al.* 1983). Piles of shed bark around the base of trees also support a rich and abundant reservoir of invertebrate prey (Dickman 1991; Majer *et al.* 2003). The shedding of bark exposes carbohydrate foods (e.g. honeydew and manna), which are used by many forest birds as sources of energy (Recher *et al.* 1983).

Tree hollows are used as nest sites by many birds (Saunders *et al.* 1982; Gibbons and Lindenmayer 2002). A positive relationship between tree size (i.e. diameter) and the presence of hollows has previously been reported for eucalypts (Bennett *et al.* 1994; Gibbons and Lindenmayer 2002). This relationship has mostly been related to tree age, with older trees more likely to be decaying, to shed larger branches and to have been exposed to events (e.g. fire, wind storms) that encourage the development of hollows. The density of hollow-bearing trees did not differ between site types, but the proportion of trees bearing hollows was greater at riparian sites. The proportion of trees with hollows increased with increasing diameter at both riparian and non-riparian sites. Areas of relatively high productivity may have higher proportions of hollow-bearing trees (Bennett *et al.* 1994), simply because such sites typically support larger trees. Differences in the proportion of trees with hollows have been found between eucalypt sub-genera, with tree hollows more likely to form in *Symphymyrtus* eucalypts than in *Monocalyptus* (Calder *et al.* 1983), but not always (Gibbons *et al.* 2000). In this study,

large (>81 cm dbh) *Symphyomyrtus* eucalypts contained comparatively higher proportions of hollows than large *Monocalyptus* trees.

Mistletoes occurred in low abundance throughout the forest landscape and especially at riparian sites. The dominance of *Symphyomyrtus* eucalypts at riparian sites is likely to contribute to the low numbers of mistletoes. The annual shedding of bark in ‘gum-barked’ eucalypts makes them less susceptible to mistletoe establishment, while rough or fibrous bark eucalypts that retain their bark are more receptive to mistletoe (Turner 1991). While a number of studies have identified the value of mistletoe flowers and fruits as a food resource for birds (Turner 1991), mistletoes also provide important nest sites for birds (Cooney *et al.* 2006). Approximately two-thirds of birds that nest in trees in Australia, have been reported nesting in mistletoe (Cooney *et al.* 2006), including 50% of the species recorded in this study.

The productivity of eucalypts differed between habitat types, being higher in riparian zones at most times for all eucalypts combined, and for some species (e.g. Narrow-leaved Peppermint *E. radiata*). This can be attributed to the high moisture availability, high nutrients and variability in reduced and oxidized soil conditions, which combine to promote plant growth (Malanson 1993; Tabacchi *et al.* 1998). Greater productivity probably also contributes to more abundant and consistent flower and fruit production, and to creating conditions that promote invertebrate abundance and diversity. The foliage of *Symphyomyrtus* eucalypts (most abundant at riparian sites) contains significantly higher nutrient levels than eucalypts in the subgenus *Monocalyptus* (Lambert and Turner 1983).

None of the resources measured were unique to either riparian or non-riparian sites. While the greater abundance of food resources (such as eucalypt flowers) and greater productivity promotes riparian sites as high quality habitats for wildlife, some features of non-riparian sites are also important. For example, prolifically flowering shrubs (e.g. *Banksia* and *Hakea*) were a feature of non-riparian habitats.

#### 5.4.2 Temporal reliability of resources

The temporal reliability of resources has been described as a key feature that makes riparian zones attractive to wildlife (Lynch and Catterall 1999). While it is necessary to

monitor resource states over several years to make firm conclusions about temporal variability, monitoring over one annual cycle provided strong evidence of the abundance of resources through time at riparian sites.

Seven of eight eucalypt species at riparian sites flowered in 2002, with four having flowering events that involved >40% of monitored trees. The one species that did not flower at riparian sites, Mealy Stringybark *E. cephalocarpa*, comprised a single tree at one site. In contrast, five of eight species at non-riparian sites flowered in the same period, with only two supporting a flowering event that involved >40% of trees. Increased moisture in riparian habitats (Brinson *et al.* 1981; Gregory *et al.* 1991) is likely to promote flowering in eucalypts. For example, in box-ironbark forest in central Victoria, flowering occurred in a greater proportion of trees with access to free-water (i.e. trees in close proximity to dams), than those without access to free-water (Wilson and Bennett 1999).

The high proportion of Symphyomyrtus eucalypts in riparian habitats, which undertake annual cycles of bark shed, provides an abundant and predictable resource. Bark shedding peaked in summer and extended throughout the year. The timing of bark peel was not synchronous between species: Manna Gum *E. viminalis* and Mountain Swamp Gum *E. camphora* peaked in late summer, Swamp Gum *E. ovata* in autumn and Mountain Grey Gum *E. cypellocarpa* in winter. The annual cycle of bark shed has a clear relationship with invertebrate availability for birds. Prior to bark shed, invertebrates are concentrated in accumulated bark on the ground around the base of tree trunks. As bark peels and detaches from the trunk, invertebrates move up to protected microhabitats between the bark and trunk (Dickman 1991). In south-east New South Wales, annual bark peel in Manna Gum *E. viminalis*, Mountain Grey Gum *E. cypellocarpa*, Swamp Gum *E. ovata*, Messmate *E. obliqua* and Narrow-leaved Peppermint *E. radiata* was synchronous for trees within species, and predictable in timing between years (Kavanagh 1987). The persistence throughout the annual cycle of relatively large amounts of bark ribbons in Symphyomyrtus eucalypts at riparian sites provides a reliable, year-round microhabitat for invertebrates and a foraging substrate for birds.

### 5.4.3 Bird patterns and community structure

Differential availability of resources occurs between riparian and non-riparian sites and birds showed clear relationships with the availability of specific food and foraging resources, and nest sites. By providing abundant and reliable resources, riparian sites supported a greater range of opportunities for birds throughout the year.

The plentiful and reliable loose bark resource (i.e. decorticating bark) at riparian sites supported a rich and abundant group of bark-foraging birds. Newly shed bark houses abundant invertebrates, and bark foragers are attracted to this in the same way that nectarivores are attracted to nectar-rich flowers (Recher and Holmes 1985; Dickman 1991; Majer *et al.* 2003). All members of the bark – invertebrates foraging group occurred at more riparian than non-riparian sites (Chapter 4), and three (Red-browed Treecreeper, White-eared Honeyeater and Crested Shrike-tit) of the six species were riparian associated species (Chapter 2). Decorticating bark was the principal foraging substrate for four of the six members of the bark – invertebrates foraging group. These species were rare, or absent, in non-riparian vegetation. Decorticating bark was also used by several species that primarily forage on other substrates (e.g. White-naped Honeyeater and Brown-headed Honeyeater), providing a stable alternative resource for species that exploit temporally variable resources such as nectar. For example, the White-naped Honeyeater foraged on eucalypt flowers when available, but decorticating bark was a major component of the substrates it used throughout the year. The reliability of this resource is reflected in the temporal stability of populations of members of the bark – invertebrates foraging group. These species were all 'residents' and showed little variation in numbers through time (Chapter 3). *Symphomyrtus* eucalypts are not confined to riparian habitats, and birds such as Crested Shrike-tit and White-eared Honeyeater commonly occur in non-riparian vegetation dominated by these species elsewhere (e.g. Candlebark *E. rubida* woodland and Mountain Ash *E. regnans* forest) (Loyn 1985b).

The presence of flowering trees attracted several nomadic nectarivores (e.g. Purple-crowned Lorikeet, Musk Lorikeet, Little Lorikeet and Swift Parrot), which were not observed in the absence of flowering eucalypts. While many nectarivores were rare (e.g. lorikeets and Swift Parrot) or mostly foraged on prolifically flowering shrubs (e.g. Red Wattlebird and Eastern Spinebill), eucalypt flowers were a main foraging

substrate for several species that belonged to the tree layer – invertebrates foraging group, including the White-naped Honeyeater and Yellow-faced Honeyeater. These species were closely associated with riparian habitats and mainly foraged on foliage and bark surfaces of trees, but they also made extensive use of eucalypt flowers when available (Chapter 4). Eucalypt flowers are likely to provide an important supplementary resource for these species with birds depending on reliability of flowering at particular times of the year (Recher and Holmes 1985; Paton 1986; French *et al.* 2003). The relationship between the abundance of nectarivores and eucalypt flowering was not clear in this study (Figure 5-1); however, heavy flowering of eucalypts in riparian habitats attracted large numbers of nectar-feeding birds (e.g. White-naped Honeyeater). Many nectarivores track flowering events at a range of spatial scales (Ford 1983; McGoldrick and Mac Nally 1998; French *et al.* 2003; Timewell and Mac Nally 2004). It is probable that within the forest landscape, non-synchronous flowering between riparian and non-riparian habitats, and of different eucalypt species, provide some form of continuity in the supply of nectar for birds. In addition, there were distinct differences in the use of shrub flowers and eucalypt flowers between nectarivores. The species richness, abundance and composition of the nectarivore assemblage often depends on the range and richness of nectar resources available (Ford 1979; Paton 1986; Reid 1986; Mac Nally and McGoldrick 1997).

#### 5.4.4 Implications for conservation

Two main implications for the conservation of bird assemblages are evident. First, the demonstration of a greater abundance of resources in riparian zones is consistent with data showing disproportionately high value for birds of these linear strips that occupy only a small proportion of the landscape (Chapter 2). Therefore, riparian zones should attract a high priority in conservation planning. Differences in vegetation productivity and resource states (e.g. eucalypt flowering) observed in this study are likely to be amplified in drier environments of other regions where there is a greater contrast in water availability between riparian and non-riparian zones.

Second, greater primary productivity and more reliable resources (i.e. abundance through time) is consistent with the concept of riparian vegetation being a refuge area during times of environmental stress such as dry conditions or drought. For example, in Mulga *Acacia aneura* vegetation in northern Australia, riparian areas were most

important for bird communities during drought and between rainfall events (Kingston 2005). The degradation of drainage depressions (i.e. riparian zones) in central Australia is believed to have contributed to the widespread extinctions of small mammals since settlement (Morton *et al.* 1995), highlighting their importance to wildlife. Riparian zones are likely to have an important role in sustaining populations through times of environmental stress by providing resources (e.g. nectar and free water) that are otherwise limited in the surrounding landscape (Nix 1993; Woinarski *et al.* 2000; Kingston 2005). By functioning as refuge habitats, riparian zones may also maximise the use of temporally unstable resources from the rest of the landscape as birds are capable of radiating from these habitats on a daily basis or for longer periods of time.



## 6 Synthesis of results and implications for conservation

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Riparian vegetation alongside Diamond Creek, Bunyip State Park

## 6.1 Overview

Riparian zones are recognised as important habitats for wildlife throughout the world (see Chapter 1). While the value placed on riparian zones has generally been based on the high richness and abundance of species occurring locally, this thesis focuses on the ecological mechanisms that underpin differences between riparian and non-riparian assemblages. By contrasting the structure of riparian and non-riparian assemblages, this study has revealed aspects of riparian zones that make them high quality habitats for birds.

The findings and implications of this study are discussed below in relation to four themes identified in Chapter 1. The first theme identifies the importance of riparian zones by comparing the species richness, abundance and composition of bird assemblages between riparian and non-riparian habitats. The second theme explores the seasonal dynamics in riparian and non-riparian bird assemblages, identifying the stability of these assemblages through time and the influence of migrant species. The third theme examines the ecological mechanisms by which riparian assemblages are richer and support more individuals than non-riparian assemblages. The fourth theme investigates differences in the availability and dynamics of resources used by birds between riparian and non-riparian habitats. Table 6-1 summarises the main findings for each of these themes.

The final section discusses the importance of riparian zones to the conservation of birds in forest landscapes. Consideration of these findings and their contribution to the body of knowledge on riparian zones is then used to discuss the appropriate management of riparian zones, particularly in forested landscapes.

**Table 6-1      Summary of objectives and key findings of study**

Theme	Objectives	Key findings
Structure of bird assemblages	<ul style="list-style-type: none"> <li>• Compare structural and floristic features of riparian and non-riparian vegetation</li> <li>• Quantify any difference in species richness and abundance between riparian and non-riparian habitats</li> <li>• Compare the species composition of avifaunal assemblages between riparian and non-riparian habitats</li> </ul>	<ul style="list-style-type: none"> <li>• Riparian zones are floristically and structurally distinct from non-riparian habitats</li> <li>• Riparian zones have more complex vegetation structure</li> <li>• Riparian zones support significantly greater species richness and abundance of birds</li> <li>• Riparian zones support a distinct species composition</li> <li>• Some species are found exclusively in the riparian zone (i.e. riparian selective species) and many are strongly linked to riparian habitats (i.e. riparian associated species)</li> <li>• A smaller number of species are found exclusively in non-riparian habitats (i.e. non-riparian selective species) or are strongly linked to non-riparian habitats (i.e. non-riparian associated species)</li> </ul>
Seasonal dynamics of bird assemblages	<ul style="list-style-type: none"> <li>• Test whether the richness and abundance of riparian bird assemblages displays less variation through time than non-riparian assemblages</li> <li>• Test whether the species composition of riparian bird assemblages displays less variation through time than non-riparian assemblages</li> </ul>	<ul style="list-style-type: none"> <li>• Riparian assemblages support significantly greater species richness and abundance through time</li> <li>• Riparian assemblages are more stable, with less temporal variation in species richness and abundance</li> <li>• The species composition of riparian bird assemblages is distinct from non-riparian bird assemblages through time</li> <li>• Species composition of bird assemblages changes during the annual cycle, but riparian assemblages are more constant through time in comparison to non-riparian assemblages</li> <li>• Riparian zones are particularly important for birds that migrate along the east coast of Australia (i.e. coastal migrants)</li> <li>• Non-riparian habitats are preferred by most species that migrate through inland Australia</li> </ul>

**Table 6.1.**      **continued.**

<b>Theme</b>	<b>Objectives</b>	<b>Key findings</b>
Ecological characteristics of bird assemblages	<ul style="list-style-type: none"> <li>Examine the ecological mechanisms by which riparian assemblages are richer and support more individual birds</li> </ul>	<ul style="list-style-type: none"> <li>Riparian zones support a greater number of foraging, nest-type and body mass groups</li> <li>Riparian zones support greater species richness in most foraging, nest-type and body mass groups</li> <li>Significant differences exist in the use of structural features of habitat, substrates and foraging heights between riparian and non-riparian habitats for selected species of birds</li> </ul>
Resource availability and dynamics	<ul style="list-style-type: none"> <li>Determine whether riparian habitats provide a greater abundance of resources used by birds when compared to non-riparian habitats</li> <li>Examine the reliability in the seasonal availability of resources in riparian and non-riparian habitats</li> <li>Determine whether primary productivity is greater and more reliable in riparian habitats when compared to non-riparian habitats</li> </ul>	<ul style="list-style-type: none"> <li>The abundance of resources is, in general, greater in the riparian zone</li> <li>Non-riparian habitats provide an important shrub flower resource</li> <li>Seasonal resources such as eucalypt flowering and bark shed are available all year or for longer periods during the year in the riparian zone</li> <li>Primary productivity is likely to be greater and more reliable in the riparian zone</li> </ul>

### 6.1.1 Structure of riparian and non-riparian bird assemblages

Strong gradients in species richness and abundance of bird assemblages along riparian-upslope transitions occur in a wide range of environments (Szaro and Jakle 1985; Mac Nally *et al.* 2000; Woinarski *et al.* 2000; Tzaros 2001), but not in all (McGarigal and McComb 1992; Pearson and Manuwal 2001; Sabo *et al.* 2005; Baker *et al.* 2006). The strength of the gradient may depend on the nature of the transition from riparian to non-riparian parts of the landscape (McGarigal and McComb 1992; Baker *et al.* 2006). In arid environments a strong gradient in water availability, and its associated effect on vegetation productivity, results in a sharp contrast between riparian and non-riparian assemblages (Knopf 1985; Szaro and Jakle 1985). Where this gradient is more subtle (i.e. in moist forest types), the contrast between assemblages is likely to be weaker (McGarigal and McComb 1992; Baker *et al.* 2006). Furthermore, in intact forest environments, riparian edge effects are unlikely to be significant in the absence of sharp vegetation boundaries (Baker *et al.* 2006).

This study demonstrated that despite a relatively subtle riparian-upslope transition (i.e. continuous eucalypt canopy over a relatively short distance in a mesic forest landscape), the riparian zone had a strong influence on the structure and floristic composition of the vegetation in this forest landscape. Riparian habitats were floristically and structurally distinct from surrounding non-riparian vegetation. Riparian zones had a more complex vegetation structure, and were characterised by a mid-storey tree layer (e.g. *Acacia* spp.) that was mostly absent from non-riparian sites, extensive fine litter and coarse woody debris, and dense ground-layer vegetation (e.g. sedges and ground ferns).

The ecological value of riparian habitats to birds was evidenced by the higher richness and abundance of bird species that they supported at all sites, and by the distinctive species composition of the avifauna which complements that occurring in surrounding non-riparian habitats (Chapter 2). Five broad groups of species were distinguished in the study area, based on their distributional patterns. Forest generalists (36% of all species) were widespread throughout the forest landscape. Riparian selective species (7%) occurred exclusively in riparian habitats. Riparian associated species (43%) were strongly linked to riparian habitats, although they also occurred in non-riparian habitats, particularly wetter forest types. Non-riparian selective species (2%) occurred

exclusively in non-riparian habitats. Non-riparian associated species (10%) were strongly linked to non-riparian habitats, although they also occurred in riparian habitats.

Differences in the species composition of bird assemblages were predominantly generated by those species with large contrasts in abundance between riparian and non-riparian habitats, but were also influenced by species occurring in one or other of the habitat types. Sabo *et al.* (2005), in a meta-analysis of the value of riparian zones to major taxonomic groups, found riparian zones to support significantly different pools of species, but not higher numbers of species; although there was significant heterogeneity in this relationship between landscape settings. In the current study, riparian zones promoted species richness at the landscape level by harboring both more species, and a different pool of species to that in surrounding forest vegetation. Despite each supporting distinct assemblages, strong linkages are maintained along the riparian-upslope gradient; evidenced by relatively few species found exclusively in either habitat type. Most forest bird species used riparian zones at some stage and almost two thirds (64%) attained higher abundance in riparian vegetation than in other vegetation communities. The overall strength of the riparian effect on the richness, abundance and species composition of bird assemblages shows that these habitats are important in contributing to landscape richness in eucalypt forest landscapes.

### 6.1.2 *Seasonal dynamics in riparian and non-riparian bird assemblages*

The effect of the riparian zone on the structure (i.e. richness, abundance) of faunal assemblages, particularly birds, has been relatively well-studied (e.g. Catterall 1993; Knopf and Samson 1994; Sabo *et al.* 2005), but little attention has been given to the temporal dynamics of this relationship. In this study, riparian assemblages supported greater species richness and abundance than non-riparian assemblages throughout the annual cycle. Patterns of bird assemblage structure (richness, abundance) showed temporal variation, but this was more stable and consistent in riparian assemblages. This pattern reflected more stable and predictable conditions in riparian zones, including the provision of more abundant and consistent food resources (e.g. eucalypt flowering) (Chapter 5).

Non-riparian assemblages displayed greater variation in richness, abundance and species composition through time. These assemblages were highly variable and

displayed no clear pattern in, or relationship between, richness and abundance through time. These assemblages also had intrinsically low richness and abundance; under these circumstances, even small influxes of birds caused considerable variation in richness and abundance through time. As a consequence of temporal limitations in resource availability (e.g. shrub flowering) in non-riparian habitats, these assemblages include many species (i.e. local movement group) that move about constantly, tracking irregular resource events (e.g. McGoldrick and Mac Nally 1998; French *et al.* 2003).

Across all sites, bird assemblages were comprised of a core of resident species, complemented by a suite of warm-season migrants during spring and summer. The influx of seasonal migrants elevated species richness and abundance in the landscape during spring and summer. While this influx of species contributed to change in species compositions through time in both riparian and non-riparian assemblages, the composition of riparian assemblages was more similar through time.

The large-scale movement pattern adopted by migratory species was associated with their preference for riparian or non-riparian habitats in the forest landscape. Species which migrate along the east coast of the Australian mainland (i.e. coastal migrants) were closely associated with riparian zones. Eight of the eleven species of coastal migrants, were riparian associated species. Coastal migrants comprised up to 30% of individuals in riparian zones during the spring/summer period. Several coastal migrants (e.g. Grey Fantail, Golden Whistler and Yellow-faced Honeyeater) are partial migrants in south-east Australia, with a proportion of the population remaining during the winter exodus. Those individuals that overwintered in the study area mostly occurred in the riparian zone.

Most species that migrate through inland Australia (i.e. inland migrants) were associated with non-riparian parts of the landscape. These species (e.g. Rufous Whistler, Black-faced Cuckoo-shrike, Olive-backed Oriole) typically have broad distributions in a wide range of wooded environments. Species within the “local movement” group (e.g. Red Wattlebird, Eastern Spinebill) contributed much of the variation evident in non-riparian assemblages. These species moved into non-riparian habitats in the landscape in response to irregular flowering events (e.g. shrub flowering).

Resources available in both the riparian zone and non-riparian parts of the landscape are potentially available to birds. In the forest landscape, riparian zones occurred as narrow, linear elements that shared boundaries with a wide-range of non-riparian vegetation communities. The strong linkages between riparian zones and the surrounding non-riparian components of the landscape are evidenced by considering the temporal dynamics of the avifauna. This study adds quantitative support to the view that riparian zones have a role in the temporal dynamics of bird communities (Catterall 1993; Lynch and Catterall 1999). Some species depend on resources in both riparian and non-riparian habitats and regularly move between these components of the landscape, including on a daily basis. For example, the Powerful Owl typically roosts in dense vegetation in gullies (e.g. Blackwood *Acacia melanoxylon* trees), but forages more widely over large areas (beyond 1 000 ha) that include both riparian and non-riparian habitats (Kavanagh 1988). Species also move into the riparian zone from the surrounding landscape in response to changing resource availability (e.g. Woinarski *et al.* 2000; French *et al.* 2003). In this study, riparian zones provided winter habitat for species (e.g. Grey Fantail, Golden Whistler) that were typically found throughout the eucalypt forest during spring and summer. However further to this, this study showed the importance of riparian zones for birds that undertake regular, large-scale migratory movements; effectively, these species (e.g. Rufous Fantail, Satin Flycatcher, Shining Bronze-Cuckoo) selected riparian zones as breeding habitat.

Significant differences in the dynamics of community structure between riparian and non-riparian assemblages in this study show that there is a disproportionate use of riparian habitats across the forest landscape. This distinguishes riparian zones in the landscape as providing high quality habitats for birds throughout the annual cycle.

### 6.1.3 *Ecological characteristics of bird assemblages*

Two ecological mechanisms were identified to account for the greater species richness in riparian assemblages. First, the riparian zone provides a greater range of opportunities to birds, and as a result, there were more ecological groups (foraging, nest-type and body mass groups) represented compared with non-riparian assemblages. The responses of birds to riparian or non-riparian habitats could be explained by their suitability to the ecological requirements of species. For example, birds that foraged among sheltered, damp litter were closely linked to riparian



habitats. Similar links were shown for birds that use domed nests in shrubs or small trees, or use open top nests in dense understorey. The consistency of the difference found across the range of ecological characteristics indicates that riparian zones offer a wider range of niches that are exploited by birds. This is augmented by the provision of distinct resources for foraging (e.g. damp litter, decorticated bark) and nesting (e.g. mid-storey vegetation) in riparian zones.

Second, greater species richness was accommodated in most foraging, nest-type and body mass groups in riparian than non-riparian assemblages. Riparian zones facilitated greater richness within ecological groups by providing conditions that promoted segregation between ecologically similar species. These conditions included the availability of more types of resources and greater abundance of some resources. For example, the complex mid-storey vegetation in riparian zones increased the number of microhabitats available for birds and benefited groups that foraged (e.g. sub-canopy – invertebrates and shrub/small tree – invertebrates foraging groups) and nested (e.g. domed – shrub/small tree, open top – dense understorey and open top – shrub/small tree nest-type groups) in the mid-storey.

The level of use of particular structural features, substrates and heights by foraging birds differed significantly between riparian and non-riparian assemblages. Structural features used more frequently in riparian zones were small trees and saplings, coarse woody debris and tree ferns. In non-riparian habitats there was greater use of ground, shrubs and tall trees. In terms of substrates, there was greater use of decorticated bark, inner foliage and fern fronds in riparian zones, while in non-riparian zones, mistletoes, open litter and flowers were used more frequently than expected.

Selected species showed significant differences in their use of structural features and substrates, and their height of foraging between riparian and non-riparian habitats. Observed differences were due to disparity in a single parameter (e.g. for the Eastern Spinebill) or multiple parameters (e.g. Brown Thornbill). Resource partitioning and niche narrowing minimises competition between similar species and enables species to co-occur (Wiens 1989). Body mass was also identified as a mechanism that facilitated segregation among ecologically similar species (e.g. sheltered ground – invertebrates foraging group).

Riparian zones provided more types of resources (e.g. potential nest sites) and greater abundance of some resources (e.g. eucalypt flowering and decorticating bark; Chapter 5), which permitted greater avian richness because there were simply more opportunities and ways to sub-divide the environment. The taxonomic diversity and wide range of ecological requirements among species strongly associated with riparian zones (i.e. riparian selective and riparian associated species) shows that the riparian influence is unlikely to be due to a specific structural feature, food or nest resource or floristic characteristic.

#### *6.1.4 Resource availability and dynamics between riparian and non-riparian habitats*

While measures of the structural complexity of vegetation may describe the spatial distribution of habitat features that provide resources, it does not quantify the availability of these resources. Explicit contrasts of resource availability between riparian and non-riparian sites provided quantitative evidence of the quality of riparian habitats in the forest landscape. Their ecological value is shown by the provision of key food and foraging resources such as nectar (i.e. eucalypt flowers) and bark substrates; nest sites, including a higher proportion of trees that are hollow-bearing; and greater primary production (i.e. new leaf growth in eucalypts).

Riparian zones provided important food and foraging resources for birds. They had a greater extent of eucalypt flowering through the year. This included individual trees bearing more flowers, more trees flowering, more species flowering and flowering occurring at more riparian than non-riparian sites. Riparian zones provided an extensive 'loose' bark resource, supporting significantly more peeling bark and hanging bark throughout the year. Loose bark houses an abundant invertebrate resource that is used by birds (Recher *et al.* 1983). The plentiful and reliable loose bark resource at riparian sites supported a rich and abundant group of bark-foraging birds. Several species which predominantly forage on loose bark (e.g. Crested Shrike-tit, White-eared Honeyeater) were mostly confined to riparian zones in the landscape. The temporal reliability of this resource was reflected in the temporal stability of populations of bark foragers through the study.

The density of hollow-bearing trees did not differ between riparian zones and non-

riparian habitats, but the proportion of trees bearing hollows was greater at riparian sites. Riparian assemblages supported a significantly greater richness and abundance of hollow-dependent birds. This might be due to the availability of suitable hollows (e.g. particular types of hollows, more hollows per tree), or it might not be associated with hollow availability (e.g. more food and/or foraging resources for hollow-using birds).

Resources exhibit greater temporal reliability in riparian zones than non-riparian parts of the landscape. This was associated with a greater abundance of resident birds in riparian habitats. It is also likely to have contributed to the seasonal movements of birds between parts of the landscape (e.g. overwintering coastal migrants moving into riparian zones). This enables birds to maximise the use of temporally unstable resources from the rest of the landscape as they can radiate out from riparian habitats on a daily basis or for longer periods of time. Greater productivity and more reliable resources are consistent with the concept that riparian zones provide important refuge areas for wildlife when conditions in surrounding parts of the landscape become stressful.

Aligned to this concept, is the potential for the riparian zone to function as ‘source’ areas for populations in the surrounding landscape (see Mac Nally *et al.* 2000). Richer and more abundant bird assemblages in riparian zones, and the provision of more abundant and reliable resources, are conditions that would be expected if riparian zones functioned as source habitats. While the current research provides enticing evidence that such a relationship exists, quantitative data on breeding success and intensive autecological studies (e.g. banding studies investigating dispersal of fledglings) are required.

## **6.2 Conservation value of riparian zones and implications for management in forest landscapes**

The importance of conserving riparian zones in forest landscapes is evident throughout this thesis. First, the vegetation in riparian zones differs in both floristic composition and structural complexity from that of adjacent non-riparian habitats. Thus, riparian zones add to the diversity of the landscape mosaic and to the diversity of habitats and resources available to forest birds. Second, a suite of bird species are strongly

associated with, or predominantly confined to, the riparian zone. These species are likely to occur in relatively lower abundance (or be absent) from the forest landscape if not for the presence of riparian vegetation. Third, most forest bird species use riparian habitats at some stage of their life, and almost two-thirds of all species (64%) attained higher densities in riparian habitats than in other forest types. Fourth, the distinctiveness of riparian vegetation and the prevalence of bird species typical of wet forests, suggest that they may function as seasonal or refuge habitats when conditions become stressful in upland habitats. This includes the potential for these habitats to function as refuges from drought and fire (Nix 1993). Last, riparian habitats in this study area are known to be used by several taxa of threatened conservation status, including the Powerful Owl *Ninox strenua*, Sooty Owl *Tyto tenebricosa* (Loyn *et al.* 2001) and Helmeted Honeyeater *Lichenostomus melanops cassidix* (Blackney and Menkhurst 1993).

In many forest landscapes, non-riparian areas potentially support a greater area and range of vegetation communities, higher spatial arrangement of patches and more successional stages. Riparian habitats characteristically comprise only a small proportion of the forest landscape (<10% of the total area in this case). Non-riparian forests, by virtue of their greater area, serve as the major population reservoirs for most species of forest birds. Consequently, the ecological role and value of non-riparian habitats should not be overlooked. Riparian habitats were not suitable for all species in this study, or in other studies (McGarigal and McComb 1992; Murray and Stauffer 1995; Mac Nally *et al.* 2000). In this study a number of species clearly were associated with non-riparian habitats, including at least 12% of species classed as non-riparian selective and non-riparian associated species.

Linkages between riparian and non-riparian habitats necessitate a 'whole of landscape' approach to management. Many species used both riparian and non-riparian habitats, and may depend on either riparian or non-riparian habitats regularly (e.g. Powerful Owl), or at particular times in the annual cycle (e.g. coastal migrant group). It is important to recognise temporal variation in the requirement of birds for forest habitats across the range of spatial scales when planning conservation programs. Entire bird assemblages will not be supported in a system of retained vegetation based totally on the retention of networks of riparian buffer strips.

This study, and the results from other studies (Recher *et al.* 1983; Woinarski *et al.* 2000), show that the conservation value of the riparian zone is fundamentally high. However, the ability of riparian zones to adequately conserve species and assemblages where upslope habitats are substantially modified is strongly influenced by the landscape context and the nature of surrounding land-use, as well as condition of the riparian zone (Fisher and Goldney 1998; Saab 1999; Lindenmayer *et al.* 2002; Martin *et al.* 2006). For example, in an extensive pine plantation in south-east Australia, the maintenance of remnant vegetation along drainage lines made an important contribution to the persistence of avifauna in the landscape. While such habitats contributed to the landscape heterogeneity of the plantation and increased native bird populations in nearby pine habitat, they did not conserve all components of the avifauna (Lindenmayer *et al.* 2002). The landscape context of the riparian zone will provide birds with resources that are either additional, complementary to, or not present in the riparian zone (Lindenmayer *et al.* 2002; Ries and Sisk 2004; Martin *et al.* 2006).

The protection of riparian zones generally receives a high priority during timber harvesting operations (Kinley and Newhouse 1997; Voller 1998; Waterhouse and Harestad 1999) and prescriptions for the retention of vegetation along streams to protect water quality and conserve biodiversity are common practice (e.g. DSE 2006). For example, prescriptions for minimum widths of buffer strips along waterways in Victorian forests range from 10 m along drainage lines to 40 m along permanent streams (DSE 2006). The adequacy of buffer strips for the conservation of fauna is yet to be determined (Bren 1995; Darveau *et al.* 1995; Vander Haegen and DeGraaf 1996; Fisher and Goldney 1998; Meiklejohn and Hughes 1999; Whitaker and Montevecchi 1999; Pearson and Manuwal 2001; Hannon *et al.* 2002; Lindenmayer *et al.* 2002; Lee *et al.* 2004), however these minimum widths are likely to be too narrow to protect the range of species potentially threatened by timber harvesting. While the protection of riparian zones is critical, such buffers will not be able to cater for the requirements of all components of the forest avifauna (e.g. non-riparian associated species). Furthermore, the use of fixed-distance prescriptions does not ensure protection of the riparian zone in its entirety. In this study, the width of the riparian zone ranged from 60 m to 230 m along a single stream (with same stream order maintained along length).

Some birds that depend on interior forest are either absent or occur in lower abundance

in riparian buffer strips than intact riparian zones elsewhere. (Darveau *et al.* 1995; Hagar 1999; Pearson and Manuwal 2001). For example, in managed Douglas-Fir forests in western USA, narrow buffers (<14 m either side of stream) did not maintain the pre-logging bird community and some riparian associated species (e.g. Black-throated Grey Warbler *Dendroica nigrescens*) were lost. Similar effects have been shown for other fauna. For example, logging had significant negative impacts on macroinvertebrate abundance and Brown Trout *Salmo trutta* (an introduced species) in streams with buffer widths up to 30 m (Davies and Nelson 1994).

High edge ratios make riparian buffer strips vulnerable to changes in the surrounding landscape and associated 'edge effects'. Such 'edge effects' include increased predation (Cain 2003, Vender Haegen 1996, Rudnicki 1993), nest parasitism (Danchin *et al.* 1998) and reduced nest success (Flaspohler *et al.* 2001), and these are likely to compound the loss of adjacent vegetation. 'Edge effects' may also have negative impacts on key habitat features of riparian zones. For example, the availability of damp, sheltered ground is closely linked to surrounding vegetation, which ameliorates exposure to climatic conditions that cause desiccation (e.g. sunlight and wind). The loss of surrounding vegetation and associated edge effects may have a negative impact on the extent of damp litter due to changes in microclimatic conditions. For example, in boreal forest in Sweden, thin buffer strips (10-15 m) suffered from desiccation in ground layer moisture throughout (Hylander *et al.* 2002). In the current study, at least eight species strongly linked to riparian habitats forage predominantly among damp litter.

Practices associated with timber harvesting in areas adjacent to riparian zones pose additional risks to the conservation value of the retained vegetation. Timber harvesting has been shown to increase sedimentation in adjacent streams, including buffered streams (e.g. Davies and Nelson 1994). The deposition of sediments in the riparian zone may potentially have a negative impact on habitat suitability for ground foraging birds, such as sheltered ground – invertebrates foragers. Regeneration burns conducted in coupes post-harvesting could also impinge on the retained buffers in the riparian zone if poorly applied. Buffer strips may also be exposed to elevated risk of windthrow (Ruel *et al.* 2001).

Given the importance of linkages between riparian and non-riparian habitats and the potential impacts of edge effects and habitat deterioration in narrow buffers, landscape

planning for fauna conservation should include the retention of large contiguous areas of vegetation that include both riparian and non-riparian elements of the landscape. The retention of large contiguous areas of forest has a number of benefits. First, the retention of a wider range of vegetation communities increases landscape heterogeneity. Second, the retained habitat is more likely to provide habitats that cater for both riparian and non-riparian species. Third, linkages are maintained between riparian and non-riparian habitats. Fourth, the riparian zone is less likely to be negatively affected by processes originating from disturbance in adjacent upslope habitats (e.g. windthrow, sedimentation).

Clearly, the maintenance of diverse and sustainable assemblages of birds in forest landscapes depends on complementary management of both riparian and non-riparian vegetation types. While this thesis concentrated on the ecological value of riparian zones to birds, the values identified would be expected to apply to other taxonomic groups. Other terrestrial faunal groups including mammals (Doyle 1990; Moore and Foley 2000; Soderquist and Mac Nally 2000) and amphibians (Parris and McCarthy 1999) have shown strong associations with riparian zones, both in Australia and internationally. This thesis highlights the importance of landscape-level planning and management for fauna conservation in forest mosaics.

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**Brown-headed Honeyeater** *Melithreptus brevirostris* (T. Wilson)



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## Appendix

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