Conservation Ecology and Breeding Biology of the White-browed Treecreeper *Climacteris affinis*

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Abstract

The White-browed Treecreeper Climacteris affinis is one of many woodland-dependent birds that are at risk from the encroachment of human-dominated land-uses into natural landscapes. The White-browed Treecreeper inhabits semi-arid woodlands in north-west Victoria, Australia, a vegetation community that has undergone extreme modification in the last century due to the expansion of agriculture in the region. Extant woodlands represent only 10% of the original woodland cover in the region, and are highly fragmented and disturbed in many districts. Thus, the survival of the White-browed Treecreeper may depend on active management. However, current knowledge of the ecology and biology of this species is virtually non-existent, and inadequate for informed and effective conservation actions. The aim of this thesis is to redress this situation and provide the ecological basis for sound conservation management of the species. The thesis consists of two parts: an investigation of habitat use at three spatial scales and a study of the social organization, nesting requirements, breeding behaviour and reproductive success of a population of White-browed Treecreepers.

Fifty-six patches of remnant woodland in north-west Victoria were surveyed to determine the factors affecting the occurrence of the White-browed Treecreeper at the regional scale. It was detected in 16 patches, and was largely confined to two core districts - Yarrara and Wyperfeld (Pine Plains). The floristic composition of the dominant tree species was an important determinant of patch occupancy, with the results providing quantitative support for the previously suspected affinity for Belah Casuarina pauper and Slender Cypress-pine Callitris gracilis – Buloke Allocasuarina luehmannii woodlands. However, the absence of the White-browed Treecreeper from several districts was due to factors other than a lack of appropriate habitat. Demographic isolation – the distance from the focal patch to the nearest population of the White-browed Treecreeper – was the most important variable in explaining variation in patch occupancy. Patches isolated from other treecreeper populations by more than 8.3 km in landscapes of non-preferred native vegetation, and 3 km in agricultural landscapes, were unlikely to support the White-browed Treecreeper. The impact of habitat loss and fragmentation on the capacity of individuals to move through the landscape (i.e. functional connectivity) is considered in relation to disruption to dispersal and migration, and the potential collapse of local metapopulations.
Habitat use was then examined in a network of patches and linear strips of Belah woodland embedded in a predominantly cultivated landscape. A minimum area of 18.5 ha of Belah woodland was identified as the most important criterion for patch occupancy at the local scale. This landscape appeared to be permeable to movement by the White-browed Treecreeper, facilitated by the extensive network of linear habitat, and clusters of small to medium fragments.

The third scale of habitat use investigated the frequency of use of 1-ha plots within tracts of occupied woodland. It is important to discriminate between habitat traits that operate at the population level, and those that act as proximate cues for habitat selection by individuals. Woodlands that have high tree density, extensive cover of low-stature shrubs, abundant lichen, a complex vertical structure, and relatively low cover of grass and herbs are likely to support larger populations of the White-browed Treecreeper. However, individuals appeared to be using tree dominance (positive) and tall shrub cover (negative) as proximate environmental stimuli for habitat selectivity. A relatively high cover of ground lichen, which probably reflects a ground layer with low disturbance and high structural complexity, was also a reliable indicator of habitat use. Predictive models were developed which could be used to plan vegetation management to enhance habitat for the White-browed Treecreeper.

The results of the regional, landscape and patch-scale investigations emphasise that factors operating at multiple spatial scales influence the suitability of remnant vegetation as habitat for the White-browed Treecreeper.

The White-browed Treecreeper is typical of many small Australian passerines in that it has high annual survival, small clutches, a long breeding season, multiple broods and relatively low reproductive rates. Reproductive effort is adjusted through the number of clutches laid rather than clutch size. They occupy relatively large, all-purpose territories throughout the year. However, unlike many group territorial birds, territory size was not related to the number of occupants.

The White-browed Treecreeper nests in tree hollows. They select hollows with a southerly orientation where possible, and prefer hollows that were higher from the ground. At Yarrara, there was considerable spatial variation in hollow abundance that, in concert with territorial constraints, restricted the actual availability of hollows to less than the absolute abundance of hollows. Thus, the availability of suitable hollows may limit reproductive productivity in some territories, although the
Facultative cooperative breeding was confirmed, with groups formed through male philopatry. Consequently, natal dispersal is female-biased, although there was no skew in the sex ratio of the fledglings or the general adult population. Helpers were observed performing all activities associated with parenting except copulation and brooding. Cooperatively breeding groups enjoyed higher fledgling productivity than simple pairs, after statistically accounting for territory and parental quality. However, the difference reflected increased productivity in the 1999-breeding season only, when climatic conditions were more favourable than in 1998. Breeding commenced earlier in 1999, and all breeding units were more likely to attempt a second brood. However, only breeders with helpers were successful in fledging second brood young, and it was this difference that accounted for the overall discrepancy in productivity. The key mechanism for increased success in cooperative groups was a reduction in the interval between first and second broods, facilitated by compensatory reductions in the level of care to the first brood. Thus, females with helpers probably achieved significant energetic savings during this period, which enabled them to re-lay sooner. Furthermore, they were able to recommence nesting when the fledglings from the first brood were younger because there were more adults to feed the dependent juveniles.

The current utility, and possible evolutionary pathways, of cooperative breeding is examined from the perspective of both breeders and helpers. Breeders benefit through enhanced fledgling productivity in good breeding conditions and a reduction in the burden of parental care, which may impart significant energetic savings. Further, breeders may facilitate philopatry as a means for ensuring a minimum level of reproductive success. Helpers benefit through an increase in their inclusive fitness in the absence of opportunities for independent breeding (i.e. ecological constraints) and access to breeding vacancies in the natal or adjacent territories (i.e. benefits of philopatry). However, the majority of breeding unit-years comprised unassisted breeders, which suggests that pairs are selectively favoured under certain environmental or demographic conditions.
Permits

This research was conducted in accordance with the instructions and regulations issued by the Australian Bird and Bat Banding Scheme (Authority No. 2244) and approval was received to undertake colour marking (leg-bands).

This research was approved by the Deakin University Animal Experimentation Ethics Committee under approval number 2/98 “Conservation ecology of the White-browed Treecreeper in north west Victoria”.

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# Table of Contents

Acknowledgements i  
Abstract iii  
Permits vi  

Chapter 1  

Introduction 1  

1.1 The White-browed Treecreeper 2  
1.2 Conservation status of southern Australian avifauna 6  
1.3 Conservation status of the White-browed Treecreeper 8  
1.4 The White-browed Treecreeper as a case study 8  
1.5 Research objectives 9  
1.6 Thesis outline 10  

Chapter 2  

Factors affecting the distribution of the White-browed Treecreeper in north-west Victoria 12  

2.1 Introduction 13  
2.2 Methods 15  
   Study Area 15  
   Survey design 21  
   Bird censuses 22  
   Habitat assessment 22  
   Landscape variables 26  
   Data analysis 27  
2.3 Results 31  
   Habitat and vegetation characteristics 31  
   Distribution of the White-browed Treecreeper 38  
   Distribution of the White-browed Treecreeper: sub-models 40  
   Distribution of the White-browed Treecreeper: final model 42  
   Revised Model 47  

vii
Chapter 3

Factors affecting the occurrence of the White-browed Treecreeper in an agricultural landscape

3.1 Introduction

3.2 Methods
   Study Area
   Rationale
   Survey design
   Site characteristics
   Data analysis

3.3 Results
   Spatial characteristics of occupied and vacant sites
   Habitat characteristics of occupied and vacant sites
   Relative abundance of treecreepers and small parrots
   Principal components analysis of the landscape variables
   Logistic regression model of White-browed Treecreeper occurrence
   Logistic regression model of White-browed Treecreeper residency
   Hierarchical partitioning of White-browed Treecreeper occurrence

3.4 Discussion
   Minimum area requirements of the White-browed Treecreeper
   Influence of stock access on occurrence of the White-browed Treecreeper
   Effect of isolation on occurrence of the White-browed Treecreeper
   Efficacy of corridors in facilitating White-browed Treecreeper movement
   Permeability of the landscape to White-browed Treecreeper movement
   Conclusions
Chapter 4

Habitat use by the White-browed Treecreeper during the non-breeding season

4.1 Introduction

4.2 Methods

   Study sites
   Censuses of the White-browed Treecreeper
   Habitat assessments
   Data analysis

4.3 Results

   Occurrence of White-browed Treecreepers
   Use of edge plots
   Use of Black Box and mallee
   Relationships among habitat plots
   Habitat use by the White-browed Treecreeper

4.4 Discussion

   Factors affecting habitat use by the White-browed Treecreeper
   Spatial variation in habitat use
   Adaptive significance of habitat use
   Conclusions

Chapter 5

Habitat use at multiple spatial scales

5.1 Introduction

5.2 Extent and grain

5.3 Contrasting effects at contrasting scales

5.4 Framework for scale dependence

5.5 Management implications of scale dependence
Chapter 6
Social organization, survival and breeding strategy of the White-browed Treecreeper at Yarrara Flora and Fauna Reserve, north-west Victoria

6.1 Introduction

6.2 Methods
   Study area
   Trapping and colour-banding
   Group composition
   Survival
   Territoriality

6.3 Results
   Group composition and cohesion
   Sex ratio
   Survival
   Territoriality
   Territory size
   Relationship between group size and territory size

6.4 Discussion
   Breeding strategy
   Survival
   Territoriality
   Territory size
   Conclusions

Chapter 7
Selection of nest sites by the White-browed Treecreeper in north-west Victoria

7.1 Introduction

7.2 Methods
   Description of nest sites
   Selection of nest sites
   Are suitable hollows limiting?
Chapter 8


8.1 Introduction 238

8.2 Methods 239
   Duration of nesting stages 239
   Nesting behaviour 240
   Data analysis 243

8.3 Results 244
   Courtship 244
   Breeding phenology 244
   Nest construction 247
   Copulation 247
   Egg laying 248
   Incubation 248
   Nestlings 255
   Post-fledging 278
   Sweeping 279

8.4 Discussion 279
   The significance of multi-broodedness 279
   Duration of nesting 283
   Diet 284
   Provisioning rates among Australian treecreepers 285
Chapter 9

Effect of helpers on reproductive success of the White-browed Treecreeper

9.1 Introduction

9.2 Methods
   Field methods
   Reproductive success
   Productivity
   Components of productivity
   Potential correlates of reproductive success
   Data analysis

9.3 Results
   Reproductive success
   Productivity
   Components of productivity
   Breeding strategy and the success of second broods
   Causes of nest failure and brood reduction
   Natal dispersal
   Parental experience and reproductive success
   Variation in territory quality
   Models of the effect of potential correlates of fledgling productivity
   Effect of breeding strategy on laying date

9.4 Discussion
   Reproductive success of the White-browed Treecreeper
   Effect of helpers on reproductive success
   Relationship between climate, laying date and effect of helpers
   How do helpers increase reproductive success?
   Conclusions
Chapter 1

Introduction
1.1 The White-browed Treecreeper

This thesis is about White-browed Treecreepers: where they live, how they make their living, and how they reproduce. The White-browed Treecreeper *Climacteris affinis* Blyth 1864 is a member of the Climacteridae, an endemic Australo-Papuan family. The Climacteridae are believed to have descended from the oldest dichotomy in the superfamily Menuroidea, which also includes the lyrebirds, scrub-birds and bowerbirds (Sibley *et al.* 1984). However, the phylogeny of the Climacteridae baffled taxonomists for much of the twentieth century. They were formerly included in the nuthatch family (Sittidae), and then aligned with the European and North American tree creepers of the family Certhiidae and the Rhabdornithidae creepers of the Philippines, due to their likeness in morphology and habits (Mayr & Amadon 1951, Keast 1957, Steinbacher *et al.* 1973). Mayr (1963) separated the Australian treecreepers into their own family, Climacteridae, and suggested they were most closely related to the genera *Acanthiza*, *Sericornis* and *Gerygone*. Harrison (1969a) disagreed, concluding “honeyeaters (Meliphagidae) are the most likely group to have given rise to the Australian treecreepers”.

Meanwhile, disagreement surrounded the classification of species within the genus *Climacteris* (Howe 1921, Mathews 1923, Keast 1957, Noske 1982a, Parker 1982). It was not until the development of molecular techniques that the cladistic relationships of the Climacteridae were clarified, with seven species of Climacteridae now recognized in two genera (Sibley *et al.* 1984). The genus *Cormobates* includes the White-throated Treecreeper *Cormobates leucophaea* and the only species outside Australia, the Papuan Treecreeper *Cormobates placens*. The Brown Treecreeper *Climacteris picumnus*, Rufous Treecreeper *Climacteris rufa* and Black-tailed Treecreeper *Climacteris melanura* comprise one species group within *Climacteris*. The White-browed Treecreeper and its most closely related congener, the Red-browed Treecreeper *Climacteris erythrops*, are assigned to a second species group.

All Climacteridae species are similar in size, morphology and, in particular, foraging behaviour, from whence they derive their common name. Treecreepers characteristically forage by hopping or “creeping” up the trunks and along the branches of trees, feeding on insects taken from on and under the bark. Almost without exception, they creep from low on the tree to its higher branches, then progress to the next tree via a short, diagonal flight. The Brown Treecreeper and
Rufous Treecreeper also forage extensively on the ground and fallen logs (Noske 1979, Luck et al. 2001). Treecreepers are confined to woodlands and forests because of their specialized foraging mode and dependence on hollows for nesting. Unlike woodpeckers, treecreepers are not able to excavate their own cavities for roosting and nesting and therefore rely on naturally-occurring hollows. Yet, within these broad structural requirements they occupy a range of habitats including rainforest, wet and dry *Eucalyptus* sclerophyll forests, open savannah woodland (mixed *Callitris* / *Casuarina* / *Eucalyptus* species), mallee (*Eucalyptus* spp.) and mulga scrub (*Acacia aneura*) (Keast 1957, Ford 1971, Noske 1979, 1982a, Cody 1994).

The White-browed Treecreeper, or *Tiru-tiru* as it is known to indigenous Australians (Higgins et al. 2001), is the only member of the Climacteridae adapted to arid environments (Keast 1957). Its biogeographic range extends across the arid and semi-arid zone of southern Australia (Blakers et al. 1984) (Fig. 1.1). Two subspecies of *affinis* are recognized (MacDonald 1969, Blakers et al. 1984): *C. a. superciliosa* occurs from north of the wheatbelt district in Western Australia through the lower Western Deserts region to northern South Australia and southern Central Australia. There is a gap in its distribution north of Spencer’s Gulf, with *C. a. affinis* replacing *superciliosa* in the east of the continent. Here, it is located in a broad band extending from south-central Queensland, south-west through western New South Wales and into north-west Victoria and adjacent parts of South Australia (Fig. 1.1).
Figure 1.1. Biogeographic distribution of the White-browed Treecreeper showing the separation of the sub-species *C. a. affinis* and *C. a. superciliosa*. The study area for this research program is indicated.

The White-browed Treecreeper is the smallest member of the Climacteridae [length 14.5 cm, wingspan c. 22 cm, weight 20–25 g (Higgins *et al.* 2001; *JQR unpublished data*)]. Like all treecreepers, it is sexually dichromatic, with females distinguished by a rufous stripe bordering the upper anterior surface of the white supercilium, and distinctive black and white streaks on the lower neck and breast that are tinged with rufous (Fig. 1.2). The male has an entirely white supercilium and the upper breast and neck are grey (Fig. 1.2). The White-browed Treecreeper emits a shrill insect-like *chirrup* and birds foraging in close proximity often exchange a soft *seep seep* contact call (Higgins *et al.* 2001; *personal observation*).
Introduction

(a) Female

(b) Male

Figure 1.2 Head and upper body of the (a) female and (b) male White-browed Treecreeper. Note the rufous above the eye and on the upper breast in the female compared with the all white ‘eye-brow’ and grey throat and upper breast in the male.
Foraging usually occurs alone or in small family groups (Harrison 1974, Blakers et al. 1984), though individuals may join other insectivores in mixed-species foraging assemblages during winter (personal observation). Throughout much of its range, the White-browed Treecreeper inhabits mulga *Acacia aneura* woodland (Marshall 1932, Harrison 1974, Cody 1994, Recher & Davis 1997) but it is also regularly reported from Belah *Casuarina pauper* woodland (Howe 1921, Ford 1971). In north-west Victoria, it is are purportedly confined to Belah and Slender Cypress-pine *Callitris gracilis* – Buloke *Allocasuarina leuhmanni* woodlands (Emison et al. 1987, LCC 1987), although early reports also recorded it in Sandalwood *Myoporum platycarpum* and mixed shrubland (MacGillivray 1910, Howe 1921). White-browed Treecreepers are sedentary and there have been no reports of long-distance movements or seasonal migration (Emison et al. 1987). Breeding occurs in the austral spring and early summer (Nest Record Scheme 2000).

There has not been any previous research dedicated specifically to the White-browed Treecreeper. Apart from the rudimentary outline of the species given above, we know very little about the White-browed Treecreeper. The information that is available is derived from large-scale surveys of distribution and coarse habitat associations (e.g. Hall 1974, Blakers et al. 1984, LCC 1987, Cody 1994) or incidental observations of questionable scientific rigour. The data on the distribution and vegetation associations of the White-browed Treecreeper in Victoria requires verification, and many facets of its ecology and biology are largely unexplored. Data pertaining to its population demographics, social organization, breeding biology, nest-site preferences, micro-habitat selection, foraging behaviour, and response to landscape modification are limited or non-existent. Filling in these knowledge chasms is the subject of this thesis.

### 1.2 Conservation status of southern Australian avifauna

General statistical patterns across a range of spatial and temporal scales, taxa and environments often reveal macroecological phenomena that provide insights into the processes and functioning of ecological systems (Brown 1999). An example is the insidious decline in bird populations in southern Australia since European colonization (Saunders 1989, Robinson 1991, Saunders et al. 1993, Barrett et al.)
In 1994, Bennett & Ford 1997, Recher 1999, Reid 1999, 2000). There have been several recent reviews of the threatening processes affecting Australian birds (e.g. Robinson & Traill 1996, Garnett & Crowley 2000, Ford et al. 2001). The inescapable pattern that these studies reveal is the link between habitat loss and species decline and local extinction: *viz a viz*, the single most destructive activity for biodiversity is wholesale land clearing (Australian and New Zealand Environment Conservation Council 2001). More than 82% of all mainland Australian and Tasmanian bird taxa have been affected by land clearance, and it continues to be a major threat for half of all taxa (Garnett & Crowley 2000). The impact of land clearing is especially pernicious in temperate and subtropical woodlands (Robinson & Traill 1996, Bennett & Ford 1997, Reid 2000, Major et al. 2001), which provide habitat for over 40% of those taxa affected by habitat loss (Garnett & Crowley 2000). A similar plight confronts the avifauna of arid and semi-arid woodlands (Reid & Fleming 1992), given the extent of landscape modification in this zone (Graetz et al. 1995, Morton et al. 1995, MCMA 2000).

The simplest way in which land clearing impinges on animal populations is through the loss of individuals in proportion to the extent of habitat loss (Bennett 1999). Depending on the amount of habitat removed, this may result in the local extinction of some species purely from the effects of random sampling (Connor & McCoy 1979, Haila et al. 1993), and species with low population density will be most at risk (Bolger et al. 1991, Gaston 1994, Connor et al. 2000). A trilogy of associated processes exacerbates the effects of pure habitat loss. The first of these is *selective clearing*. Typically, native vegetation on fertile soils and in accessible locations is cleared first and most extensively, resulting in the disproportionate loss of some habitats. Habitat specialists within selectively cleared vegetation are particularly susceptible to population decline and extinction, even at relatively low levels of habitat loss. Second, the effects of *habitat fragmentation*, that is, the subdivision of tracts of habitat into smaller remnants with an increase in isolation of remnants, may increase the rate of decline of some species over the effects of habitat loss alone (e.g. Newmark 1991, Andren 1994, Bennett 1999). Finally, habitat loss often precipitates a *decline in habitat quality* for individual species, and ecological communities in their entirety, through disturbance to ecosystem processes, biotic invasions and changes in species interactions (Saunders et al. 1991, Hobbs 1993, Ford et al. 2001, Major et al. 2001). The relative importance of these three processes on population
extinction, and the extent of habitat loss that must occur before they take effect, are contentious issues in conservation biology (Andren 1994, Fahrig 1997, 2001, MacNally 1999, Trzcinski et al. 1999, Villard et al. 1999). The effect of each of these components of habitat change on the White-browed Treecreeper will be considered in the course of this thesis.

1.3 Conservation status of the White-browed Treecreeper

Research on the White-browed Treecreeper assumes greater urgency in the context of its conservation status. In 1996, the Victorian population of the White-browed Treecreeper was listed as a threatened taxon under the Flora and Fauna Guarantee Act 1988 (Walker 1996). This listing represented a timely and prudent application of the precautionary principle in conservation management but lacked hard scientific data for a regional decline in range or abundance. However, in light of the mounting evidence of the effects of habitat loss on animal populations cited above, a persuasive argument for its listing was that 90% of its putatively preferred habitat of Belah and Pine-Buloke woodlands has been cleared (LCC 1987, Walker 1996, MCMA 2000). Further recognition that the species is vulnerable has followed. Reid (1999) listed the White-browed Treecreeper as one of two species of “special concern” in his diagnosis of birds in the sheep-wheat belt of New South Wales. Garnett and Crowley (2000) classified the eastern sub-species C. a. affinis as “near threatened”, due to a significant and continuing decline in abundance in over 50% of its former range and estimated the entire population to be about 20,000 breeding birds. They also commented that it is patchily dispersed throughout its range, confined largely to fragments of remaining habitat, and is likely to persist only in low densities where it is present.

1.4 The White-browed Treecreeper as a case study

The White-browed Treecreeper has many attributes that suggest it would be educative as a case study that addresses conservation issues faced by many woodland species threatened by human activities. First, it is listed as a threatened species, which infers that it is sensitive to human-induced changes in the landscape. Second,
it is representative of a community (i.e. semi-arid woodlands / temperate woodlands) that is in decline and threatened by many processes, especially habitat loss and fragmentation. Therefore, the results of this study may be applied to other species with similar habitat requirements. Third, as a group, treecreepers may be particularly sensitive to habitat loss and changes in the landscape (e.g. Noske 1991, Barrett et al. 1994, Walters et al. 1999). Thus, treecreepers have potential to be used as focal species (sensu Lambeck 1997) for particular threatening processes. It is anticipated that the results of this research would have implications for the conservation of the wider semi-arid woodland community, and passerine bird conservation in general.

1.5 Research objectives

Effective conservation action for threatened species requires sound ecological knowledge (Bennett 1987, Fahrig & Merriam 1994, Simberloff 1994, Ford et al. 2001). Hence, the general aim of this thesis is to provide the ecological foundations necessary for informed decision-making in the conservation management of the White-browed Treecreeper. Two key objectives were identified that would contribute significantly to achieving this aim:

1. To identify the biophysical and habitat characteristics of the landscape that affect the distribution of the White-browed Treecreeper across a range of spatial scales; and

2. To clarify the demographic characteristics and breeding behaviour, and measure the reproductive success, of a purportedly viable population of the White-browed Treecreeper.

The first objective is concerned with the concept of habitat selection in a multi-scale hierarchy, and the second objective pertains to population demography and breeding biology. Clearly, effective conservation management hinges not only on both components in isolation, but on the synergy and interaction between habitat selection and breeding biology.
1.6 Thesis outline

The concept of habitat selection at a range of spatial scales is addressed in the first part of the thesis (Chapters 2 – 5). An underlying theme through this part of the research is to assess the sensitivity of the White-browed Treecreeper to human-induced changes in the landscape. Specifically, the principal research questions posed are:

- What is the current distribution of the White-browed Treecreeper in Victoria and which factors affect its occurrence at a regional scale? (Chapter 2)

- What are the spatial characteristics that influence patch occupancy in a local network of habitat remnants? How influential is landscape connectivity in facilitating patch occupancy? (Chapter 3)

- Which habitat and vegetation attributes affect fine-scale habitat selection within occupied patches? (Chapter 4)

Chapter 5 is a synthesis of Chapters 2 – 4 with an emphasis on the implications of habitat selection across a range of spatial scales for the conservation management of the White-browed Treecreeper.

The second part of the thesis (Chapters 6 – 10) relates to questions of demography and breeding parameters. The main research topics in this section are:

- To describe the social organization (e.g. territoriality, group composition) and basic demographic characteristics (e.g. adult survival, sex ratio) of a self-sustaining White-browed Treecreeper population. (Chapter 6)

- What factors influence nest-site selection and are nest-sites limiting population growth? (Chapter 7)

- To document the reproductive biology and nesting behaviour of the White-browed Treecreeper, including an exploration of strategies of parental care. In what way might differences in parental care affect the fitness of the young and the parents? (Chapter 8)
• To quantify reproductive success in a population of the White-browed Treecreeper and examine the effect of breeding strategy (i.e. breeding pairs with cooperative helpers versus unassisted pairs) on reproductive productivity? (Chapter 9)

An overview of Chapters 6 – 9 is presented in Chapter 10. The theme of this synthesis is to evaluate the factors that may have limited, or promoted, the incidence of cooperative breeding in the White-browed Treecreeper, and evaluate the selective advantage offered by the respective breeding strategies.

The final chapter draws together the major findings of the research (Chapter 11). The implications of these findings for management of the White-browed Treecreeper are discussed with particular reference to the synergies between anthropogenic landscape modification, habitat selection and requirements for successful breeding. Priorities for further research are highlighted.
Chapter 2

Factors affecting the distribution of the White-browed Treecreeper in north-west Victoria
2.1 Introduction

Anthropogenic destruction of natural habitats threatens the conservation of biological diversity around the globe (Groombridge 1992, Olsen & Dinerstein 1998). The conversion of native vegetation to human-dominated land-uses produces landscapes in which suitable habitat for many species exists only as discrete patches of remnant native vegetation embedded in a matrix of modified land (Diamond 1975a, Sullivan & Shaffer 1975, Forman et al. 1976). This imperils biodiversity by reducing the absolute amount of habitat available for wildlife (habitat loss), transforming the spatial configuration of remaining habitat (habitat fragmentation) and distorting the relative abundance of vegetation communities through preferential clearing of particular vegetation types (habitat composition) (Bennett 1999, Ford et al. 2001).

The extent of biodiversity loss in particular patches of habitat is often correlated with patch-specific spatial characteristics, such as size (Fahrig & Merriam 1994, Bender et al. 1998, Connor et al. 2000), shape (Gates & Gysel 1978, Major et al. 1999a) or isolation (Fahrig & Merriam 1985, Dunning et al. 1995, Collinge 1996). Processes that reduce the quality of remnant vegetation as wildlife habitat (e.g. grazing, altered fire regimes, loss of mature trees) are often associated with, or closely follow, the agents of habitat loss. Further, the disintegration of ecosystem processes in fragmented landscapes (Saunders et al. 1991, Hobbs 1993) may compound the decline in habitat quality, exacerbating the impacts of habitat loss on wildlife.

However, the composition of faunal communities is not determined solely by patch-specific attributes. Factors operating at the landscape-scale also exert significant influence on species diversity, in individual patches and on a regional scale (e.g. Saunders 1989, Bennett 1990, Hinsley et al. 1995, Trzcinski et al. 1999). In particular, the structure and composition of the landscape surrounding remnant habitat has implications for the capacity of animals to move through the landscape (Saunders 1990, Bierregaard et al. 1992, Forman 1995a, Lindenmayer et al. 1999). This is encapsulated in the concept of landscape connectivity (Forman & Godron 1981, Noss 1983).

Landscape connectivity encompasses both structural connectivity, defined by the physical arrangement of landscape elements, and functional connectivity, which relates to the ease with which individuals can move through the matrix (Taylor et al. 2001).
1993, Forman 1995b). Functional connectivity is dependent on species attributes, such as dispersal strategy, dispersal mortality, vagility and inclination to cross patch boundaries, as well as the temporal and spatial scale of the system under investigation (Wiens et al. 1985, Temple 1990, Wiens 1996, Ruckelshaus et al. 1997, Tischendorf & Fahrig 2000). The extent of habitat fragmentation, that is, the amount of habitat in a landscape, isolation of patches and the configuration of remaining habitat, also influences functional connectivity. Moreover, the nonlinear relationship between habitat loss and fragmentation (With et al. 1997, Hargis et al. 1998) may lead to critical thresholds of habitat loss for particular species, beyond which functional connectivity cannot be maintained (Andrén 1994, With & Crisp 1995, Jansson & Angelstam 1999, With and King 1999). Recognition of such thresholds would greatly assist management of threatened species because they may indicate conditions under which the regional persistence of the species is compromised.

Conservation biologists are cognizant of the need to reconcile empirical evidence of species decline with sound ecological theory (Caughley 1994). One way in which this is being addressed is through the convergence of metapopulation theory (Levins 1969, Hanski & Gilpin 1991a, 1997) and population biology (Shaffer 1981, Gilpin & Soule 1986) into models that incorporate spatial and demographic characteristics of populations (e.g. Karieva 1990, Dolman & Sutherland 1994, Doak 1995, Turner et al. 1995, Hanski et al. 2000, McCarthy et al. 2000). However, there is still a gulf between spatial theory and its application to conservation problems in fragmented landscapes (Hanski 1998, Harrison & Bruna 1999, Debenski & Holt 2000). Harrison and Bruna (1999) suggest that the way forward is to continue seeking facts and patterns in systems of conservation concern and to build on the ever-increasing body of knowledge from which generalized theories grow. From a pragmatic perspective, spatial theory may provide insights into the agents of decline and therefore expedite effective conservation management.

The White-browed Treecreeper population in north-west Victoria is one such system of conservation concern. Ninety percent of the species’ putatively preferred habitat, Belah and Pine-Buloke woodlands, has been cleared for agriculture in north-west Victoria (LCC 1987, MCMA 2000). Consequently, Belah and Pine-Buloke woodlands are now severely depleted and highly fragmented, with only a handful of expansive tracts (> 500 ha) remaining in the region. Thus, although the primary
threatening process is easy to identify (i.e. habitat loss), the ecological basis and mechanistic functioning of habitat loss and fragmentation on the White-browed Treecreeper population are poorly understood, thus hampering management actions. Information on the White-browed Treecreeper’s current distribution, abundance, habitat preferences or extent of decline in north-west Victoria is limited, and much of the existing information is anecdotal in nature (LCC 1987, Walker 1996). To fill this knowledge-gap, this chapter presents the results of the first empirical study designed to identify the factors that determine the distribution and occurrence of the White-browed Treecreeper in north-west Victoria. This is achieved by:

- describing the distribution of the White-browed Treecreeper in north-west Victoria, thus providing a baseline from which future change can be measured.
- developing models of patch occupancy using logistic regression and hierarchical partitioning, based on vegetation floristics, woodland structure and spatial characteristics of landscape pattern.
- interpreting patch occupancy in the context of spatial theory.

### 2.2 Methods

**Study Area**

The study area covered the historical range of the White-browed Treecreeper in Victoria, as determined from records in the Atlas of Victorian Wildlife (DNRE 1997a), an area of approximately 22,400 km² (Fig. 2.1). The climate in north-west Victoria is semi-arid (mean annual rainfall: 250 to 350 mm). Rainfall is irregular between years and between seasons. There are more days with rain in winter (June – August) but heavy rainfall may occur during occasional summer storms. Winters are mild (mean maximum temperature: 15° - 17° C), although overnight temperatures may fall below freezing, and summers (December – February) are hot, with daytime maximum temperatures regularly exceeding 35° C.
Figure 2.1. Historical records of the White-browed Treecreeper in north-west Victoria, collated into 5' cells of latitude and longitude (Source: Atlas of Victorian Wildlife, DNRE 1997a). The survey districts used in this survey are also indicated.
Altitude varies from 100 m ASL in the south to less than 50 m ASL in the north of the study area. Sand dunes are the main physiographic landform in the region, though small alluvial plains occur along streams and larger plains impinge from the east. Topographic relief is low throughout, seldom exceeding 10 m, although the larger dunes may reach heights of 40 m (LCC 1987).

The dune-fields are dominated by mallee communities (e.g. Chenopod mallee – characterized by Oil Mallee *Eucalyptus oleosa*, White Mallee *E. gracilis*, Red Mallee *E. calycogona* and Dumosa Mallee *E. dumosa*) that typically have a low height profile, high stem density (due to the multi-stemmed growth form that defines mallee) and a sparse understorey of shrubs and hummock grasses (LCC 1987).

Extensive tracts of heath or scrub communities, which consist of a low, dense shrub layer (e.g. Desert Banksia *Banksia ornata*, Broombush *Melaleuca uncinata*, or Green Tea-tree *Leptospermum coriaceum*) in which trees are absent or infrequent are also common on the dunes or sandy plains.

Belah woodland occurs on the north-south trending sandstone ridges in the north of the study region. This community has an overstorey of widely-spaced Belah *Casuarina pauper* trees that may reach 25 m in height, with a diverse sub-canopy (5 – 10 m) that may include Sugarwood *Myoporum platycarpum*, Hooked Needlewood *Hakea tephrosperma*, Cattlebush *Alectryon oleifolia*, Leafless Ballart *Exocarpos aphyllus* and Twin-leaf Emu-bush *Eremophila oppositifolia* (Fig. 2.2a). The upper shrub layer (2 – 5 m) is commonly dominated by Desert Cassia *Senna artemisioides*, Narrow-leaf Hop-bush *Dodonaea angustissima* or Sweet Quandong *Santalum acuminatum*. Numerous Chenopodiaceae (e.g. Spiny Fan-flower *Scavola spinescens*, Hedge Saltbush *Rhogodium spinescens*) and daisy-bushes (e.g. Mueller Daisy-bush *Olearia muelleri*, Pimelea Daisy-bush *O. pimeleoides*) are widespread in the well-developed lower shrub layer (~1 m).

Buloke *Allocasuarina luehmannii* and/or Slender Cypress-pine *Callitris gracilis* are the dominant overstorey species (15 – 20 m high) on the lunettes (smooth crescent-shaped dunes on the eastern side of existing or ancient lake basins) that are prevalent in southern parts of the study area (LCC 1987). Pine-Buloke woodland (Fig. 2.2b) has a more open understorey (2 – 5 m) community of wattles (e.g. Small Cooba *Acacia ligulata*, Umbrella Wattle *A. oswaldii*, Mallee Wattle *A. montana*, Grey Mulga *A. brachybotrya*) and other shrubs (e.g. Weeping Pittosporum *Pittosporum*...
phillyreoides, Moonah Melaleuca lanceolata) than Belah woodland. Further, Pine-Buloke woodlands are characterized by a grassy ground cover rather than a low shrub layer, although introduced annuals have largely replaced the native tussock grasses and herbs in most remnants (LCC 1987).

Other types of woodland scattered through the region are mainly confined to one or two districts. Along the watercourses and floodplains of the Wyperfeld district, Black Box Eucalyptus largiflorens woodlands are common (Fig. 2.2c). These typically have a high stem density, no shrub layer and a grassy understorey. Gypseous woodland, consisting of Sugarwood and Cattlebush, occur on the Copi Plains evaporative basin in the far north-west of the study area (Fig. 2.2d). Savanna woodland of scattered Slender Cypress-pine, Cattlebush or larger mallee species are present on the plains of the Copi Plains, Pink Lakes and Timberoo districts.

North-west Victoria is sparsely populated but human activities have dramatically altered the natural vegetation (LCC 1987). Belah and Pine-Buloke woodlands were preferentially cleared for crop cultivation because the loamy soils on which they grow are more fertile than the sand dunes of the surrounding mallee and heath. Cypress-pine was also harvested for timber. Consequently, Belah and Pine-Buloke woodlands are now confined to relatively small and isolated patches, apart from a few large tracts in conservation reserves. Over-grazing, fire and weed invasion have further decreased the naturally low regeneration rates of Belah and Pine-Buloke woodlands, reducing the extent and quality of many woodland remnants (Chesterfield & Parsons 1985). Belah and Pine-Buloke woodlands are now so depleted and degraded that they have been classified as endangered vegetation communities (MCMA 2000). Termination of natural flooding regimes and excessive grazing has degraded Black Box woodlands, and clearing, over-grazing and weed invasion have severely depleted and disturbed Gypseous and Savanna woodlands (MCMA 2000).
(a) Belah woodland (Mallanbool Flora and Fauna Reserve)

(b) Pine-Buloke woodland (Timberoo Flora and Fauna Reserve)

*Figure 2.2.* Typical woodland communities in north-west Victoria.
Regional distribution

(c) Black Box woodland (Wyperfeld National Park)

(d) Gypseous woodland (predominantly Cattlebush) (Murray-Sunset National Park - Copi Plains area)

Figure 2.2. (continued) Typical woodland communities in north-west Victoria.
Survey design

The floristic composition and size of all patches of remnant woodland in the study area were estimated from 1:100,000 maps of eco-vegetation class (EVC) (DNRE 1997b). Only patches larger than 50 ha were considered, in order to decrease the probability that White-browed Treecreepers were not detected in a patch because of patch size limitations, which were not of primary interest in this survey.

Sampling effort was stratified by geographic location, woodland type and patch size. Geographic location was divided into six districts that included most of the historic records of the White-browed Treecreeper (Fig. 2.1), plus some additional areas with anecdotal reports of White-browed Treecreeper occurrence, or ostensibly suitable woodland vegetation.

The second stratum was defined by woodland type. Selection of patches was weighted towards Belah and Pine-Buloke woodlands, as most records of the White-browed Treecreeper in Victoria are from these vegetation communities (Emison and Bren 1989, Robertson et al. 1989, DNRE 1997a). However, other types of woodland were surveyed in the districts in which they occurred (e.g. Gypseous, Savanna, Black Box). Other woodland types were included because the White-browed Treecreeper inhabits woodlands dominated by a variety of tree species in other parts of its range, such as Mulga Acacia aneura (Whitlock 1924, Ford 1971, Recher & Davis 1997), Sugarwood (Schodde 1957, Hobbs 1961), mallee (Terrill & Rix 1950, Condon 1951, 1962) and Black Box (MacGillivray 1924, Mack 1961). Dense mallee scrub and River Red Gum Eucalyptus camaldulensis forest were not considered because White-browed Treecreepers were not recorded in these communities in north-west Victoria when they were surveyed extensively in the 1980s (LCC 1987, Robertson et al. 1989).

The third stratum was patch size, categorized as small (50 – 150 ha), medium (150 – 400 ha) or large (> 400 ha). Many of the ‘cells’ in the stratified design (i.e. district X woodland type X patch size) were empty; that is, there were no patches that fulfilled the criteria. Where there was a surplus of appropriate patches, those to be surveyed were randomly selected. In total, 56 patches were surveyed.
**Bird censuses**

Searches for the White-browed Treecreeper were conducted using fixed-width line transects of 500 by 60 m (3 ha). Line transects are more time efficient and reliable than other census techniques for detection of inconspicuous species (Davies 1982, Arnold 1984). Survey effort within a patch was related to area because the primary objective was to determine the occupancy status of the White-browed Treecreeper, rather than measure species richness. The number of transects per patch followed a non-linear relationship, such that one transect was placed in patches of 50-150 ha, two in 151-250 ha, three in 251-450 ha, four in 451-850 ha, five in 851-1650 ha and six in >1651 ha. Transects were initially allocated according to area estimates from maps. However, after more accurate measures of area were obtained from ground-truthing or aerial photographs, it became clear that the distribution of transects sometimes differed from the desired relationship.

A total of 97 transects was distributed within the 56 woodland patches. Transects were positioned by randomly selecting cells from a grid of 25-ha cells superimposed over maps of the patches. Transects within the same patch were separated by a minimum of 500 m. Two rounds of censuses were completed: in June / July (austral winter) and in October – December (austral spring/summer) 1997. Censuses were conducted by walking slowly for 30 minutes along the transect mid-line between 0600 – 1200 during spring / summer, or at any time during the day in winter. All birds observed were recorded as either inside (< 30 m from the transect mid-line) or outside the transect (> 30 m). Aural records were considered to be outside the transect unless otherwise verified.

**Habitat assessment**

Quantification of woodland structure, tree species composition, shrub layer attributes and measures of habitat complexity for each transect was conducted using the point-centered quarter method (PCQM) (Mueller-Dombois & Ellenberg 1974) as a basis for habitat assessment. This is a plotless technique that utilizes point-to-plant distances in four ‘quarters’ at sampling points along a transect to quantify plant densities. In sparsely vegetated, aggregated and species-poor communities, such as the semi-arid woodlands encountered in this study, PCQM is more efficient, reliable
and robust than plot sampling or other distance methods (Mueller-Dombois & Ellenberg 1974, Bullock 1996).

Eleven sampling points were designated at 50 m intervals along each transect. Total tree density was calculated from the distance to the closest tree in each quarter at each sampling point, following the equations in Mueller-Dombois and Ellenberg (1974). Thus, each density estimate was derived from 44 point-to-tree distances. This was repeated for shrubs. Characteristics of each tree or shrub were recorded to quantify a range of habitat variables (Table 2.1). The density of dead standing trees (DST) was calculated using the nearest individual method at each sampling point (Mueller-Dombois & Ellenberg 1974) because the scarcity of dead trees on many transects precluded the consistent application of PCQM. These estimates are not reliable as absolute densities due to the small number of sampling points, but allow for comparisons between sites. Tree-species composition was interpreted using the importance value (IV) of each species (Mueller-Dombois & Ellenberg 1974, Villard et al. 1995) (Table 2.1). As IV is based on ratios rather than absolute values, it standardizes for density and dominance, thereby providing a direct comparison of relative species composition between transects that is independent of woodland structure.

A number of habitat complexity variables were measured within a 10-m radius circular plot at each sampling point (Table 2.1). For each variable, the mean value across the 11 sampling points was calculated for each transect. Within each circular plot, the proportional cover of each vegetation stratum was visually assessed using a semi-quantitative scale (0-1, 1-5, 5-25, 25-50, 50-75, >75%) (Table 2.1). The midpoint of the cover classes was used to estimate the mean percentage cover for each stratum per transect (Mueller-Dombois & Ellenberg 1974, Villard et al. 1995). The number of vegetation strata present was considered as a separate variable. Finally, the distance from each sampling point to the closest foliage of any type was estimated in eight directions (successive 45° rotations) through a PVC tube (40 cm long by 4 cm diameter) held parallel to the ground at eye height. A ‘foliage index’ was then calculated as the sum of the distances, in which the amount of foliage, or the “bushiness” of the understorey, is inversely correlated to the index.

Two avian factors were considered, namely the mean abundance of the Brown Treecreeper and Yellow-throated Miner *Manorina flavigula*. Mean abundance per
transect (3 ha) was estimated as the total number of individuals detected “on-transect” from both survey rounds, divided by two. The congeneric Brown Treecreeper is potentially a direct competitor of the White-browed Treecreeper for food resources and nesting hollows, and the Yellow-throated Miner is a large aggressive honeyeater that may exclude other species from its territory.
<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Transformation</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Woodland structure</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree density (stems ha(^{-1}))</td>
<td>Number of tree stems (&gt; 12 cm DBH) per ha, derived from the 44 point-to-tree distances.</td>
<td>Log(_{10})</td>
</tr>
<tr>
<td>Tree DBH (cm)</td>
<td>Mean diameter at breast height of the 44 trees used for density estimation; measured using a calibrated DBH tape.</td>
<td>None</td>
</tr>
<tr>
<td>Tree height (m)</td>
<td>Height classes: 0-2 m, 2-5 m, 5-10 m, 10-15 m and 15-20 m. Mean height calculated from class midpoint.</td>
<td>None</td>
</tr>
<tr>
<td>Canopy cover (%)</td>
<td>Percent foliage cover of tree canopy (&gt; 5 m).</td>
<td>Arcsine</td>
</tr>
<tr>
<td>Hollows (%)</td>
<td>Proportion of the 44 trees used for density estimation that contain obvious hollows.</td>
<td>Arcsine</td>
</tr>
<tr>
<td>DST density (stems ha(^{-1}))</td>
<td>Number of dead standing trees (&gt; 12 cm DBH) per ha, derived from 11 point-to-tree distances.</td>
<td>Log(_{10})</td>
</tr>
<tr>
<td><strong>Tree species composition</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Importance Value (IV)</td>
<td>Sum of the relative density and relative dominance per species, where relative density is the percentage of stems, and relative dominance the percentage of total basal area represented by each species. IV calculated for Belah, Buloke, Slender Cypress-pine, Cattlebush, Sugarwood, Black Box, mallee, and all other species combined.</td>
<td>None</td>
</tr>
<tr>
<td><strong>Shrub layer attributes</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shrub density (stems ha(^{-1}))</td>
<td>Number of shrubs (&gt; 0.5 m high) per ha, derived from the 44 point-to-shrub distances.</td>
<td>Log(_{10})</td>
</tr>
<tr>
<td>Shrub height (m)</td>
<td>Mean height of the 44 shrubs used for density estimation; measured with 1-m ruler or calibrated 3-m pole.</td>
<td>None</td>
</tr>
<tr>
<td>Shrub width (m)</td>
<td>Mean diameter of foliage (measured across widest axis) per shrub.</td>
<td>Log(_{10})</td>
</tr>
<tr>
<td>Shrub cover (%)</td>
<td>Percent foliage cover of low (0.5-2 m) and high shrub (2-5 m).</td>
<td>Arcsine</td>
</tr>
<tr>
<td>Foliage index (score)</td>
<td>Mean of the foliage index score (see text) from the 11 sampling points.</td>
<td>Log(_{10})</td>
</tr>
<tr>
<td><strong>Habitat complexity</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of strata</td>
<td>Mean number of vegetation strata [ground layer, low shrub, high shrub, low canopy, high canopy] per sampling point.</td>
<td>None</td>
</tr>
<tr>
<td>Log density (# ha(^{-1}))</td>
<td>Number of fallen logs (&gt; 8 cm diameter) per ha.</td>
<td>None</td>
</tr>
<tr>
<td>Bare ground (%)</td>
<td>Percent of ground with exposed soil, sand, litter, moss, bryophyte or lichen.</td>
<td>Arcsine</td>
</tr>
<tr>
<td>Ground cover (%)</td>
<td>Percent cover of grass, non-woody herbs and forbs &lt; 0.5 m high.</td>
<td>Arcsine</td>
</tr>
<tr>
<td>Stump density (# ha(^{-1}))</td>
<td>Number of stumps resulting from tree cutting per ha.</td>
<td>Log(_{10})</td>
</tr>
<tr>
<td>Avian factors (inds. ha(^{-1}))</td>
<td>Mean abundance of the Brown Treecreeper and the Yellow-throated Miner.</td>
<td>BTC: (\sqrt{4})</td>
</tr>
</tbody>
</table>
### Landscape variables

For each of the 56 habitat patches, five landscape variables were measured, sourced from aerial photographs (scale: 1:50,000), EVC maps (scale: 1:100,000) and ground measurements (Table 2.2). ‘Patch Size’ was the area of discrete woodland, excluding other forms of natural vegetation (e.g. mallee scrub, heathland, grassland). In mosaics of woodland of different floristic composition, Patch Size included only the focal woodland type. ‘Belah / Buloke Woodland’ measured the area of Belah or Pine-Buloke woodland as a percentage of a 100 km² landscape centred on the focal patch. Three indices of patch isolation were measured: a) ‘Mainland Isolation’ – distance to the nearest patch of native vegetation of any type greater than 100 ha; b) ‘Nearest Neighbour’ - mean distance to the three closest woodland patches of any size; and c) ‘Demographic Isolation’ - distance to the nearest patch known to be occupied by the White-browed Treecreeper (from census results and incidental observations).

Each patch was assigned to one of four ‘Landscape Context’ categories based on the land use surrounding the majority of the patch: 1 – agriculture; 2 – open grassland / dry lakebeds; 3 – native woody vegetation (non-woodland); and 4 – woodland of different tree species composition to the focal patch.

### Table 2.2. Mean (± s.e.) and range in values (in parentheses) of landscape variables for woodland patches within each district.

<table>
<thead>
<tr>
<th></th>
<th>Timberoo</th>
<th>Wyperfeld</th>
<th>Yarrara</th>
<th>Women</th>
<th>Pink Lakes</th>
<th>Copi Plains</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. patches</td>
<td>8</td>
<td>12</td>
<td>8</td>
<td>4</td>
<td>14</td>
<td>10</td>
<td>56</td>
</tr>
<tr>
<td>Patch Size (ha)</td>
<td>302 ± 183 (1522)</td>
<td>257 ± 74 (801)</td>
<td>423 ± 214 (1842)</td>
<td>198 ± 22 (94)</td>
<td>171 ± 46 (548)</td>
<td>282 ± 68 (589)</td>
<td>266 ± 45 (1846)</td>
</tr>
<tr>
<td>Belah / Buloke Woodland (%)</td>
<td>5.4 ± 2.1 (17.5)</td>
<td>15.3 ± 2.9 (26.5)</td>
<td>7.2 ± 1.9 (16.0)</td>
<td>4.0 ± 0.3 (1.0)</td>
<td>3.6 ± 0.6 (6.3)</td>
<td>2.8 ± 0.8 (5.3)</td>
<td>6.8 ± 1.0 (27.8)</td>
</tr>
<tr>
<td>Mainland Isolation (km)</td>
<td>2.4 ± 0.6 (5.2)</td>
<td>0.7 ± 0.4 (4.2)</td>
<td>0.5 ± 0.3 (2.4)</td>
<td>1.8 ± 0.8 (3.8)</td>
<td>1.0 ± 0.4 (4.0)</td>
<td>0.6 ± 0.2 (2.0)</td>
<td>1.0 ± 0.2 (6.0)</td>
</tr>
<tr>
<td>Nearest Neighbour (km)</td>
<td>4.6 ± 1.1 (8.9)</td>
<td>1.6 ± 0.3 (3.1)</td>
<td>2.7 ± 0.4 (2.8)</td>
<td>4.2 ± 0.9 (3.9)</td>
<td>2.1 ± 0.3 (4.2)</td>
<td>3.7 ± 0.6 (6.5)</td>
<td>2.9 ± 0.3 (9.8)</td>
</tr>
<tr>
<td>Demographic Isolation (km)</td>
<td>6.8 ± 2.9 (24.0)</td>
<td>8.2 ± 3.3 (29.4)</td>
<td>1.0 ± 0.4 (2.8)</td>
<td>63.1 ± 1.5 (6.3)</td>
<td>18.4 ± 2.6 (34.2)</td>
<td>26.8 ± 2.2 (21.8)</td>
<td>16.8 ± 2.3 (66.8)</td>
</tr>
</tbody>
</table>
**Data analysis**

**Habitat characteristics**

In the larger patches, habitat and vegetation variables were averaged across multiple transects, such that each patch contributed a single datum to the analysis for every variable. Floristic composition of the tree community was summarized in two ways. First, the Importance Values (IV) were used in k-means cluster analysis to identify groups of patches that had similar composition of tree species. Second, IV were used to construct dissimilarity matrices for non-metric multidimensional scaling (NMDS) (Shepard 1962, Clarke 1993). NMDS is an ordination technique that reduces the multi-dimensionality inherent in community data to a smaller number (usually two or three) of dimensions or axes, with each patch represented by a set of coordinates corresponding to its floristic composition.

Habitat variables that are measured on different scales are best summarized using principal components analysis (PCA), after standardizing each variable. Three sets of variables were summarized in separate PCAs: (i) woodland structure, (ii) shrub layer attributes and (iii) habitat complexity (see Table 2.1 for variables included). The first three principal components were then extracted from each PCA (with Varimax rotation). The NMDS co-ordinates and principal component scores were used to compare habitat and vegetation characteristics of patches among the geographic districts, and as predictor variables in multivariate modelling. Cluster analysis and PCA were performed using SPPS V10.0 and NMDS using PRIMER (Carr 1997).

**Distribution of the White-browed Treecreeper**

Presence or absence of the White-browed Treecreeper was the response variable in all analyses. A patch was considered occupied if White-browed Treecreepers were detected on (inside or outside) at least one transect during at least one census. This liberal approach to patch occupancy was used because a positive record demonstrated the capacity of the species to reach the patch and, given their sedentary habits, probably signified residence within the patch. Geographic bias in White-browed Treecreeper distribution was initially examined by comparing the proportion of patches that were occupied among the districts, using $\chi^2$ analysis. A similar analysis was conducted to identify preferences for types of woodland by comparing occupancy among the tree species cluster groups.
Multivariate models of White-browed Treecreeper distribution

A predictive model of patch occupancy was developed for the White-browed Treecreeper using multivariate logistic regression (Hosmer & Lemeshow 1989, Nicholls 1989). The number of predictor variables available for model building was large; therefore, five sets of variables (sub-models) were defined a priori, each representing a different component of the environment, viz woodland structure, tree species composition, shrub layer attributes, habitat complexity and landscape structure. This enabled an assessment of the influence of each set of variables on White-browed Treecreeper patch occupancy. A ‘final’ model was then built from predictor variables selected from the sub-models (Fig. 2.3).

**Figure 2.3.** Schematic representation of the sub-modelling strategy. Parameters selected from the sub-models were combined in a final logistic regression to construct a predictive model of patch occupancy for the White-browed Treecreeper.

The distribution of the predictor variables was examined prior to analysis, and variables that departed significantly from a normal distribution were transformed (Table 2.1). Only one variable from a set of inter-correlated variables ($|r| > 0.5$) was used in the model building process. Logistic regression progressed by forward stepwise selection of variables based on the log-likelihood ratio (Nicholls 1989). The
goodness-of-fit of a selected model was examined using the Hosmer-Lemeshow test (SPSS v.8). Plots of the standardized residuals, leverage values and Cook’s-D coefficient of sensitivity were used to assess adherence to the assumption of normally distributed errors, the fit of the model, and to identify potential outliers and influential cases (Nicholls 1989).

For each sub-model, a ‘pair’ of logistic regressions was conducted. The first regression included the predictor variables directly (as listed in Tables 2.1 and 2.2). The second regression included the NMDS axes co-ordinates or principal component scores. The preferred regression in each pair was determined from the change in log-likelihood ($G$-statistic), Nagelkerke $R^2$ value and correct classification rate (CCR) associated with the saturated (all variables entered) and the fitted sub-model. The predictor variable responsible for the largest change in log-likelihood in the preferred regression of each sub-model pair was selected for inclusion in the ‘final’ model.

After the model parameters were estimated, the logit link function was used to calculate the probability of occurrence of the White-browed Treecreeper in a patch:

$$ Pr (x) = \frac{e^u}{1 + e^u} $$

where $u$ is the linear equation defined by the significant regression parameters:

$$ u_i = a + \beta x_i + \beta y_i \ldots $$

where $a$ is the model constant and $\beta$ is the parameter estimate for predictor variables $x$ and $y$.

The performance of the final model was assessed from Nagelkerke $R^2$ and CCR. However, estimating classification errors in the same data that was used to derive the model parameters will be biased. In the absence of novel data, a jack-knife technique was applied to the final model to evaluate the extent of the bias (Efron & Gong 1983). This involved removing each case from the data one at a time, re-fitting the model parameters, and applying the new parameters to the excluded case. The ‘jack-knife probability’ is then used to calculate the classification error. SPSS v.8.0 was used for all logistic regression modelling.

Multivariate regressions that seek the best single model are prone to multicollinearity among the predictor variables, which can lead to spurious deductions regarding causality (MacNally 1996, 2000). Therefore, explanatory relationships between the
predictor variables and patch occupancy by the White-browed Treecreeper were sought by using hierarchical partitioning (Chevan & Sutherland 1991). This is a complementary approach to multivariate regression that is based on mathematical hierarchical theorem (see Chevan & Sutherland 1991 for mathematical proof). In hierarchical partitioning, all possible combinations of the predictor variables in a multivariate setting are considered simultaneously to identify the most likely causal factors and highly collinear predictor variables can be identified (MacNally 2000).

Because this study used logistic regression models, the log-likelihood value was the goodness-of-fit measure used in hierarchical partitioning to compare the $2^K$ models (where $K$ is the number of predictor variables). The variation in White-browed Treecreeper patch occupancy was partitioned to estimate the independent contribution ($I_X$) of each predictor variable. The relative importance of predictor variables can be assessed by comparing the $I_X$ associated with each variable. In addition, variation in White-browed Treecreeper occurrence due to the joint effect ($J_X$) of two or more predictor variables was distinguished from variable-specific ($I_X$) effects. The predictor variables most likely to influence patch occupancy are those with high $I_X$, whilst highly collinear variables will have large ratios of $J_X : I_X$ (Chevan & Sutherland 1991).

Chevan and Sutherland (1991) acknowledge that hierarchical partitioning is a supplement to, rather than a substitution for, other multivariate statistical techniques. Thus, for each sub-model, hierarchical partitioning was used to examine the independent contribution of each variable to validate the results of the logistic regressions. The inferences from hierarchical partitioning were favoured where there were discrepancies between the methods (MacNally 2000). Hierarchical partitioning was performed using the HIERARCH program (Chevan 1991).
2.3 Results

Habitat and vegetation characteristics

The floristic composition of woodland patches was elegantly summarized in six clusters (Table 2.3). The dominant tree species in each cluster was used to name the woodland types, except for ‘Gypseous’ where Cattlebush and Sugarwood are co-dominant. Belah woodland was the most frequently surveyed woodland type (32% of patches), followed by Slender Cypress-pine (21%), Buloke (18%), mallee savanna (16%), Gypseous (9%) and Black Box (4%). Characteristics of woodland structure, shrub attributes and habitat complexity are summarized for each woodland type in Table 2.4.

<table>
<thead>
<tr>
<th>Importance Value</th>
<th>Black Box</th>
<th>Belah</th>
<th>Buloke</th>
<th>Gypseous</th>
<th>Cypress-pine</th>
<th>Mallee</th>
</tr>
</thead>
<tbody>
<tr>
<td>Allocasuarina luehmannii</td>
<td>0.0</td>
<td>3.3</td>
<td>149.3</td>
<td>0.0</td>
<td>15.5</td>
<td>19.5</td>
</tr>
<tr>
<td>Callitris gracilis</td>
<td>0.0</td>
<td>6.3</td>
<td>27.5</td>
<td>8.0</td>
<td>144.2</td>
<td>14.8</td>
</tr>
<tr>
<td>Casuarina pauper</td>
<td>0.0</td>
<td>166.7</td>
<td>7.0</td>
<td>7.4</td>
<td>1.0</td>
<td>8.2</td>
</tr>
<tr>
<td>Alectryon oleifolius</td>
<td>0.0</td>
<td>10.8</td>
<td>7.5</td>
<td>94.4</td>
<td>3.2</td>
<td>23.5</td>
</tr>
<tr>
<td>Myoporum platycarpum</td>
<td>0.0</td>
<td>4.1</td>
<td>0.0</td>
<td>83.8</td>
<td>5.4</td>
<td>3.4</td>
</tr>
<tr>
<td>Mallee Eucalyptus spp.</td>
<td>0.0</td>
<td>6.9</td>
<td>3.7</td>
<td>3.4</td>
<td>22.4</td>
<td>118.3</td>
</tr>
<tr>
<td>Eucalyptus largiflorens</td>
<td>185.5</td>
<td>0.0</td>
<td>0.9</td>
<td>0.0</td>
<td>0.3</td>
<td>0.0</td>
</tr>
<tr>
<td>Other species</td>
<td>14.5</td>
<td>1.9</td>
<td>4.1</td>
<td>3.0</td>
<td>8.0</td>
<td>12.2</td>
</tr>
</tbody>
</table>

Number of patches 2 18 10 5 12 9
Table 2.4. Habitat characteristics (mean ± s.e.) of surveyed patches, summarized by woodland type.

<table>
<thead>
<tr>
<th>Woodland type</th>
<th>Black Box</th>
<th>Belah</th>
<th>Buloke</th>
<th>Gypseous</th>
<th>Cypress-pine</th>
<th>Mallee</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of patches</td>
<td>2</td>
<td>18</td>
<td>10</td>
<td>5</td>
<td>12</td>
<td>9</td>
<td>56</td>
</tr>
<tr>
<td><strong>Woodland structure</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree density (stem ha(^{-1}))</td>
<td>91.4 ± 11.1</td>
<td>109.5 ± 10.5</td>
<td>65.4 ± 12.5</td>
<td>24.5 ± 6.7</td>
<td>47.6 ± 9.1</td>
<td>33.9 ± 9.0</td>
<td>68.0 ± 6.3</td>
</tr>
<tr>
<td>Tree dbh (cm)</td>
<td>24.8 ± 1.33</td>
<td>27.4 ± 0.83</td>
<td>31.0 ± 1.45</td>
<td>26.3 ± 3.95</td>
<td>27.9 ± 2.02</td>
<td>23.0 ± 1.45</td>
<td>27.3 ± 0.75</td>
</tr>
<tr>
<td>Tree height (m)</td>
<td>7.5 ± 0.1</td>
<td>8.9 ± 0.2</td>
<td>8.9 ± 0.3</td>
<td>5.7 ± 0.6</td>
<td>8.5 ± 0.2</td>
<td>6.9 ± 0.2</td>
<td>8.2 ± 0.2</td>
</tr>
<tr>
<td>Canopy cover (%)</td>
<td>31.5 ± 3.7</td>
<td>24.7 ± 2.2</td>
<td>16.4 ± 1.4</td>
<td>3.6 ± 0.4</td>
<td>15.6 ± 1.8</td>
<td>12.1 ± 2.2</td>
<td>17.6 ± 1.3</td>
</tr>
<tr>
<td>Hollows (%)</td>
<td>4.0 ± 4.0</td>
<td>9.8 ± 1.4</td>
<td>5.1 ± 1.5</td>
<td>5.9 ± 3.6</td>
<td>2.7 ± 0.7</td>
<td>9.6 ± 2.6</td>
<td>6.9 ± 0.8</td>
</tr>
<tr>
<td>DST density (stem ha(^{-1}))</td>
<td>65.7 ± 12.6</td>
<td>15.7 ± 2.3</td>
<td>16.0 ± 2.0</td>
<td>5.2 ± 2.1</td>
<td>15.0 ± 2.8</td>
<td>4.5 ± 1.1</td>
<td>14.7 ± 1.8</td>
</tr>
<tr>
<td><strong>Shrub strata</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shrub density (stem ha(^{-1}))</td>
<td>0.0 ± 0.0</td>
<td>1185 ± 280</td>
<td>98 ± 43</td>
<td>41 ± 18</td>
<td>240 ± 99</td>
<td>187 ± 119</td>
<td>484 ± 114</td>
</tr>
<tr>
<td>Low shrub cover (%)</td>
<td>0.1 ± 0.1</td>
<td>19.8 ± 3.0</td>
<td>5.0 ± 1.7</td>
<td>5.6 ± 1.6</td>
<td>7.4 ± 2.5</td>
<td>6.7 ± 3.3</td>
<td>10.4 ± 1.5</td>
</tr>
<tr>
<td>High shrub cover (%)</td>
<td>1.8 ± 0.4</td>
<td>4.9 ± 0.8</td>
<td>3.5 ± 1.4</td>
<td>7.5 ± 2.3</td>
<td>4.1 ± 1.5</td>
<td>5.5 ± 2.1</td>
<td>4.7 ± 0.6</td>
</tr>
<tr>
<td>Foliage index (score)</td>
<td>177 ± 25</td>
<td>139 ± 15</td>
<td>261 ± 39</td>
<td>339 ± 76</td>
<td>237 ± 41</td>
<td>263 ± 38</td>
<td>221 ± 17</td>
</tr>
<tr>
<td><strong>Complexity</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of strata</td>
<td>3.0 ± 0.6</td>
<td>4.5 ± 0.1</td>
<td>4.0 ± 0.3</td>
<td>3.4 ± 0.1</td>
<td>3.9 ± 0.3</td>
<td>3.5 ± 0.2</td>
<td>4.0 ± 0.1</td>
</tr>
<tr>
<td>Bare ground (%)</td>
<td>31.7 ± 5.0</td>
<td>75.3 ± 2.6</td>
<td>38.3 ± 4.2</td>
<td>51.5 ± 11.8</td>
<td>36.7 ± 7.5</td>
<td>42.3 ± 6.7</td>
<td>51.4 ± 3.3</td>
</tr>
<tr>
<td>Ground cover (%)</td>
<td>53.6 ± 3.4</td>
<td>14.3 ± 2.4</td>
<td>48.2 ± 5.0</td>
<td>45.1 ± 6.4</td>
<td>50.6 ± 5.8</td>
<td>53.1 ± 8.1</td>
<td>38.5 ± 3.1</td>
</tr>
<tr>
<td>Log density (# ha(^{-1}))</td>
<td>97.0 ± 7.2</td>
<td>108.3 ± 7.3</td>
<td>84.1 ± 9.1</td>
<td>80.2 ± 30.0</td>
<td>111.0 ± 21.1</td>
<td>48.1 ± 16.5</td>
<td>91.9 ± 6.9</td>
</tr>
<tr>
<td>Stump density (# ha(^{-1}))</td>
<td>5.1 ± 5.1</td>
<td>66.5 ± 12.8</td>
<td>45.6 ± 17.4</td>
<td>21.9 ± 16.5</td>
<td>66.0 ± 11.5</td>
<td>22.3 ± 10.3</td>
<td>49.4 ± 6.5</td>
</tr>
<tr>
<td><strong>Avian factors</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Br. T’creep (ind ha(^{-1}))</td>
<td>1.08 ± 0.42</td>
<td>1.63 ± 0.83</td>
<td>1.40 ± 0.57</td>
<td>0.87 ± 0.33</td>
<td>0.25 ± 0.17</td>
<td>0.72 ± 0.44</td>
<td>1.06 ± 0.30</td>
</tr>
<tr>
<td>Y-thr. Miner (ind ha(^{-1}))</td>
<td>0.0 ± 0.0</td>
<td>0.15 ± 0.15</td>
<td>0.20 ± 0.20</td>
<td>0.0 ± 0.0</td>
<td>0.25 ± 0.15</td>
<td>0.94 ± 0.35</td>
<td>0.29 ± 0.09</td>
</tr>
</tbody>
</table>
Multidimensional scaling of the importance values produced a reasonable three-dimensional solution (stress = 0.13). Each of the main tree species was significantly correlated with at least one dimension (i.e. axis) of the ordination (Table 2.5).

Ordination plots of the NMDS co-ordinates illustrated the distribution of woodland types across the study region (Fig. 2.4). A variety of woodland types occurred in the Pink Lakes, Copi Plains and Timbooro districts. In the Wemen district, woodlands were dominated by either Belah or Buloke, most patches in Wyperfeld were Buloke or Cypress woodland, and in the Yarrara district, woodland patches were exclusively dominated by Belah.

Belah and Buloke woodlands were complementary along a north-south geographical gradient, such that Belah was prevalent in the northern districts of Yarrara, Copi Plains and Wemen, whereas Buloke was more common in the south. Pink Lakes represented a transitional zone, with pure stands of Belah and Buloke, as well as mixed woodlands that contained both species. Slender Cypress-pine was distributed throughout the study region, but patches containing mature trees were common only in the Wyperfeld, Pink Lakes and Copi Plains districts. Mallee savanna was widespread in the Timbooro and Pink Lakes districts. Gypseous woodland only occurred at Copi Plains and Black Box woodland was confined to the Wyperfeld district.

<table>
<thead>
<tr>
<th>Tree Species</th>
<th>Axis 1</th>
<th>Axis 2</th>
<th>Axis 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Allocasuarina luehmannii</td>
<td>0.277*</td>
<td>0.328*</td>
<td>-0.713***</td>
</tr>
<tr>
<td>Callitris gracilis</td>
<td>0.757***</td>
<td>0.157</td>
<td>0.045</td>
</tr>
<tr>
<td>Casuarina pauper</td>
<td>-0.516***</td>
<td>-0.864***</td>
<td>0.096</td>
</tr>
<tr>
<td>Alectryon oleifolius</td>
<td>-0.369**</td>
<td>0.056</td>
<td>0.344*</td>
</tr>
<tr>
<td>Myoporum platycarpum</td>
<td>-0.401**</td>
<td>0.204</td>
<td>0.373**</td>
</tr>
<tr>
<td>Mallee Eucalyptus spp.</td>
<td>0.169</td>
<td>0.477***</td>
<td>0.409**</td>
</tr>
<tr>
<td>Eucalyptus largiflorens</td>
<td>-0.230</td>
<td>0.213</td>
<td>-0.301*</td>
</tr>
<tr>
<td>Other species</td>
<td>0.339*</td>
<td>0.152</td>
<td>0.065</td>
</tr>
</tbody>
</table>

* P < 0.05, ** P < 0.01, *** P < 0.001
Between 85 and 95% of the total variation in the woodland structure, shrub layer and habitat complexity variables was explained by the first three components of the respective principal components analyses (Table 2.6). All habitat and vegetation variables were highly correlated \((r > 0.75)\) with at least one principal component (Table 2.6). Ordinations of the woodland patches in environmental space defined by the principal components suggest there was little geographic bias in the habitat variables across the study region. There was considerable overlap in the environmental space occupied by patches from different districts and patches from the same district were scattered, suggesting that a variety of habitat attributes were present within each district. Further, specific habitat features (e.g. dense woodland or tall shrubs) were not restricted to only one or two districts (Fig. 2.5).

However, some patterns in the ordinations were evident. Woodlands in the Copi Plains district were of lower tree density and canopy cover than the other districts (low value for woodland structure PC1) (Fig. 2.5a). Patches in the Yarrara district

**Figure 2.4.** Multidimensional scaling ordination of tree species importance value, differentiated by geographic district.
were characterised by a high density of low shrubs (high value for shrub layer PC1),
which contrasted with many patches in Copi Plains, Pink Lakes and Wyperfeld that
were devoid of shrubs (Fig. 2.5b). Patches in the Yarrara district were also distinct
from most other districts based on measures of habitat complexity (Fig. 2.5c). There
was typically a high proportion of bare ground (high value for PC1) and many
residual stumps (high value for PC2) from forestry activity in patches at Yarrara,
whereas ground layer vegetation (grasses and forbs) was more prevalent (low value
for PC1) in patches in other regions. A distinction between patches in Wyperfeld and
Copi Plains was evident based on the cover of ground layer vegetation (Fig. 2.5c).
Table 2.6. Principal components analyses of sets of variables representing woodland structure, shrub layer attributes and habitat complexity. The variables with loadings that contribute most to each component are designated by bold type.

<table>
<thead>
<tr>
<th></th>
<th>Component 1</th>
<th>Component 2</th>
<th>Component 3</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Woodland structure</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eigenvalue</td>
<td>2.288</td>
<td>1.705</td>
<td>1.141</td>
</tr>
<tr>
<td>% variation explained</td>
<td>38.1</td>
<td>28.4</td>
<td>19.0</td>
</tr>
<tr>
<td>Component loadings</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree density</td>
<td>0.870</td>
<td>-0.168</td>
<td>0.284</td>
</tr>
<tr>
<td>Tree dbh</td>
<td>-0.172</td>
<td>0.940</td>
<td>0.029</td>
</tr>
<tr>
<td>Tree height</td>
<td>0.416</td>
<td>0.844</td>
<td>0.019</td>
</tr>
<tr>
<td>Hollows</td>
<td>0.092</td>
<td>0.048</td>
<td>0.948</td>
</tr>
<tr>
<td>Dead tree density</td>
<td>0.750</td>
<td>0.074</td>
<td>-0.354</td>
</tr>
<tr>
<td>Canopy cover</td>
<td>0.870</td>
<td>0.270</td>
<td>0.189</td>
</tr>
<tr>
<td><strong>Shrub layer</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eigenvalue</td>
<td>2.647</td>
<td>2.003</td>
<td>1.028</td>
</tr>
<tr>
<td>% variation explained</td>
<td>44.1</td>
<td>33.4</td>
<td>17.1</td>
</tr>
<tr>
<td>Component loadings</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shrub density</td>
<td>0.954</td>
<td>0.125</td>
<td>0.147</td>
</tr>
<tr>
<td>Shrub height</td>
<td>0.155</td>
<td>0.962</td>
<td>0.173</td>
</tr>
<tr>
<td>Shrub width</td>
<td>0.232</td>
<td>0.953</td>
<td>0.127</td>
</tr>
<tr>
<td>Foliage index</td>
<td>-0.845</td>
<td>-0.212</td>
<td>-0.263</td>
</tr>
<tr>
<td>Low shrub cover</td>
<td>0.899</td>
<td>0.240</td>
<td>0.285</td>
</tr>
<tr>
<td>High shrub cover</td>
<td>0.370</td>
<td>0.225</td>
<td>0.900</td>
</tr>
<tr>
<td><strong>Habitat complexity</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eigenvalue</td>
<td>1.936</td>
<td>1.367</td>
<td>1.172</td>
</tr>
<tr>
<td>% variation explained</td>
<td>38.7</td>
<td>27.3</td>
<td>23.4</td>
</tr>
<tr>
<td>Component loadings</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of strata</td>
<td>0.233</td>
<td>0.847</td>
<td>-0.264</td>
</tr>
<tr>
<td>Bare ground</td>
<td>0.973</td>
<td>0.049</td>
<td>0.048</td>
</tr>
<tr>
<td>Ground cover</td>
<td>-0.962</td>
<td>-0.165</td>
<td>-0.077</td>
</tr>
<tr>
<td>Fallen log density</td>
<td>0.103</td>
<td>0.001</td>
<td>0.942</td>
</tr>
<tr>
<td>Cut stump density</td>
<td>-0.021</td>
<td>0.787</td>
<td>0.455</td>
</tr>
</tbody>
</table>
Figure 2.5. Distribution of habitat attributes across the study region, as represented by the first two principal components of sets of variables describing a) woodland structure, b) shrub layer and c) habitat complexity.
**Distribution of the White-browed Treecreeper**

White-browed Treecreepers were recorded at 30 of the 97 transects, located in 16 of the 56 (28.6%) patches. The distribution of occupied patches suggests that the White-browed Treecreeper is largely confined to two core districts: Yarrara and the Pine Plains area in Wyperfeld National Park (Fig. 2.6). However, the White-browed Treecreepers also persists near the township of Walpeup in the Timbooroo district and in isolated patches in the north of the Pink Lakes district (Fig. 2.6).

The White-browed Treecreeper was present in a significantly greater proportion of patches in the Yarrara (87.5% occupied) and Wyperfeld (50%) districts than the other four districts (Pink Lakes 14%; Timbooroo 12.5%; Wemen 0%; Copi Plains 0%) \( (\chi^2 = 17.35, df = 5, P = 0.004) \). This geographic bias did not strictly reflect the availability of suitable habitat. When the analysis was restricted to the woodland types in which the White-browed Treecreeper was detected (i.e. exclude Mallee and Gypseous woodland), a strong trend for the skew in distribution towards the Yarrara and Wyperfeld districts remained \( (\chi^2 = 9.64, df = 5, P = 0.086) \). Furthermore, the White-browed Treecreepers was not detected in any of the 16 patches of Belah, Buloke or Cypress-pine woodland in the Wemen and Copi Plains districts or the southern part of the Pink Lakes district.

There was a strong trend for the frequency of occupancy by the White-browed Treecreeper to be influence by woodland type \( (\chi^2 = 9.51, df = 5, P = 0.090) \) (Fig. 2.7). A greater proportion of patches of Belah woodland was occupied (56%) than patches dominated by either Buloke (30%) or Cypress-pine (17%). White-browed Treecreepers were not detected in Gypseous or Mallee woodland. A single White-browed Treecreeper was detected during one census in one of the two Black Box woodlands. Given the limited sampling in this woodland type, the biological significance of this observation is questionable. After removing Black Box woodlands from the analysis, the bias towards Belah woodlands is more pronounced \( (\chi^2 = 9.19, df = 4, P = 0.056) \). When districts in which the White-browed Treecreeper was not detected are excluded, the trend for preferential occupancy of Belah woodlands persists \( (\chi^2 = 8.07, df = 4, P = 0.089) \).
Figure 2.6. Occurrence of the White-browed Treecreeper in 56 woodland patches in north-west Victoria in 1997. Woodland patches not surveyed (see Fig. 2.1) are not displayed for simplicity. Letters refer to geographic districts: CP – Copi Plains; Y – Yarrara; PL – Pink Lakes; T – Timberoon; Wy – Wyperfeld; We – Wemen.
Region distribution

Figure 2.7. Patch occupancy by the White-browed Treecreeper in woodlands of different floristic composition. Number of patches surveyed is indicated above the bars.

Distribution of the White-browed Treecreeper: sub-models

In all sub-models, the regression that included the ‘raw’ predictor variables was preferred over the summary variables derived from PCA or NMDS. The ability of the saturated sub-models to describe White-browed Treecreeper patch occupancy varied from 68% (shrub layer sub-model) to 93% (landscape factors sub-model) of patches correctly classified (Table 2.7). Landscape factors produced the best fit to the observed distribution patterns, with only four patches incorrectly classified. The change in the log-likelihood ratio and the classification error were similar for the woodland structure and tree-species composition sub-models. Note that in the tree-species composition sub-model, Belah IV and Buloke IV were summed due to their complementary distribution. The habitat complexity sub-model returned a smaller change in log-likelihood, but its ability to predict the occupancy status of patches was equal to that of the tree-species sub-model. Occupancy patterns of the White-browed Treecreeper were not predicted accurately by parameters describing shrub attributes.

The selection of the most influential independent variable from each sub-model according to hierarchical partitioning was concordant with the results from logistic regression (Table 2.7). That is, the variables responsible for the most pronounced
change in the log-likelihood ratios in the logistic regressions were also the source of the largest independent effects in the hierarchical partitions. Thus, Demographic Isolation, Canopy Cover, Belah / Buloke IV, Ground Cover and Shrub Density were selected to develop the final model (Table 2.7). As the landscape variables overwhelmingly produced the best fit to the observed patterns of patch occupancy, the second most important predictor variable in the hierarchical partition of landscape factors, Landscape Context (Fig. 2.8), was included in the final model.

Table 2.7. Summary of the saturated, and best single-variable, sub-model of the occurrence of the White-browed Treecreeper. $G$ is the change in log-likelihood from the null model, CCR is the correct classification rate, $R^2$ refers to the Nagelkerke statistic, and HP$_I$ is the percentage of the total independent-effects in hierarchical partitioning attributable to the predictor variable.

<table>
<thead>
<tr>
<th>Sub-model</th>
<th>Saturated sub-model</th>
<th>Best single-variable sub-model</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$G$</td>
<td>CCR %</td>
</tr>
<tr>
<td>Landscape factors</td>
<td>49.256</td>
<td>92.9</td>
</tr>
<tr>
<td>Woodland structure</td>
<td>22.996</td>
<td>80.4</td>
</tr>
<tr>
<td>Tree species composition</td>
<td>20.093</td>
<td>76.8</td>
</tr>
<tr>
<td>Habitat complexity</td>
<td>16.110</td>
<td>76.8</td>
</tr>
<tr>
<td>Shrub layer</td>
<td>8.939</td>
<td>67.9</td>
</tr>
</tbody>
</table>
Figure 2.8. Distribution of independent and joint effects calculated from hierarchical partitioning of variables included in the landscape factors sub-model of patch occupancy by the White-browed Treecreeper. DI – Demographic Isolation; LC – Landscape Context; BBW – Belah / Buloke Woodland; NN – Nearest Neighbour; PS – Patch Size; MI – Mainland Isolation.

**Distribution of the White-browed Treecreeper: final model**

The saturated model (all variables) accurately described White-browed Treecreeper occurrence in north-west Victoria (Table 2.8). However, none of the predictor variables were significant at $\alpha = 0.05$, and the parameter estimates had large standard errors. A more parsimonious model was developed by forward stepwise selection, in which Demographic Isolation was entered first, followed by Belah / Buloke Importance Value (Table 2.8). Thus, the final model is expressed as:

$$u = 0.751 - (2.563 \times \ln\{\text{Demographic Isolation} + 1\}) + (0.025 \times \text{Belah / Buloke IV})$$

where $u$ is related to the probability of occurrence by the logit link-function.
Table 2.8. Final model of the occurrence of the White-browed Treecreeper in north-west Victoria. Standard error of the parameter estimates are given in parentheses.

<table>
<thead>
<tr>
<th>Model a</th>
<th>G</th>
<th>R²</th>
<th>Constant</th>
<th>Dem`phic Isol’n</th>
<th>Bel / Bul IV</th>
<th>Canopy Cover</th>
<th>Landscape Context b</th>
<th>Classification Error (%) c</th>
</tr>
</thead>
<tbody>
<tr>
<td>Saturated</td>
<td>53.13</td>
<td>0.878</td>
<td>-18.375 (15.197)</td>
<td>-5.633 (3.107)</td>
<td>0.020 (0.025)</td>
<td>48.332 (36.659)</td>
<td>na</td>
<td>0.354 (4.291)</td>
</tr>
<tr>
<td>Wald χ²</td>
<td>1.462</td>
<td>3.288</td>
<td>0.628</td>
<td>1.738</td>
<td>2.589</td>
<td>0.007</td>
<td>0.029</td>
<td>0.1463</td>
</tr>
<tr>
<td>P</td>
<td>0.227</td>
<td>0.070</td>
<td>0.428</td>
<td>0.187</td>
<td>0.459</td>
<td>0.934</td>
<td>0.864</td>
<td>0.231</td>
</tr>
<tr>
<td>Forward stepwise</td>
<td>44.99</td>
<td>0.791</td>
<td>0.751 (1.040)</td>
<td>-2.563 (0.794)</td>
<td>0.025 (0.0095)</td>
<td>89</td>
<td>81</td>
<td>93</td>
</tr>
<tr>
<td>Wald χ²</td>
<td>0.522</td>
<td>10.417</td>
<td>6.911</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P</td>
<td>0.470</td>
<td>0.001</td>
<td>0.008</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

a In the saturated model, all predictor variables were entered into the model. In the forward stepwise model, variables were entered at α = 0.05 and removed at α = 0.1 in subsequent steps, based on the change in log-likelihood.

b Parameter estimates predict probability of occurrence relative to patches in an agricultural matrix.

c CCR is the percentage of patches correctly classified by the model (assuming that Pr (x) > 0.5 = occupied); sensitivity is the percentage of occupied patches correctly classified; specificity is the percentage of vacant patches correctly classified.
The classification error calculated from the jack-knife procedure for the final model was 86%. This suggests the final model is relatively robust. However, the model is better at predicting the patches that were not occupied (“jack-knife specificity” = 93%) than correctly predicting occupancy (“jack-knife sensitivity” = 69%). The “jack-knife predicted occupancy” differed from the final model output for only two patches, in which the probability of occupancy fell below the 0.5 cut-off (Pr (x) = 0.49 and 0.39, respectively). Thus, if a more conservative cut-off for occupancy was employed (e.g. Pr (x) > 0.3 = occupied), the results from the jack-knife procedure would be qualitatively identical to the final model.

The final model predicts that the probability of occurrence of the White-browed Treecreeper:

i) increases with proximity to another patch that supports a population (Fig. 2.9a, 2.9b), and

ii) increases with increasing representation of Belah or Buloke (Fig. 2.9c).

Hierarchical partitioning supports the selection of Demographic Isolation as the primary explanatory variable of patch occupancy, accounting for 58% of the total independent explanatory power of the model (Fig. 2.10). Moreover, Demographic Isolation functions mainly as an independent variable, with very low joint contribution. Contrary to the logistic regression, hierarchical partitioning ascribes a marginally higher independent contribution to Canopy Cover than to Belah / Buloke IV (Fig. 2.10). However, both variables have a high ratio of independent to joint effects, suggesting they may be interchangeable in a purely predictive model. The total contribution of Landscape Context was substantially less than Canopy Cover or Belah / Buloke IV but nearly all of its influence was attributable to independent effects (Fig. 2.10). This suggests Landscape Context may have subtle, but ecologically significant, effects on the occurrence of the White-browed Treecreeper.
Figure 2.9a. Influence of Demographic Isolation on the predicted probability of patch occupancy, as derived from the final logistic regression model, and observed occurrence. Filled squares indicate occupied patches; empty squares denote patches in which White-browed Treecreepers were not detected. The solid vertical line designates the maximum distance from the nearest occupied patch at which White-browed Treecreepers were detected. The dashed and dotted horizontal lines represent Pr(x) of 0.5 and 0.3, respectively.

Figure 2.9b. Influence of Demographic Isolation on predicted probability of patch occupancy by the White-browed Treecreeper, as derived from the final logistic regression model. Models were fitted for five values of Belah / Buloke Importance Value (0, 50, 100, 150 and 200). The vertical and horizontal lines are as for Fig. 2.9a.

Figure 2.9c. Influence of Belah / Buloke Importance Value on the predicted probability of patch occupancy by the White-browed Treecreeper, as derived from the final logistic regression model. Five Demographic Isolation distances are modelled, corresponding to the mean distance for all patches surveyed (16.8 km), the threshold distance of 8.3 km, 5 km, 3 km and 1 km.
Demographic Isolation was significantly less at occupied patches than vacant patches (Mann-Whitney U-test: $z = -5.07$, $P < 0.001$; Table 2.9). This difference was consistent when confined to districts ($z = -4.34$, $P < 0.001$) or woodland types ($z = -4.64$, $P < 0.001$) in which White-browed Treecreepers were detected (Table 2.9). The furthest from another occupied patch that White-browed Treecreepers were detected was 8.3 km (Fig. 2.9a). This may represent an ‘isolation threshold’, with White-browed Treecreepers unable to colonize or persist in patches isolated by more than this distance. This distance relates to patches of Belah woodland within a mosaic of non-preferred natural vegetation (e.g. mallee). However, in agricultural landscapes, the furthest distance that White-browed Treecreepers were detected from another occupied patch was only 3 km.

Occupied patches had significantly higher proportional composition of Belah or Buloke (BBIV) than unoccupied patches ($z = -3.28$, $P = 0.001$; Table 2.9). This discrepancy was maintained when the analysis was restricted to those districts ($z = -$
3.032, \( P = 0.002 \) or woodland types (\( z = -2.170, \ P = 0.030 \) in which White-browed Treecreepers were detected (Table 2.9). The latter result suggests that the White-browed Treecreeper may preferentially occupy patches with a higher proportion of Belah or Buloke over patches in which these tree species are a minority of the overall tree community. Note that at the isolation threshold distance of 8.3 km, very high values of BBIV are required for the predicted probability of patch occupancy to approach 0.5 (Fig. 2.9b).

Table 2.9. Mean ± standard error of the distance to the nearest patch occupied by White-browed Treecreepers (Demographic Isolation) and proportional representation of Belah or Buloke (Belah / Buloke IV) in patches occupied and not occupied by the White-browed Treecreeper.

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>Demographic Isolation</th>
<th>Belah / Buloke IV</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>All patches</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Occupied</td>
<td>16</td>
<td>1.9 ± 0.7</td>
<td>144.7 ± 15.2</td>
</tr>
<tr>
<td>Not occupied</td>
<td>40</td>
<td>22.7 ± 2.8</td>
<td>69.8 ± 11.9</td>
</tr>
<tr>
<td>Total</td>
<td>56</td>
<td>16.8 ± 2.3</td>
<td>91.2 ± 10.5</td>
</tr>
<tr>
<td><strong>Occupied districts</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Occupied</td>
<td>16</td>
<td>1.9 ± 0.7</td>
<td>144.7 ± 15.2</td>
</tr>
<tr>
<td>Not occupied</td>
<td>26</td>
<td>15.0 ± 2.2</td>
<td>68.5 ± 14.5</td>
</tr>
<tr>
<td>Total</td>
<td>42</td>
<td>10.0 ± 1.7</td>
<td>97.5 ± 12.1</td>
</tr>
<tr>
<td><strong>Occupied woodland types</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Occupied</td>
<td>16</td>
<td>1.9 ± 0.7</td>
<td>144.7 ± 15.2</td>
</tr>
<tr>
<td>Not occupied</td>
<td>26</td>
<td>25.7 ± 3.9</td>
<td>96.4 ± 15.5</td>
</tr>
<tr>
<td>Total</td>
<td>42</td>
<td>16.6 ± 3.0</td>
<td>114.8 ± 11.7</td>
</tr>
</tbody>
</table>

**Revised Model**

Demographic Isolation is a quasi-dependent variable that can only be determined retrospectively from census data. Thus, its inclusion in the final model presents a dilemma for the practical application of the model to predict patch occupancy by the White-browed Treecreeper in novel landscapes. Therefore, a revised model was developed with surrogate variables for Demographic Isolation chosen from the landscape sub-model, namely Belah / Buloke Woodland and Nearest Neighbour.
These variables were included with Canopy Cover, Belah / Buloke IV and Landscape Context in logistic regression and hierarchical partitioning. Belah / Buloke Woodland was entered into the fitted model on the first step, followed by Belah / Buloke IV and finally Canopy Cover (Table 2.10). The classification error of the revised model was 11%, equivalent to the final model, and the change in log-likelihood was also comparable to the final model (Table 2.10). Thus, the final model is expressed as:

\[
u = -21.9 + (25.9 \times \text{Arcsine} \{\text{Belah / Buloke Wdl}\}) + (0.048 \times \text{Belah / Buloke IV}) + (16.5 \times \text{Arcsine} \{\text{Canopy Cover}\})\]

where \(u\) is related to the probability of occurrence by the logit link-function.

**Table 2.10. Parameters in the revised logistic regression model of White-browed Treecreeper occurrence in north-west Victoria.**

<table>
<thead>
<tr>
<th>Model</th>
<th>(G)</th>
<th>(R^2)</th>
<th>Variables</th>
<th>Wald (\chi^2)</th>
<th>(P)</th>
<th>Parameter estimate (se)</th>
<th>Classification Error (%)</th>
<th>CCR</th>
<th>Sens</th>
<th>Spec</th>
</tr>
</thead>
<tbody>
<tr>
<td>Null</td>
<td></td>
<td></td>
<td>Constant</td>
<td>9.595</td>
<td>0.002</td>
<td>-0.916 (0.296)</td>
<td>71</td>
<td>0</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td>Forward stepwise</td>
<td>39.19</td>
<td>0.72</td>
<td>Constant</td>
<td>7.825</td>
<td>0.005</td>
<td>-21.901 (7.829)</td>
<td>89</td>
<td>81</td>
<td>93</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Bel / Bul Wdl</td>
<td>6.288</td>
<td>0.012</td>
<td>25.863 (10.314)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Bel / Bul IV</td>
<td>5.509</td>
<td>0.019</td>
<td>0.048 (0.020)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Canopy Cover</td>
<td>5.054</td>
<td>0.025</td>
<td>16.527 (7.352)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(a\) CCR is the percentage of patches correctly classified; sensitivity is the percentage of occupied patches correctly classified; specificity is the percentage of vacant patches correctly classified.

This model predicts that the probability of occurrence of the White-browed Treecreeper:

i) increases with increasing Belah / Buloke Woodland in the local landscape (Fig. 2.11a);

ii) increases with increasing representation of Belah or Buloke in the woodland (Fig. 2.11b); and

iii) increases with increasing Canopy Cover in the woodland (Fig. 2.11c).
Figure 2.11. Predicted probability of White-browed Treecreeper occurrence as a function of (a) Belah / Buloke Woodland, (b) Belah / Buloke Importance Value and (c) Canopy Cover. Mean probability is plotted ± standard error (dotted lines).
Results from the hierarchical partitioning were in agreement with the order of variable entry into the model and the selection of variables in the fitted model (Fig. 2.12).

Figure 2.12. Hierarchical partition of the environmental variables used to develop the revised model of patch occupancy by the White-browed Treecreeper. BBW – Belah / Buloke Woodland; BBIV – Belah / Buloke Importance Value; CC – Canopy Cover; NN – Nearest Neighbour; LC – Landscape Context.

The proportion of Belah or Pine-Buloke woodland within a 100 km² landscape surrounding a patch, and density of the foliage of the canopy were both significantly greater at occupied patches than unoccupied patches (Mann-Whitney U-test: Belah / Buloke Woodland: $z = -3.488, P < 0.001$; Canopy Cover: $z = -3.165, P = 0.002$; Table 2.11). These differences were again maintained if the comparisons were restricted to occupied districts (Belah / Buloke Woodland: $z = -3.086, P = 0.002$; Canopy Cover: $z = -2.655, P = 0.008$) or woodland types (Belah / Buloke Woodland: $z = -3.101, P = 0.002$; Canopy Cover: $z = -2.007, P = 0.045$) (Table 2.11).
Table 2.11. Mean ± standard error of the percentage of Belah or Pine-Buloke woodland in the landscape (Belah / Buloke Woodland) and density of the canopy foliage (Canopy Cover) in patches occupied and not occupied by the White-browed Treecreeper.

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>Belah / Buloke Woodland</th>
<th>Canopy Cover</th>
</tr>
</thead>
<tbody>
<tr>
<td>All patches</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Occupied</td>
<td>16</td>
<td>11.7 ± 2.0</td>
<td>50.1 ± 2.8</td>
</tr>
<tr>
<td>Not occupied</td>
<td>40</td>
<td>4.8 ± 0.9</td>
<td>37.9 ± 1.9</td>
</tr>
<tr>
<td>Total</td>
<td>56</td>
<td>6.8 ± 1.0</td>
<td>41.6 ± 1.8</td>
</tr>
<tr>
<td>Occupied districts</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Occupied</td>
<td>16</td>
<td>11.7 ± 2.0</td>
<td>50.1 ± 2.8</td>
</tr>
<tr>
<td>Not occupied</td>
<td>26</td>
<td>5.7 ± 1.4</td>
<td>40.7 ± 2.1</td>
</tr>
<tr>
<td>Total</td>
<td>42</td>
<td>8.0 ± 1.2</td>
<td>44.5 ± 1.8</td>
</tr>
<tr>
<td>Occupied woodland types</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Occupied</td>
<td>16</td>
<td>11.7 ± 2.0</td>
<td>50.1 ± 2.8</td>
</tr>
<tr>
<td>Not occupied</td>
<td>26</td>
<td>5.7 ± 1.4</td>
<td>43.1 ± 1.7</td>
</tr>
<tr>
<td>Total</td>
<td>42</td>
<td>8.0 ± 1.2</td>
<td>46.0 ± 1.6</td>
</tr>
</tbody>
</table>

2.4 Discussion

Status of the White-browed Treecreeper

This research provides the first quantitative analysis of the distribution of the White-browed Treecreeper and factors affecting its occurrence in north-west Victoria. The species is limited in geographic extent and selectively occupies Belah or Pine-Buloke woodlands. The districts in which White-browed Treecreepers are most prevalent (Yarrara and Wyperfeld) retain a relatively high proportion of the preferred woodland types. However, the absence, or under-representation, of White-browed Treecreepers elsewhere is not due to habitat constraints alone, as suitable woodland was present in each district surveyed.

Range contraction within the region is evident from comparisons of the current distribution (Fig. 2.6) with wildlife atlas records (DNRE 1997a) and anecdotal reports of historical distribution (Fig. 2.1). Although the White-browed Treecreeper
Regional distribution

is locally common in the Yarrara and Wyperfeld districts, they were not detected in the Wemen or Copi Plains districts, areas where they have historically been present. Their occurrence in the Timberoo and Pink Lakes districts is sporadic. Their presence near the township of Walpeup in the Timberoo district may represent a northern extension of the Wyperfeld population or a small, discrete local population. Their persistence in two patches of Belah woodland in middle of the Murray-Sunset National Park (Fig. 2.6) may be residual populations of a formerly more extensive distribution, or southern outliers of the population in the Yarrara district.

White-browed Treecreepers were not recorded in sufficient numbers to allow reliable density estimates, precluding quantitative statements on abundance trends. However, this observation alone suggests that population density was low in occupied patches, save for a few notable exceptions. Moreover, the status of the White-browed Treecreeper in north-west Victoria is probably more precarious than these survey results suggest because occurrence in a particular patch may not equate to a viable population. This study did not measure population persistence or reproductive success. Thus, several occupied patches may be demographic sinks, where local mortality exceeds reproduction and the population is maintained by immigration from more productive areas (Pulliam 1988). Therefore, the persistence of the regional population may be dependent on only a handful of productive, source populations (e.g. Dunning et al. 1992, Trine 1998).

Thus, this study supports the classification of the White-browed Treecreeper as vulnerable in north-west Victoria on the basis of limited distribution and abundance, and evidence of range contraction. This survey provides baseline data against which future surveys can be compared to evaluate trends in the Victorian population. Although the species is not currently listed as nationally threatened, this decline at the periphery of its biogeographic range may herald reductions in range and abundance across its wider geographic distribution (Gaston 1994). Its recent classification as a species ‘at risk’ in New South Wales attests to this (Reid 1999, Garnett & Crowley 2000).
**Factors affecting the distribution of the White-browed Treecreeper**


Demographic Isolation was the single most important factor in explaining White-browed Treecreeper distribution within north-west Victoria, with probability of occupancy positively related to proximity to the nearest occupied patch. This complements studies in the Northern Hemisphere on nuthatches and tree-creepers, species that share many ecological and behavioural traits with Australian treecreepers (Steinbacher *et al.* 1973, Keast 1981). The distribution and / or breeding density of the Tree-creeper *Certhia familiaris* (Hinsley *et al.* 1995) and European Nuthatch *Sitta euopaea* (Verboom *et al.* 1991, Bellamy *et al.* 1998, Matthysen 1999) are strongly related to measures of isolation. Stith *et al.* (1996) documented a negative correlation between inter-patch distance and patch occupancy in the Florida Scrub-jay *Aphelocoma coerulescens*, a species that is similar to the White-browed Treecreeper in that it has specific habitat requirements and poor dispersal capabilities. In Australia, habitat loss causes disruption to the social structure of the Grey-crowned Babbler *Pomatostomus temporalis* resulting in distribution patterns determined largely by demographic isolation (D. Robinson, personal communication).

Patch occupancy patterns are sensitive to temporal and spatial variation in population size (Soulé *et al.* 1988, Newmark 1991, Hinsley *et al.* 1996a; but see MacNally *et al.* 2000). Larger populations are likely to be dispersed across more patches in a given area than smaller populations, provided specific habitat requirements are met in the patches. By definition, Demographic Isolation is negatively correlated with the number of patches occupied in a given area. Therefore, it follows that Demographic Isolation will be closely associated with district-level population size. Thus, variation in district-level population size is likely to be a significant factor contributing to differential patch occupancy between the districts in this study. However, the
identification of Demographic Isolation as the pre-eminent patch-level explanatory variable is important in itself, and is useful for identifying the processes responsible for the distribution of the White-browed Treecreeper and reasons for its decline.

Debate about the relative importance of habitat fragmentation and habitat loss has recently grown (e.g. Andrén 1994, Fahrig 1997, Trzcinski et al. 1999, Villard et al. 1999). Much of the controversy revolves around terminology. For example, Fahrig (1997) considers habitat destruction as the ultimate cause of the distinct processes of habitat loss and habitat fragmentation, the latter defined strictly as the division of habitat into a larger number of smaller patches. Under this specification, effects of habitat loss will almost always exceed those of fragmentation (Fahrig 1997, Bender et al. 1998, Trzcinski et al. 1999). An alternative terminology regards habitat loss and insularization as components of the general phenomenon of habitat fragmentation (Wilcox 1980, Lynch & Whigham 1984, Wiens 1989a, Bennett 1999). Studies following this terminology usually conclude that bird distributions are influenced by several measures of habitat fragmentation, including indices of habitat configuration, patch isolation and habitat loss (e.g. Askins et al. 1987, McIntyre 1995, Opdam et al. 1995, Villard et al. 1995, 1999, Jansson & Angelstam 1999, Rosenberg et al. 1999).

However, landscape metrics typically co-vary (Gustafson and Parker 1992, Hargis et al. 1998) and there are practical impediments to experimentally divorcing their effects (Wiens 1996, Harrison & Bruna 1999). Thus, explicit allocation of influence to particular landscape features relies on statistical techniques, usually regression or factor analyses (e.g. van Dorp & Opdam 1987, Bennett & Ford 1997, Rosenberg et al. 1999, Trzcinski et al. 1999, Villard et al. 1999) or simulation models (e.g. Andrén 1994, With & Crist 1995, Fahrig 1997, 1998, With et al. 1997). I used a relatively new technique, hierarchical partitioning, to distinguish the independent effects of several landscape parameters on the distribution of the White-browed Treecreeper. Hierarchical partitioning allows explicit recognition of multicollinearity that is hidden in regression analyses (MacNally 1996, 2000) and quantifies the variable-specific effect of each predictor variable on the response variable (Chevan & Sutherland 1991).

In the hierarchical partition of the landscape factors (Fig. 2.8), Demographic Isolation accounted for 55% of the explained variability in White-browed
Treecreeper patch occupancy. This was much greater than the independent contribution of Belah / Buloke Woodland (11%), Nearest Neighbour (9%) or Mainland Isolation (6%). Moreover, most of the explanatory power of Demographic Isolation is unique to itself, for its independent contribution is much larger than its joint contribution. This is not the case for the other three variables, which have large joint effects relative to their independent contribution, indicating a high degree of collinearity. Landscape Context (13%) and Patch Size (6%) have much lower explanatory power but nearly all of their impact is independent of the other predictor variables.

These results are consistent with predictions that the arrangement of habitat will influence the persistence of habitat specialists in landscapes with low habitat cover (e.g. 10 – 30%) (Andrén 1994, With & Crist 1995, Fahrig 1998, Jansson & Angelstam 1999). However, the current habitat configuration results primarily from the destruction of entire patches of habitat and thus could be regarded as habitat loss rather than fragmentation (sensu Fahrig 1997). Clearly, the inter-dependence of local population size, and hence patch isolation, with the amount of habitat in a landscape deems that the retention of habitat is the critical issue for White-browed Treecreeper conservation. However, for landscapes at or below a species-specific threshold of habitat cover, viability of local populations may be influenced by the configuration of remnant habitat in the landscape.

The importance of demographic isolation in describing patch occupancy at a regional scale implies that poor dispersal ability relative to the degree of patch isolation restricts access to remote habitat, resulting in discontinuity in their distribution (Ruckelshaus et al. 1997, Hokit et al. 1999). For those patches that are accessible, the decision to settle in a patch appears to be determined by woodland floristics. The preference for Belah or Buloke woodlands apparent in the regression analysis was supported by hierarchical partitioning but the latter emphasised that White-browed Treecreepers may be selecting habitat on the basis of the structural characteristics of a woodland (i.e. Canopy Cover) rather than floristic composition per se. This reflects the sporadic presence of White-browed Treecreepers in patches dominated by Black Box and Cypress-pine, which also have high canopy cover. Thus, patch suitability is determined by a different set of environmental factors at different spatial scales (Wiens et al. 1987, Bellamy et al. 1998, Howell et al. 2000).
The influence of land-use in the surrounding landscape on patch occupancy becomes apparent when patches incorrectly classified by the final model are examined. Of particular interest are three patches in a woody vegetation matrix with low predicted probability of presence, but in which White-browed Treecreepers were detected (solid squares less than Pr (x) = 0.5 in Fig. 2.9a). If Landscape Context is entered into the final model, two of these patches are correctly re-classified as occupied. This suggests the negative effect of demographic isolation may be mitigated in a matrix of non-preferred, woody vegetation. That is, functional connectivity for the White-browed Treecreeper is higher in native vegetation mosaics than agricultural landscapes (Stouffer & Bierregaard 1995, Saari et al. 1998, Renjifo 1999).

Isolation caused by unsuitable natural habitat will probably not impede dispersal (or movement) as much as isolation caused by the destruction of natural habitat (Wilcox & Murphy 1985). This is reflected in the lower Demographic Isolation threshold in agricultural landscapes (3 km) compared with natural mosaics (8.3 km). In an agricultural matrix, the dearth of foraging substrates, of refuge from increased numbers of predators (Janzen 1986, Kurki et al. 2000) and of trees to link their short tree-to-tree flights may severely restrict the capacity of White-browed Treecreepers to move across expanses of open ground. An appropriate management response may be to apply a more conservative probability cut-off for predicting presence (e.g. Pr (x) = 0.3) for patches in a mosaic of natural vegetation types (Fig. 2.9a).

Alternatively, the Demographic Isolation threshold of 8.3 km may not reflect the dispersal capabilities of individuals in natural mosaics, but rather local extinction in the intervening patches. Currently, I am not able to distinguish between these possibilities. However, if the natural mosaic threshold of 8.3 km was due to local extinctions, the shorter threshold of 3 km may be more appropriate for mosaics of native vegetation as well.

Mechanisms of demographic isolation

Metapopulation dynamics (reviews in Hanski and Gilpin 1991a, 1997, Fahrig & Merriam 1994, Opdam 1991, Hanksi 1998) provides a useful framework for interpreting the mechanistic functioning of spatially subdivided populations. In the Yarrara and Wyperfeld districts, the district-level population was centred on one or
two large local populations (e.g. Yarrara FFR, Mallanbool FFR or Wyperfeld SE). Furthermore, the White-browed Treecreeper was detected in nearly all patches of suitable woodland surveyed. Thus, in a metapopulation context, it appears that local populations (i.e. within a discrete patch) rarely suffer extinction, although patch occupancy data collected over several years is required to verify this supposition (e.g. Verboom et al. 1991, Villard et al. 1995, Bellamy et al. 1996a, Hames et al. 2001). This differs from classic metapopulation dynamics in which local populations repeatedly undergo extinction and re-colonization (Hanski 1994, 1998).

I suggest that the spatial organization in these districts may be best described as an amalgam of the mainland-island (Boorman & Levitt 1973, Harrison et al. 1988, Hanski 1994) and patchy population (Harrison 1991) modifications of the classic metapopulation structure (Levins 1969). Persistence in the district is primarily maintained by one or two mainland populations that provide a reliable source of recruits to a network of smaller satellite patches within the demographic isolation threshold (i.e. mainland-island system). The frequency of recruits from the mainland populations may be supplemented by exchange of individuals among a collection of patches that are within the demographic isolation threshold distance (i.e. patchy population structure).

Dispersal underpins the dynamics of spatially sub-divided populations (Hansson 1991, Davis & Howe 1992, Pither & Taylor 1998). Isolated patches are predicted to have fewer immigrants than patches close to other occupied patches (Hanski & Gilpin 1991b), thus reducing the likelihood of an isolated, declining local population being rescued by immigrants (Brown and Kodric-Brown 1977) or vacant patches being re-colonized following local extinction (Hanksi 1994). Thus, when spatial isolation exceeds the functional connectivity threshold, dispersal is disrupted, the metapopulation collapses and eventually the species disappears from that district as it successively dies out from individual patches – a non-equilibrium metapopulation (Harrison 1991).

It is likely that disrupted dispersal, and the subsequent collapse of the metapopulation structure, has contributed to the disappearance of the White-browed Treecreeper from previously occupied districts in north-west Victoria. Walters and colleagues (Walters et al. 1999, Cooper & Walters 2002) concluded that disrupted dispersal was the most likely cause for declines of the Brown Treecreeper in fragmented
landscapes in north-east NSW. Australian treecreepers are reluctant to cross expanses of open ground: presumably, they have lower thresholds of isolation than more vagile species (With & Crist 1995). As habitat is lost from the landscape, their inability to disperse to patches now beyond the demographic isolation threshold compromises persistence of the ‘patchy metapopulation’. This may herald a hierarchy of decline across the region in a step-wise process of progressive disappearances from individual patches, local districts (landscape scale) and potentially whole regions (Saunders 1989).

Factors operating on individuals (e.g. exotic predators, decline in habitat quality, stochasticity) are usually responsible for extinctions from patches, whereas collapse of the metapopulation dynamic through disrupted dispersal (and thus decreased colonization) functions at the landscape scale (e.g. Verboom et al. 1991). Furthermore, the rate of landscape change will significantly affect regional population survival (Fahrig 1992). It appears that the White-browed Treecreeper has not been able to adjust its rate or distance of dispersal or inter-patch migration to match the rapidly changing landscape of north-west Victoria (LCC 1987). Clearly, empirical data on the extent, distance and success of dispersal and behaviour during dispersal events are essential for progress in understanding the process of range contraction in the White-browed Treecreeper.

Application of regression models

Spatially explicit patch-occupancy models are becoming increasingly common tools in the management of threatened wildlife: for example, the Spotted Owl Strix occidentalis (Gutierrez & Harrison 1996), Leadbeater’s Possum Gymnobelideus leadbeateri (Lindenmayer et al. 1991) and Greater Glider Petauroides volans (Possingham et al. 1994). However, all models are limited by the environmental coverage of the data set, quality of their ecological data, process used for independent variable selection, interpretation of predicted probabilities and validation of the model (Nicholls 1989). There is an unavoidable compromise in the design of surveys for rare or sparsely distributed species between survey extent (number of sites), environmental coverage and sampling intensity (temporal
replication). This survey emphasized survey extent at the expense of sampling intensity and geographic coverage in favour of a wider range of habitat types.

Sampling intensity was inadequate to detect White-browed Treecreepers in four patches (including Timberoo Flora and Fauna Reserve) in which occupancy was subsequently confirmed by incidental observations or dedicated additional searching. Encouragingly, the model is fairly robust to these misclassifications, as repeating the analysis with these patches coded as occupied did not change the parameters selected or the overall conclusions. The predicted probability of patch occupancy in the final model was highly correlated with that of the “corrected occupancy” model ($r = 0.916$, $P<0.001$). Importantly, the misclassified patches were in Wyperfeld and Timberoo, districts in which White-browed Treecreepers were detected in other patches. It is salient that additional searching with playback calls conducted in the more remote districts did not reveal other “missed” populations. However, it is imperative that conservation ecologists and land managers thoroughly evaluate predicted probabilities from patch occupancy models, especially predicted absences, prior to implementing strategies based on their predictions.

The predictions of the model developed here have not been tested against a novel set of patches because virtually all available patches of Belah and Buloke woodland in the region that satisfied the size criterion were used in model development. However, the model would benefit from rigorous testing in another region, notwithstanding potential regional variation in the habitat specificity of White-browed Treecreepers.

**Conclusions**

The White-browed Treecreeper was largely confined to two core districts - Yarrara and Wyperfeld – in north-west Victoria, which represents a contraction in range compared with historical records. The floristic composition of the dominant tree species was an important determinant of patch occupancy, with the results providing quantitative support for the previously suspected affinity for Belah and Pine – Buloke woodlands. However, the absence of the White-browed Treecreeper from several districts was not due to a lack of appropriate habitat. Demographic isolation was the most important variable in explaining variation in patch occupancy.
Three general principles of conservation biology are reinforced by the results presented here. First, maximizing the amount of habitat is the cornerstone to the persistence of regional populations of particular species, and hence biodiversity (Burkey 1989, Collinge 1996, Fahrig 1997, Bender et al. 1998). Second, the degree of structural isolation of spatially sub-divided habitat should be less than the dispersal capabilities of the species of interest (i.e. functional isolation) (Burkey 1989, Taylor et al. 1993, Forman 1995a). Patches isolated from other treecreeper populations by more than 8.3 km in mosaics of natural habitat, or 3 km in agricultural landscapes, appeared to be functionally isolated for the White-browed Treecreeper. Third, patterns of patch occupancy must be considered in a landscape context (Noss 1983, Hobbs 1993, 1994). The spatial configuration of habitat, the amount of habitat in the landscape and the land-use in the matrix between patches have a significant bearing on the capacity of a particular patch to support the White-browed Treecreeper.
Chapter 3

Factors affecting the occurrence of the White-browed Treecreeper in an agricultural landscape
3.1 Introduction


This chapter is concerned with the effects of habitat fragmentation on patch occupancy patterns of the White-browed Treecreeper at a landscape scale. This study was conducted in the fragmented agricultural landscape around Yarrara in north-west Victoria. Belah woodland occurs on the more fertile soils of the region and was therefore preferentially cleared for crop farming during the last century (LCC 1987), resulting in the destruction of 90% of Belah woodland in north-west Victoria (MCMA 2000). This massive change in land use radically altered both the landscape composition (relative proportion of vegetation types) and physiognomy (arrangement of vegetation patches) (sensu Dunning et al. 1992) in the Yarrara district. However, Belah woodland has been protected under native vegetation clearance controls since the implementation of the Mallee Area Review (LCC 1987). Therefore, fragmentation of the Belah woodland should have ceased 10 to 15 years before this study, although illegal clearing may have continued regardless.

The general aim of this chapter is to assess the ability of the White-browed Treecreeper to move through and persist in a predominantly agricultural landscape. The response of a particular species to habitat fragmentation will be a function of its minimum area requirements, sensitivity to edge environments, interspecific
interactions, ability to move through the modified landscape, and the speed at which the fragmentary processes progress (Bridgewater 1987, Loyn 1987, Lynch 1987, Robinson et al. 1992, Burel 1993, Taylor et al. 1993, Margules et al. 1994). Therefore, a crucial step in conservation planning for the White-browed Treecreeper is an appreciation of how these processes interact at a landscape scale. Thus, the specific objectives of this chapter were:

- to identify the spatial characteristics that influence occupancy in remnant vegetation patches,
- to determine the minimum area requirements for patch occupancy, and
- to assess the permeability of the landscape to White-browed Treecreeper movement, as inferred from the occupancy patterns of different landscape elements.

### 3.2 Methods

**Study Area**

This study was conducted in a 480 km\(^2\) area in the Yarrara district of north-west Victoria (Fig. 3.1). The climate is semi-arid (mean annual rainfall: 275-300 mm) with mild winters (mean daily minimum in July: 4.4\(^\circ\)) and hot summers (mean daily maximum in January: 31.9\(^\circ\)). Elevation is low (≈ 60 m ASL) and topographical relief relatively flat throughout the study area. The predominant land use in the study area is cereal cropping. Native vegetation is confined to small fragments on private land, linear strips along road verges and fence-lines, and the large remnants that comprise Yarrara Flora and Fauna Reserve (FFR) (2210 ha), Mallanbool FFR (512 ha) and Meringur FFR (393 ha) (Fig. 3.1). Two main native vegetation types occur in the study area: Belah woodland and mallee woodland / scrub. The Murray-Sunset National Park, a few kilometres south of the study area, is an extensive tract (≈700,000 ha) of mainly mallee scrub that includes pockets of Belah woodland.
Figure 3.1. Remnant native vegetation in the Yarrara district. Location of remnants surveyed are indicated by red circles.
**Rationale**

The response of the White-browed Treecreeper to habitat fragmentation was assessed by survey techniques. The rationale underlying the survey approach was that if the White-browed Treecreeper is able to move through the fragmented landscape, it will occur in remnants outside the large reserves, provided habitat is available. The spatial characteristics of remnant vegetation that influence viability as habitat will be inferred from the relative frequency of White-browed Treecreeper occurrence in different parts of the landscape. Further, the extent to which the White-browed Treecreeper occurs outside the large reserves and the distance of occupied habitat from the major reserves will reflect the permeability of the landscape with respect to this species. The mechanisms by which treecreepers move through the landscape may be indicated by the spatial characteristics of the remnants that are occupied (e.g. distance from nearest vegetation, area of surrounding vegetation). Similarly, the use of linear habitat as conduits for movement (i.e. ‘corridors’) may be assessed by comparing occupancy in connected remnants with remnants that are entirely surrounded by farmland, or by direct observation of individuals in linear habitat.

**Survey design**

The survey was confined to Belah woodland to minimize the effects of vegetation differences between sites. Survey sites were categorized according to their spatial attributes and landscape context into one of the following ‘landscape elements’:

- continuous woodland – extensive tracts (> 300 ha) of relatively undisturbed vegetation located in the reserves,
- contiguous woodland – heavily grazed vegetation contiguous with the reserves,
- linear – linear vegetation (20-40 m wide) along roadsides, fence-lines and road reserves that may or may not connect blocks of native vegetation,
- fragments < 100 ha.

Using a categorical approach to landscape context provided a workable solution to two analytical problems: a) assigning a discrete area to linear sites that are part of an indefinite network, and b) differentiating between continuous and contiguous sites that differ in grazing history and landscape context but are not independent in terms
of size, because contiguous woodland was included in the area measurements of continuous woodland.

The method used to survey the bird fauna at most sites was identical to that employed for the regional survey (Chapter 2). Briefly, all species seen or heard while walking slowly (1 km hr$^{-1}$) along the mid-line of a fixed-width line-transect (500 m by 60 m) were recorded. Individuals observed within the transect were counted for abundance estimations, but species detected outside the transect were duly noted for site occupancy status. Seven fragments were too small to accommodate a 500 m transect. These sites were comprehensively searched until the presence or absence of White-browed Treecreepers was confidently ascertained (usually 15 to 25 minutes). Numbers of individuals of other species present in the fragment were recorded incidentally.

One transect was placed in each fragment and linear site, but continuous woodland were surveyed proportional to size according to a non-linear relationship. Thus, Meringur FFR and Mallanbool FFR each contained three transects whereas six transects were surveyed in Yarrara FFR. In addition, one transect was located in contiguous woodland adjacent to the northern and eastern boundaries of Yarrara FFR, and the southern margin of Mallanbool FFR. All transects were randomly positioned within the remnants, with the linear sites randomly selected from aerial photos of the local network. In total, 32 line transects and 7 area searches were conducted in each survey round, distributed across 3 large reserves (15 transects), 18 fragments (11 transects and 7 area searches) and 6 linear sites (6 transects). Surveys were carried out in May 1999 (non-breeding season), August 1999 (commencement of the breeding season) and January 2000 (end of the breeding season).

**Site characteristics**

Nine landscape variables were used to describe the spatial characteristics and landscape context of each transect (Table 3.1). All landscape data was sourced from 1:50,000 or 1:40,000 aerial photographs taken variously from 1987 to 1992. A polar planimeter was used to measure the area of remnant vegetation patches. Native vegetation on private land that was contiguous with public reserves was included in a single estimate of area for the entire tract of vegetation. Discrete area measurements
for the linear sites were not attempted. Mallee vegetation was differentiated from Belah based on differences in colour and grain on the photographs and knowledge of the locality. All remnant vegetation within a 3-km radius of each transect was traced onto a transparent disc placed over the aerial photograph. Three kilometres was chosen as the appropriate distance to define the landscape context of a site because distributional data at the regional scale indicate that this is a threshold distance beyond which isolation effects are observed in agricultural landscapes (Chapter 2). The amount of native vegetation and Belah woodland within 3 km of the transect was then measured. The area of the focal remnant was included in these measurements despite the likely correlation with Total Area and Belah Area because excluding the focal remnant would be an unrealistic interpretation of the area of vegetation or habitat available to treecreepers. The total distance of linear vegetation within 3 km was also measured. Measurements of Mainland Isolation and Demographic Isolation were not confined to the 3-km limit.

Table 3.1. Landscape variables measured for transect sites.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Area</td>
<td>Area of a remnant, including all native vegetation</td>
<td>ha</td>
</tr>
<tr>
<td>Belah Area</td>
<td>Area of Belah woodland within a remnant</td>
<td>ha</td>
</tr>
<tr>
<td>Mainland Isolation</td>
<td>Distance to the nearest tract of continuous woodland</td>
<td>km</td>
</tr>
<tr>
<td>Demographic Isolation</td>
<td>Distance to the nearest site occupied by White-browed Treecreepers</td>
<td>km</td>
</tr>
<tr>
<td>Structural Isolation</td>
<td>Either (i) an isolate, i.e. entirely surrounded by cultivated land, or (ii) connected, i.e. linked to other landscape elements via native vegetation</td>
<td>categorical</td>
</tr>
<tr>
<td>% Native Vegetation</td>
<td>Percentage of native vegetation within a 3-km radius, excluding linear vegetation</td>
<td>%</td>
</tr>
<tr>
<td>% Habitat Cover</td>
<td>Percentage of Belah woodland within a 3-km radius, excluding linear vegetation</td>
<td>%</td>
</tr>
<tr>
<td>Habitat:Veg</td>
<td>Ratio of Belah woodland to native vegetation within a 3-km radius</td>
<td>ratio</td>
</tr>
<tr>
<td>Linear Vegetation</td>
<td>Sum of linear distance of native vegetation within a 3-km radius</td>
<td>km</td>
</tr>
</tbody>
</table>

a Natural log (x + 1) used in all analyses.
b Square root transformation used in all analyses.
c Area (km$^2$) of vegetation (x) was measured from aerial photos and converted to percentages by converting to ha, and dividing the value by the area of a circle: $\% = (x / \pi r^2 * 100) * 100$, where $r = 3$ km. Percentages were then arcsine transformed for all analyses.
d Reflected square root transformation used in all analyses: $\sqrt{(\text{maximum value} + 1) - x}$, where $x$ is the value for each case.
The point-centered quadrant method (PCQM: see Chapter 2) was initially used to quantify the vegetation along each line transect. However, due to inconsistencies in applying this method to the small fragments and linear sites, variation in vegetation attributes between sites was ultimately assessed qualitatively. The health of the shrub understorey in remnants was assumed to be related to the history and intensity of stock grazing. Thus, Stock Access, as indicated by presence or absence of effective fencing, was included as a binomial variable. Belah dominated the canopy stratum at all sites, though the relative abundance of mid-canopy trees (e.g. Cattlebush and Sugarwood) varied slightly between sites. The most conspicuous difference between sites was tree density, which was categorized on an interval scale of 1 (low) – 3 (high), with data from the PCQM assessments used to establish benchmarks.

Landscape, vegetation and bird data from multiple transects within continuous woodland sites were averaged so that each site (e.g. tract of continuous woodland, small fragment) contributed only one datum for each variable. A summary of site characteristics is presented in Table 3.2.
Table 3.2. Summary of landscape and habitat variables, grouped by landscape element. Data presented are the mean ± s.e., and minimum and maximum values in parentheses, and the number of sites in each category of structural isolation, stock access and tree density.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Continuous</th>
<th>Contiguous</th>
<th>Linear</th>
<th>Fragment</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n = 3</td>
<td>n = 3</td>
<td>n = 6</td>
<td>n = 18</td>
<td>n = 30</td>
</tr>
<tr>
<td><strong>Landscape variables</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total Area</td>
<td>1082 ± 568</td>
<td>-</td>
<td>-</td>
<td>22.5 ± 5.4</td>
<td>174 ± 107</td>
</tr>
<tr>
<td>(393 – 2210)</td>
<td></td>
<td></td>
<td></td>
<td>(0.6 – 83.0)</td>
<td>(0.6 – 2210)</td>
</tr>
<tr>
<td>Belah Area</td>
<td>919 ± 479</td>
<td>-</td>
<td>-</td>
<td>18.2 ± 4.0</td>
<td>147 ± 91</td>
</tr>
<tr>
<td>(369 – 1874)</td>
<td></td>
<td></td>
<td></td>
<td>(0.6 – 50.5)</td>
<td>(0.6 – 1874)</td>
</tr>
<tr>
<td>Mainland Isolation</td>
<td>-</td>
<td>0.0</td>
<td>2.83 ± 1.14</td>
<td>2.41 ± 0.47</td>
<td>2.24 ± 0.42</td>
</tr>
<tr>
<td>(0.0 – 7.1)</td>
<td></td>
<td></td>
<td>(0.0 – 6.8)</td>
<td>(0.0 – 7.1)</td>
<td></td>
</tr>
<tr>
<td>Demographic Isolation</td>
<td>1.4 ± 0.8</td>
<td>0.0</td>
<td>1.53 ± 0.85</td>
<td>1.51 ± 0.31</td>
<td>1.35 ± 0.26</td>
</tr>
<tr>
<td>(0.6 – 3.0)</td>
<td></td>
<td></td>
<td>(0.0 – 5.0)</td>
<td>(0.0 – 5.0)</td>
<td></td>
</tr>
<tr>
<td>Structural Isolation</td>
<td>All connected</td>
<td>All connected</td>
<td>All connected</td>
<td>9 isolates</td>
<td>9 isolates</td>
</tr>
<tr>
<td>% Native Vegetation</td>
<td>29.4 ± 7.1</td>
<td>28.4 ± 2.9</td>
<td>18.4 ± 5.2</td>
<td>16.9 ± 3.0</td>
<td>19.6 ± 2.3</td>
</tr>
<tr>
<td>(19.7 – 43.2)</td>
<td></td>
<td>(24.6 – 34.2)</td>
<td>(4.1 – 36.5)</td>
<td>(4.0 – 52.4)</td>
<td>(4.0 – 52.4)</td>
</tr>
<tr>
<td>% Habitat Cover</td>
<td>24.6 ± 6.4</td>
<td>24.4 ± 4.2</td>
<td>14.6 ± 5.2</td>
<td>11.7 ± 2.7</td>
<td>14.8 ± 2.2</td>
</tr>
<tr>
<td>(17.4 – 37.2)</td>
<td></td>
<td>(18.2 – 32.3)</td>
<td>(0.8 – 30.5)</td>
<td>(0.2 – 44.6)</td>
<td>(0.2 – 44.6)</td>
</tr>
<tr>
<td>Habitat:Veg</td>
<td>83.4 ± 3.9</td>
<td>84.7 ± 5.9</td>
<td>64.2 ± 12.8</td>
<td>60.4 ± 6.0</td>
<td>65.9 ± 4.7</td>
</tr>
<tr>
<td>(75.7 – 88.3)</td>
<td></td>
<td>(74.1 – 94.5)</td>
<td>(19.7 – 96.7)</td>
<td>(5.0 – 92.6)</td>
<td>(5.0 – 96.7)</td>
</tr>
<tr>
<td>Linear Vegetation</td>
<td>10.4 ± 1.0</td>
<td>13.9 ± 1.5</td>
<td>18.0 ± 2.5</td>
<td>18.5 ± 1.4</td>
<td>17.1 ± 1.1</td>
</tr>
<tr>
<td>(8.8 – 12.4)</td>
<td></td>
<td>(11.2 – 16.4)</td>
<td>(11.6 – 28.8)</td>
<td>(6.6 – 30.7)</td>
<td>(6.6 – 30.7)</td>
</tr>
</tbody>
</table>

**Habitat variables**

<table>
<thead>
<tr>
<th>Stock Access</th>
<th>Grazing</th>
<th>No grazing</th>
<th>Tree Density</th>
<th>Low</th>
<th>Medium</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>3</td>
<td>10</td>
</tr>
</tbody>
</table>

* Contiguous and linear sites excluded from area measurements, therefore n = 21; Continuous sites excluded from Mainland Isolation measurements, therefore n = 27.

**Data analysis**

The occupancy status of sites was defined in two ways: (i) presence / absence of White-browed Treecreepers, pooled over the three survey rounds so that one
observation was sufficient to assign “occupied” status, and (ii) reporting rate, the
number of surveys in which White-browed Treecreepers were detected. Presence /
absence data indicated that a site was accessible and used by White-browed
Treecreepers whilst reporting rate assessed the likelihood of permanent residency.
Relative abundance of the White-browed Treecreeper, Brown Treecreeper and small
parrots at each site were determined as simple counts of individuals within the
transect. Numbers of individuals counted in area searches of small fragments were
corrected to 3 ha, an area equivalent to the line transects.

Occupancy status was compared between landscape elements using the contingency
coefficient, a measure of association based on the $\chi^2$ statistic for nominal data
(SPSS v.10). The landscape characteristics of occupied sites were compared with
vacant sites using $t$-tests, after appropriate data transformations. Tree density and
stock access were compared between occupied and vacant sites using contingency
coefficient $\chi^2$ tests.

The probability of occurrence of the White-browed Treecreeper at a site was
analysed using logistic regression (binomial response variable, logit link function)
(Hosmer and Lomeshaw 1989, Nicholls 1989) and hierarchical partitioning (Chevan
& Sutherland 1991; Chapter 2). All nine landscape variables were highly inter-
correlated. Belah Area was considered more ecologically relevant than Total Area
and was therefore used to distinguish between fragments in the categorical variable
‘Landscape Element’ (i.e. Continuous, Contiguous, Linear, Fragment > 20 ha or
Fragment < 20 ha). To reduce the number of correlated independent variables in the
logistic regression, six landscape variables were included in a principal components
analysis (PCA), after appropriate data transformations. Varimax rotation of the final
solution maximized the interpretability of the extracted orthogonal components.

Parameter selection in the logistic regression progressed by forward stepwise
selection ($P < 0.05$ for inclusion of parameters, $P < 0.1$ for exclusion of parameters)
based on the log-likelihood ratio. Residual diagnostics were examined to compare
the fitted model to the observed data and assess adherence to data assumptions
(Nicholls 1989). Six parameters were available for model building: two principal
components and four categorical variables (i.e. Landscape Element, Structural
Isolation, Stock Access and Tree Density). Indicator contrast was used for each of
the categorical variables, with the reference category for each variable corresponding to the “natural” state (i.e. Landscape Element = continuous, Structural Isolation = connected, Stock Access = no, and Tree Density = high).

Two hierarchical partitions were performed. The first was used as a validation of the logistic regression and therefore included similar variables. However, an advantage of hierarchical partitioning is its ability to partition the explanatory power of each predictor variable into independent and joint effects, thereby identifying collinearity among predictor variables (Chevan & Sutherland 1991, MacNally 1996). In addition, the relative importance of the independent effects of correlated variables may be assessed. Therefore, a second partition was run that included Landscape Element, Stock Access and three inter-correlated landscape variables that were formerly included in a principal component, namely Demographic Isolation, Habitat Cover and Habitat:Vegetation ratio.

3.3 Results

Spatial characteristics of occupied and vacant sites

The White-browed Treecreeper was detected at 15 of the 30 sites (Fig. 3.2). The proportion of occupied and vacant sites differed significantly among the categories of Landscape Element (Contingency $\chi^2 = 0.577$, $n = 30$, $P = 0.005$; Fig. 3.2a). More sites were occupied than expected from a random distribution in continuous woodland and fragments $> 20$ ha, whereas occupied sites were under-represented in fragments $< 20$ ha.

Reporting rate also differed significantly between categories of Landscape Element, driven by large differences between small fragments and continuous woodland (Contingency $\chi^2 = 0.721$, $n = 30$, $P = 0.001$; Fig. 3.2b). The White-browed Treecreeper was detected in each of the three tracts of continuous woodland in every survey round. Two of the contiguous sites were also occupied in every survey, but the White-browed Treecreeper was not detected at all in the third contiguous site. The White-browed Treecreeper was detected in most fragments larger than 20 ha and
in four of the six linear sites, but frequency of occurrence in these landscape elements was inconsistent (Fig. 3.2).

**Figure 3.2.** Occurrence of the White-browed Treecreeper in the five categories of Landscape Element based on (a) presence / absence and (b) reporting rate.
Fragments with less than 20 ha of Belah woodland were rarely occupied by the White-browed Treecreeper (Fig. 3.3). The smallest occupied fragment was 21 ha in Total Area, of which 18.5 ha was Belah woodland. White-browed Treecreepers were detected in this fragment during all surveys. Therefore, 18.5 ha of Belah woodland was considered the critical threshold in fragment area for residency by a pair of White-browed Treecreepers (Fig. 3.3). The marked effect of remnant area was reflected in the significant difference in the mean area of occupied and vacant remnants (Total Area: $t_{19} = -4.68$, $P < 0.001$; Belah Area: $t_{11.45}$ (equal variances not assumed) $= -4.48$, $P = 0.001$; Fig. 3.4). The significant effect of area remained when the continuous woodland sites were excluded from the analysis (Total Area: $t_{16} = -3.82$, $P = 0.002$; Belah Area: $t_{16} = -4.34$, $P = 0.001$).

![Figure 3.3](image)

**Figure 3.3.** Reporting rate of the White-browed Treecreeper versus Belah Area (shown on a logarithmic scale), excluding linear and contiguous sites. The dashed line indicates the critical threshold in fragment area of 18.5 ha.

The mean distance to the nearest continuous tract of woodland did not differ significantly between occupied and vacant sites (Mainland Isolation: $t_{25} = 1.28$, $P = 0.213$; Fig. 3.4). Occupied sites were not significantly closer to other occupied
habitat than vacant sites (Demographic Isolation: $t_{25} = 1.37, P = 0.182$; Fig. 3.4) and White-browed Treecreepers were not detected significantly more often in fragments with linking linear habitat (44% occupied) than fragments entirely surrounded by farmland (22% occupied) (Fisher’s exact test $1$-tail $= 0.310$).

The occurrence of White-browed Treecreepers was not significantly affected by the percentage of native vegetation within 3 km of a site ($t_{28} = -1.23, P = 0.227$; Fig. 3.4). There was a trend for occupied sites to have a larger proportion of Belah woodland within 3 km than vacant sites (% Habitat Cover: $t_{28} = -1.77, P = 0.087$; Fig. 3.4). The ratio of Belah woodland to native vegetation within 3 km was higher around occupied sites when all sites were included ($t_{28} = 2.71, P = 0.011$; Fig. 3.4), but the difference was not significant when continuous sites were excluded ($t_{22} = 1.85, P = 0.077$). This suggests remnant area may have confounded this comparison, although a strong trend remains when restricted to fragments and linear sites. The total distance of linear vegetation within 3 km of the site did not differ significantly between occupied and vacant sites ($t_{28} = 1.70, P = 0.101$). However, there was a trend for more linear vegetation in the vicinity of vacant sites (Fig. 3.4).

**Habitat characteristics of occupied and vacant sites**

The proportion of occupied and vacant sites did not differ significantly between the categories of tree density ($\chi^2 = 0.288, n = 30, P = 0.258$), although the proportion of sites occupied decreased with increasing tree density (Fig. 3.5). White-browed Treecreepers were more likely to occupy sites from which stock was excluded (i.e. not grazed) (Fisher’s exact test $1$-tail, $n = 30, P = 0.040$; Fig. 3.5). In a sub-set of 23 sites for which vegetation data was collected using the PCQM transects, stock access was negatively correlated with shrub stem density ($r_s = -0.798, P < 0.001$), % shrub cover (0.5 – 5.0 m high) ($r_s = -0.755, P < 0.001$) and % herb cover (0 – 0.5 m high) ($r_s = -0.506, P = 0.014$). This suggests the White-browed Treecreeper may be responding to understorey condition. However, this association is confounded by the significant correlation between patch area and stock access (Total area - stock access: $r_s = -0.723, n = 21, P < 0.001$; Belah area - stock access: $r_s = -0.696, n = 21, P < 0.001$).
Figure 3.4. Comparison of landscape variables between occupied and vacant sites. Sample size for each box-plot is shown below the x-axis. The box represents 50% of the values with the median indicated by the horizontal line. The whiskers extend to the highest and lowest values, excluding outliers, which are indicated by an asterix.
Figure 3.5. White-browed Treecreeper occupancy in sites categorized according to (a) Tree Density and (b) Stock Access. Total number of sites = 30 in both graphs.
Relative abundance of treecreepers and small parrots

The average number of White-browed Treecreepers per 3 ha transect per survey varied between 0 and 1.33 individuals (Fig. 3.6a). Although there was a significant positive correlation between White-browed Treecreeper abundance and Belah Area ($r = 0.626$, $n = 21$, $P = 0.002$), above the critical threshold in fragment area of 18.5 ha, abundance did not increase with patch area ($r = 0.280$, $n = 10$, $P = 0.434$). This reflects a non-linear threshold effect of area on the presence of the White-browed Treecreeper rather than a linear relationship between density and increasing patch area. Note that some of the occupied fragments have zero abundance (Fig. 3.6a). This indicates individuals were detected outside the transect, and therefore not included in abundance calculations, but were present at the site.

The Brown Treecreeper, a potential competitor of the White-browed Treecreeper for foraging habitat and nest hollows, was present in nearly all of the fragments, including fragments as small as 1.5 ha (Fig. 3.6b). Abundance of the Brown Treecreeper was not linearly correlated with Belah Area ($r = -0.132$, $n = 21$, $P = 0.569$), but was highest in mid sized fragments (10 to 50 ha), resembling a quadratic relationship (Fig. 3.6b). Abundance of the Brown Treecreeper was usually higher than the White-browed Treecreeper in the fragments but this was reversed in continuous woodland. The lower abundance of the Brown Treecreeper in continuous woodland partly reflects the position of the transects, which tended to sample interior habitat in which the Brown Treecreeper was not as prolific.

Several species of small to medium parrot (Budgerigar *Melopsittacus undulatus*, Cockatiel *Nymphicus hollandicus*, Red-rumped Parrot *Psephotus haematonotus*, Mulga Parrot *Psephotus varius* and Blue Bonnet *Psephotus haematogaster*) may also compete with White-browed Treecreepers for nest hollows (Higgins 1999; personal observation). The combined abundance of these parrots was significantly negatively correlated with Belah Area ($r = -0.476$, $n = 21$, $P = 0.029$) and generally peaked in fragments of between 10 and 20 ha (Fig. 3.6c). The outliers in two very small fragments (Fig. 3.6c) were due to an irruption of Budgerigars in north-west Victoria during spring 1999 (Tzaros in preparation). However, the negative correlation remains significant even if Budgerigars are excluded ($r = -0.435$, $n = 21$, $P = 0.049$).
Figure 3.6. Mean abundance within transects of the (a) White-browed Treecreeper, (b) Brown Treecreeper, and (c) sum of small parrots per survey, versus Belah Area. Filled symbols indicate the White-browed Treecreeper occurred at that site. Open symbols indicate the White-browed Treecreeper was not detected. The dashed line indicates the critical threshold in fragment area for the White-browed Treecreeper.
Principal components analysis of the landscape variables

A total of 89% of the variation in the isolation and landscape context variables was accounted for by the first two components of the PCA (Table 3.3). The first component (Landscape PC1) was positively correlated with the amount of linear vegetation within 3 km and mainland isolation, and negatively with the amount of native vegetation and Belah woodland within 3 km (Table 3.3). Sites with a high value for component 1 are embedded in an agricultural matrix with little native vegetation in the surrounding landscape. Most of the remnant vegetation in these landscapes exists as a network of linear strips. The second component (Landscape PC2) was positively correlated with demographic isolation and mainland isolation, and negatively with the ratio of Belah woodland to native vegetation and the amount of Belah woodland within 3 km (Table 3.3). Sites with a high value for component 2 are a long way from sites occupied by the White-browed Treecreeper, and are surrounded largely by agricultural land. Thus, the components are describing similar landscape gradients but emphasize slightly different landscape features.

Table 3.3. Principal components analysis of isolation and landscape context variables for sites surveyed for the White-browed Treecreeper (n = 30). Significant correlations ($P < 0.01$) between the components$^1$ and variable loadings are designated in bold.

<table>
<thead>
<tr>
<th></th>
<th>Landscape PC 1</th>
<th>Landscape PC 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eigenvalues</td>
<td>2.896</td>
<td>2.470</td>
</tr>
<tr>
<td>% of variance explained</td>
<td>48.3</td>
<td>41.2</td>
</tr>
</tbody>
</table>

**Component loadings**

<table>
<thead>
<tr>
<th></th>
<th>Landscape PC 1</th>
<th>Landscape PC 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mainland isolation</td>
<td>0.714</td>
<td>0.601</td>
</tr>
<tr>
<td>Demographic isolation</td>
<td>0.341</td>
<td>0.906</td>
</tr>
<tr>
<td>% Native vegetation</td>
<td>-0.826</td>
<td>-0.464</td>
</tr>
<tr>
<td>% Habitat</td>
<td>-0.778</td>
<td>-0.599</td>
</tr>
<tr>
<td>Habitat : Native vegetation</td>
<td>0.461</td>
<td>0.792</td>
</tr>
<tr>
<td>Linear vegetation</td>
<td>0.878</td>
<td>0.291</td>
</tr>
</tbody>
</table>

$^1$ Correlations refer to transformed variable as per Table 3.1. Thus, direction of association with raw value of Habitat : Native vegetation is negative.

The five landscape element categories were randomly dispersed in an ordination of the principal components, except for the contiguous sites, which clustered at low
values of Landscape PC2 (Fig. 3.7). This suggests that isolation and landscape context were not biased towards any particular landscape element. The clustering of the contiguous sites was expected as these sites were defined \textit{a priori} by their close proximity to continuous woodland and ergo, White-browed Treecreepers.

\textbf{Figure 3.7.} Ordination of survey sites based on the first two principal components (Landscape PC1 and Landscape PC2) describing site isolation and landscape context.

\textit{Logistic regression model of White-browed Treecreeper occurrence}

Four parameters were fitted in the first model developed for White-browed Treecreeper occurrence (presence / absence): Landscape Element, Landscape PC2, Stock Access and Structural Isolation. However, the standard errors of the parameter estimates in this model were very large, and the model may have been ‘over-fitted’ given that four of the six parameters were selected in a model with only 30 cases (Nicholls 1989). Hence, the step with the smallest standard error to $\beta$-coefficient ratios was chosen as the most appropriate model. This occurred on the second step, after the inclusion of Landscape Element and Landscape PC2 (Table 3.4).
Table 3.4. A logistic regression model of White-browed Treecreeper occurrence in remnant Belah woodland in the Yarrara district of north-west Victoria. Variables were selected by forward stepwise selection based on the log-likelihood ratio (LL).

<table>
<thead>
<tr>
<th>Variables entered</th>
<th>Model LL</th>
<th>Change in LL</th>
<th>d.f.</th>
<th>P</th>
<th>β</th>
<th>s.e.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Step 1</strong></td>
<td>23.75</td>
<td>17.84</td>
<td>4</td>
<td>0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Constant</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>9.20</td>
<td>57.52</td>
</tr>
<tr>
<td>Landscape Element</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Continuous</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>Contiguous</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-8.51</td>
<td>57.54</td>
</tr>
<tr>
<td>Linear</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-8.51</td>
<td>57.53</td>
</tr>
<tr>
<td>Fragment &gt;20 ha</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-7.59</td>
<td>57.53</td>
</tr>
<tr>
<td>Fragment &lt;20 ha</td>
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<td></td>
<td></td>
<td></td>
<td>-11.60</td>
<td>57.53</td>
</tr>
<tr>
<td><strong>Step 2</strong></td>
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<td>0.008</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Constant</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>10.63</td>
<td>53.16</td>
</tr>
<tr>
<td>Landscape Element</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Continuous</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>Contiguous</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-12.27</td>
<td>53.21</td>
</tr>
<tr>
<td>Linear</td>
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<td></td>
<td>-9.59</td>
<td>53.17</td>
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<td>Fragment &gt;20 ha</td>
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<td></td>
<td></td>
<td></td>
<td>-7.18</td>
<td>53.16</td>
</tr>
<tr>
<td>Fragment &lt;20 ha</td>
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<td></td>
<td></td>
<td></td>
<td>-13.51</td>
<td>53.18</td>
</tr>
<tr>
<td>Landscape PC2</td>
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<td></td>
<td></td>
<td></td>
<td>-1.97</td>
<td>1.01</td>
</tr>
</tbody>
</table>

This model predicts that the probability of occurrence of the White-browed Treecreeper:

i) decreases outside continuous woodland, but is highest in fragments > 20 ha and linear sites;

ii) decreases with increasing demographic isolation (i.e. distance from nearest conspecific population);

iii) increases with increasing ratio of Belah woodland in the remnant native vegetation in the landscape; and

iv) increases with increasing amount of Belah woodland in the landscape.

This model still has large standard errors for the Landscape Element categories because White-browed Treecreepers were not universally present or absent in
particular landscape elements, introducing a large degree of error in the predicted probabilities based on categorical parameter estimates. However, the ability of the model to accurately categorize sites into occupied or vacant was very good (only 10% classification error). The residual diagnostics and Nagelkerke $R^2$ value (0.75) indicated a reasonable model fit. The only fragment under 20 ha that was occupied returned a high residual and co-efficient of sensitivity (Cook’s D). This case was also the only site where White-browed Treecreepers were incorrectly predicted to be absent (“false absence”), a potentially critical measure of model adequacy in conservation biology. However, this was the largest fragment in the Fragment < 20 ha category, and the Total Area of the fragment (including adjacent mallee) was greater 20 ha. Thus, the general conclusions of the model remain well supported.

Patch area was the mechanistic process underpinning the model. Predicted probability of occurrence reflected the area of Belah woodland, and when linear sites were excluded, patch area on its own efficiently predicted occupancy (Fig. 3.8a). It could be anticipated that area effects might be mitigated in fragments that are less isolated (due to increased rates of recolonisation or visitation) or that more isolated fragments might not be occupied irrespective of size. This notion was rejected, as the fragment area threshold for White-browed Treecreeper occurrence was not influenced by Demographic Isolation, and most of the larger remnants were occupied, irrespective of isolation (Fig. 3.8b). In fact, there was no apparent effect of isolation on occurrence in the fragments. The may be explained by all except three of the fragments being within the demographic isolation threshold in agricultural landscapes of 3 km, as identified in Chapter 2 (Fig. 3.8b).

However, Landscape PC2, which reflects the influence of several isolation measures, did refine the predicted probability of occurrence in linear sites (Fig. 3.8c). The linear sites in which the White-browed Treecreeper was detected were all within 500 m of occupied habitat. In contrast, the two vacant linear sites were isolated by more than the demographic threshold (3 km) at 3.2 km and 5.0 km, and further still from continuous woodland at 4.5 km and 7.1 km, respectively. The Habitat : Native vegetation ratio for occupied linear sites ranged from 0.67 to 0.97 compared with 0.20 and 0.32 for the vacant sites. Belah woodland comprised only 0.8% and 2.6% of the landscape within 3 km of the vacant linear sites against a mean of 21.1% (range 7.0% to 30.5%) for occupied sites.
**Figure 3.8a.** Predicted probability of White-browed Treecreeper occurrence from the logistic regression model (Table 3.4) versus Belah Area, excluding linear sites. Sites at which White-browed Treecreepers were observed are indicated by filled squares; vacant sites are indicated by open squares. Note that the contiguous sites are included as additional points but do not represent discrete habitat patches. The dashed line indicates the observed fragment area threshold.

**Figure 3.8b.** The occurrence of the White-browed Treecreeper as a function of Demographic Isolation and Belah Area, excluding linear and contiguous sites. The horizontal dashed line represents the demographic isolation threshold from the regional scale analysis (Chapter 2). Other symbols as for Fig. 3.8a.

**Figure 3.8c.** Predicted occurrence of the White-browed Treecreeper as a function of Landscape PC2 and Landscape Element. Sites at which White-browed Treecreepers were predicted to be present are indicated by filled circles; sites at which they were predicted to be absent are indicated by open circles. Note that Landscape PC2 only influences predicted group membership in the linear sites.
**Logistic regression model of White-browed Treecreeper residency**

Reporting rate was used to construct a model of the probability of permanent residency by the White-browed Treecreeper at a site. However, reporting rate was equivalent to the extremes of presence or absence at 24 sites. White-browed Treecreepers were present only once from the three surveys at four sites, and twice at two sites (Fig. 8.2b). The four sites with a reporting rate of one were re-classified as vacant and the logistic regression re-run. The same two parameters were selected in the fitted residency model - Landscape Element and Landscape PC2 – as the occurrence model. However, as three of the four sites with a single observation were linear sites, the predicted probability of residency in linear sites ($\beta = -14.01$) was substantially less than the probability of occurrence in linear sites ($\beta = -9.59$). However, other aspects of the model remained virtually unchanged (correlation ($r$) between predicted probabilities of occurrence and residence models = 0.809, $P < 0.001$), including the model performance statistics.

**Hierarchical partitioning of White-browed Treecreeper occurrence**

Hierarchical partitioning imparts a slightly different perspective on the data to that of the regression model. The first hierarchical partition, which was used as a validation of the occurrence model, confirmed the primary importance of Landscape Element in determining patch occupancy (Fig. 3.9a). Predictor variables that explain much of the variation in the response variable in their own right are identified by large independent partitions. This is clearly evident for Landscape Element, which re-iterates the importance of the size of habitat remnants for suitability. The secondary importance of Landscape PC2 (isolation and landscape context) was also corroborated in the hierarchical partition.

Structural Isolation and Tree Density exerted little influence on site occupancy, and much of their influence could not be distinguished from other predictor variables (i.e. joint effects) (Fig. 3.9a). However, the influence of Stock Access on site occupancy was substantial and almost equal to that of Landscape PC2 (Fig. 3.9a). The negative joint effects for Landscape PC2 and Stock Access indicate that other variables may be ‘masking’ or suppressing the detection of the full extent of their independent effect on patch occupancy (Chevan & Sutherland 1991).
One advantage of hierarchical partitioning is that the inter-dependence of predictor variables, and their relative independent contribution to variation in the response variable, can be quantified (Chevan & Sutherland 1991, MacNally 1996). Thus, three of the isolation / landscape context variables formerly combined in Landscape PC2 were entered separately in a second hierarchical partition (Fig. 3.9b). Once again, the significance of Landscape Element was evident. However, contrary to the logistic regressions and the first partition, the second largest independent effect was explained by Stock Access, with each of the three isolation variables accounting for considerably less of the variation in site occupancy (Fig. 3.9b). This indicates that once area effects have been considered, stock access is the next single most important variable in explaining site occupancy by the White-browed Treecreeper.

The independent effects of Habitat : Native vegetation, Demographic Isolation and % Habitat Cover were relatively minor but their cumulative effect may have been substantial. The ratio of suitable habitat (i.e. Belah woodland) to native vegetation explained more of the variation in site occupancy than the proportion of Belah woodland \textit{per se}, with Demographic Isolation of intermediate importance (Fig. 3.9b). This result is counter-intuitive because it suggests that, all else being equal, differences between landscapes with equal native vegetation cover but dissimilar composition of vegetation types explained more of the variation in patch occupancy than differences between landscapes with differing amounts of habitat cover. In practice, the ratio of Belah woodland to native vegetation declines with decreasing native vegetation cover. Thus, in the context of this study, the ratio of Belah woodland to native vegetation provides a more powerful measure of isolation and landscape context.
Figure 3.9. Hierarchical partition of the variation in White-browed Treecreeper site occupancy among (a) the predictor variables used in the logistic regression model of occurrence, and (b) Landscape Element, Stock Access and three variables that were components of Landscape PC2 in the regression models ($n = 30$ sites). The solid portion of each bar represents independent effects; the stippled portion represents joint effects.
3.4 Discussion

Minimum area requirements of the White-browed Treecreeper

The occupancy patterns of the White-browed Treecreeper in the Yarrara district reflect their habitat requirements, historical land-use and management practices, and biogeographic principles. Landscape Element was the foremost descriptive parameter of the probability of White-browed Treecreeper occurrence at a site. The area of Belah woodland at a site underpinned this result, as it was the primary discriminatory factor among categories of Landscape Element. Landscape elements with greater than 20 ha of Belah woodland had a significantly higher probability of White-browed Treecreeper occupancy in logistic regression models, and Landscape Element had a higher independent effect on site occupancy than isolation, landscape context or habitat variables in the hierarchical partitioning. The area-sensitivity of the White-browed Treecreeper is predictable, given the negative effects of fragmentation on several of its congeners (Barrett et al. 1994, Freudenberger 1999, Reid 1999, Walters et al. 1999, Watson et al. 2000). Furthermore, area effects such as those detected in this study concur with a raft of empirical and theoretical studies demonstrating the importance of patch size on avian species richness, and consequently the probability of occurrence of individual species in fragments of diminishing size (Diamond 1975, Opdam et al. 1985, Bolger et al. 1991, Newmark 1991, Stouffer & Bierregaard 1995, Bellamy et al. 1996b, Winter & Faaborg 1999, Ney-Nifle & Mangel 2000).

The area-dependency of patch occupancy represents a step function because White-browed Treecreepers were not detected in any fragments with less than 18.5 ha of Belah woodland, yet all except two patches above this critical threshold in fragment area were occupied (Fig. 8.3). It is possible, indeed probable, that the threshold area for occupancy varies in space and time as a function of regional abundance (Hinsley et al. 1996a). Thus, in landscapes with a smaller regional population, the threshold fragment area may be larger because individuals may preferentially occupy larger patches. Conversely, if the abundance of White-browed Treecreepers in the Yarrara district increases, it is feasible that smaller fragments may be occupied (thereby reducing the threshold area) because individuals are forced to colonize smaller fragments in their quest for unused habitat.
The critical threshold in fragment area observed in the Yarrara landscape of 18.5 ha is more than twice the mean territory size of a breeding pair in continuous habitat (8.4 ha; Chapter 6). Further, fragments of approximately 20 ha accommodated only one established pair plus one unpaired individual each, and fragments in the 40 to 50 ha range were also estimated to be under their carrying capacity based on territory size in continuous woodland. This suggests population density is positively correlated with remnant area (Bender et al. 1998, Connor et al. 2000), although the relationship is non-linear. It also implies that the critical threshold in fragment area does not merely reflect the area of habitat necessary to encompass a pair’s territory requirements. What are the ecological mechanisms that may be responsible for this disparity?

First, altered vegetation composition and structure in the fragments may deplete invertebrate abundance, thereby limiting food availability for the White-browed Treecreeper. Under these conditions, a breeding pair may require a larger territory to maintain an equivalent resource base compared with continuous woodland. However, my data was not suited to testing this hypothesis because territory size was not quantified in the fragments and invertebrate abundance was not investigated. However, studies of the relationship between invertebrate abundance and patch area have produced equivocal results (e.g. Lovejoy et al. 1986, Main 1987, Keals & Majer 1991, Bierregaard et al. 1992, Margules et al. 1994, Davies et al. 2000).

Studies that have related resource availability to avian abundance and productivity have also produced inconsistent results. For example, Zanette et al. (2000) concluded that the Eastern Yellow Robin Eopsaltria australis experienced food shortages that impinged on their reproductive success in forest fragments in north-eastern New South Wales, Australia. However, Walters et al. (1999), working in the same fragmented system, rejected food availability as limiting in the Brown Treecreeper, another area-sensitive, predominantly ground-foraging insectivore. Similarly, Burke and Nol (1998) and Sabine et al. (1996) produced contrasting results for the effect of habitat fragmentation on food availability for the insectivorous Ovenbird Seiurus aurocapillus in forest fragments in south-east Canada. Such contrasting conclusions reiterates the diversity of responses to fragmentation between similar species and within the same species in different landscapes (Wiens 1989). Thus, although food constraints may inflate the territory size requirements of the White-browed
Treecreeper in fragments, it would be imprudent to assume so without corroborative evidence or quantifying resource availability.

Second, territory size in continuous woodland may have been underestimated due to temporally dynamic home ranges; that is, shifts in the boundaries of territories over time. The mean territory size of a breeding pair in continuous woodland was determined from fixes collected over approximately one year. It may be that although only 6 to 10 ha is used in any given year, territory boundaries gradually shift and change shape, so that over a longer timeframe a larger area is necessary to accommodate a pair. Thus, pairs may be excluded from permanently occupying smaller fragments due to the cumulative territory requirements over several years.

Third, Reed (1999) contends that a lack of interspecific competition during evolutionary development may leave species vulnerable to changed competitive interactions in fragmented landscapes. Changes in avifaunal composition associated with decreasing remnant size are well established (e.g. Ambuel & Temple 1983, Lynch & Whigham 1984, Loyn 1987, Askins 1993, Major et al. 2001). Species that prefer edge habitat or feed in the agricultural matrix but nest or roost in native vegetation (e.g. parrots) are likely to be more prevalent in fragments than continuous woodland (Ambuel & Temple 1983, Janzen 1986, Lynch & Saunders 1991). Such compositional changes were detected in this study with the relative densities of Brown Treecreepers and small parrots higher in the fragments than in continuous woodland. These potential competitors of the White-browed Treecreeper were present in even the smallest fragments.

This may alter community interactions in small fragments in two ways. An increase in interference competition (Wiens 1989) between the dominant Brown Treecreeper and the White-browed Treecreeper (Noske 1979; personal observation) in small fragments may preclude the latter from permanently occupying fragments below the observed threshold. Alternatively, increases in both exploitative and interference competition (Wiens 1989) with Brown Treecreepers (e.g. for foraging substrate) and parrots (e.g. for nest hollows) may force White-browed Treecreepers to seek food and hollows over a larger area. Thus, a secondary consequence of altered community dynamics for the White-browed Treecreeper may be larger home ranges, thereby excluding them from fragments below the threshold observed.
Fourth, the observed area threshold may be a sampling effect arising from the vulnerability of small populations to extinction, and stochastic fluctuations in occupancy from year-to-year (Diamond 1984, Gilpin & Soule 1986, Haila et al. 1993). It is doubtful that any of the occupied fragments support resident populations of more than 10 breeding birds. The populations in these fragments are therefore at severe risk of local extinction due to demographic or genetic stochasticity (Franklin 1980), exacerbated by the effects of environmental fluctuations (Shaffer 1981). Assuming time to extinction is correlated with population size and population size is dependent on area (Diamond 1984), larger patches will be occupied more often than smaller patches. Differential residency may be exacerbated if settlement of dispersing birds is non-random, which may occur if individuals actively prospect for better quality habitat (i.e. larger patches) (Reed et al. 1999) or are attracted to patches already occupied by conspecifics (Stamps 1988, Ray et al. 1991). Thus, the probability of sampling a patch when it is occupied increases with fragment size leading to the observed patch occupancy patterns, although smaller patches may be occupied ephemerally.

Fifth, changes in community composition in fragmented landscapes are frequently attributed to edge effects that restrict the inhabitable area for some species to the interior core of a patch (Forman & Godron 1981, Yahner 1988) or alter population processes (e.g. Major et al. 1999a). Changes in microclimate and vegetation structure (Lovejoy et al. 1986, Saunders et al. 1991, Matlack 1993), increased nest predation (Ambuel & Temple 1983, Wilcove 1985, Andren & Angelstam 1988, Luck et al. 1999) and brood parasitism (Brittingham & Temple 1983) may induce an edge effect. However, several lines of evidence suggest edge effects were unlikely to be important in this study. White-browed Treecreepers were observed foraging at the extreme margins of both fragments and continuous woodland, and several nests were located within 50 m of fragment edges. In addition, White-browed Treecreepers were consistently recorded in linear vegetation (Fig. 3.2), habitat that is effectively all “edge”. This suggests that they are not restricted by habitat requirements or ‘psychologically constrained’ to interior habitat in their day to day behaviour.

Predation of White-browed Treecreeper nests was unlikely to have been more intense at edges or in fragments, although it was not tested empirically. This is because the primary predators of White-browed Treecreeper nests are reptiles, which respond
more to habitat features than spatial factors (Kitchener et al. 1980, Hadden & Westbrooke 1996). Thus, because most fragments are grazed and have a disturbed ground layer, they are unlikely to support a large reptile community. Moreover, in fragments that are fenced or in continuous habitat, reptile density is unlikely to be higher at edges because edges are more likely to have a disturbed shrub and ground layer. A reduction in reptilian predators in the fragments may be counteracted by an increase in feral predators (May & Norton 1996). However, cats and foxes are less able to access the nest hollows of the White-browed Treecreeper, although fledglings may be vulnerable to mammalian predators. These observations concur with several recent studies that have shown that “forest interior” species may persist in fragmented landscapes if predation does not increase with fragmentation as conventionally predicted (e.g. Matthyssen & Adriaensen 1998, Nour et al. 1998, Tewsbury et al. 1998, Friesen et al. 1999).

Finally, the observed area threshold of 18.5 ha may not represent the equilibrium rate of patch extinction and recolonization (sensu MacArthur & Wilson 1967) by the White-browed Treecreeper. The size of the smallest fragment that is occupied will increase with time from physical fragmentation of the habitat (Terborgh & Winter 1980, Diamond 1984, Bolger et al. 1991). The critical threshold in fragment area for a species under consideration will depend on the point along this temporal gradient at which the study is conducted. I can not be certain that the end point of this process has been reached for the White-browed Treecreeper in the Yarrara district. In other words, the time lag or extinction debt of the fragmentation process may not yet be fully realized (Burel 1993, Tilman et al. 1994, Brooks et al. 1999) and the fragment area threshold may continue to increase. This serves as a salutary reminder that presence of a species does not verify the existence of viable, self-sustaining breeding populations in area-sensitive birds (Wiens 1989).

**Influence of stock access on occurrence of the White-browed Treecreeper**

The effects of stock access on patch occupancy were confounded by fragment area: only 16% of fragments under 50 ha - and 7% smaller than 25 ha - were fenced. However, the hierarchical partitioning analysis indicated that the independent effect of stock access was substantial. The probability of White-browed Treecreeper
occurrence was negatively associated with stock access. The harmful impacts of stock grazing and trampling on soil properties (Braunack & Walker 1985, Graetz & Tongway 1986, Yates et al. 2000) and vegetation composition and structure (Crisp & Lange 1976, Parsons 1989, Yates et al. 2000) in semi-arid communities are well established. The limited data collected in this study supports these impacts of grazing in Belah woodland. Further, several studies have documented changes in invertebrate community composition and abundance associated with increased grazing (e.g. Abbott et al. 1979, Majer 1989, Abensperg-Traun et al. 1996, Bromham et al. 1999).

Grazed and disturbed woodland contiguous with ungrazed woodland supported resident populations of the White-browed Treecreeper. This suggests that it is not solely a habitat effect that prevents White-browed Treecreepers from inhabiting many grazed remnants. It may be that the effects of grazing are most acute in fragments that are of marginal utility in terms of size; that is, in the 15 to 25 ha range (Fig. 3.10). Unfortunately, fenced (i.e. ungrazed) fragments of this size are rare ($n = 1$), hence it is difficult to draw substantiated conclusions. However, in this size range, subtle differences in invertebrate density due to differential grazing intensity may determine whether fragments have adequate resources to support a pair of White-browed Treecreepers. Thus, stock access and grazing history must be considered as an overlay on the factors discussed previously that influence area requirements. That is, grazing practices may shift the balance between territory size, habitat quality, food availability and interspecific competition.

The contention that grazing only influences habitat occupancy in smaller fragments is supported by the limited effect of grazing on occupancy in larger remnants of Belah woodland (Fig. 3.10). There is little information on the impact of grazing to be garnered from fragments in the 0-15 ha range as they are currently all grazed. However, this presents an elegant opportunity to test the hypothesis that grazing effects influence the fragment area threshold, by removing stock access from fragments of 5-25 ha and monitoring White-browed Treecreeper occupancy once the shrub layer regenerates. The hypothesis predicts that fragments in the 15-25 ha range should be colonized, but occupancy of smaller fragments would still be precluded by other area-related effects.


Figure 3.10. Occurrence of the White-browed Treecreeper in grazed and ungrazed fragments of 0-15 ha, 15-25 ha and 25-50 ha, linear sites and continuous woodland. The number of sites in each category is indicated above the bars.

Effect of isolation on occurrence of the White-browed Treecreeper

Declines in bird species richness and the probability of occurrence of particular species with increasing isolation of habitat patches are common (e.g. Howe 1984, Askins et al. 1987, van Dorp & Opdam 1987, Newmark 1991, Verboom et al. 1991, Hinsley et al. 1995, Beyer at al. 1996, Jansson & Angelstam 1999) but not inevitable (e.g. Martin 1980, Matthysen 1999, Watson et al. 2000). This study found only limited evidence for an isolation effect on White-browed Treecreeper occurrence at the landscape scale. Isolation and landscape context did not explain additional variation in occupancy in the fragments above the effects of patch area and habitat quality. This suggests that the fragments surveyed of appropriate size, vegetation type and quality were accessible to White-browed Treecreepers.
However, contrary evidence emerged from the linear sites. Differential occurrence in linear vegetation was best predicted by Landscape PC2, a surrogate for isolation and landscape context variables (Fig. 3.8c). Values of Demographic Isolation, Mainland Isolation, Habitat cover and Habitat : Native vegetation for occupied linear sites were mutually exclusive to vacant linear sites. Linear sites that were distant from a potential source of immigrants and surrounded by less habitat were less likely to be used than less isolated habitat. This suggests that the probability of White-browed Treecreepers reaching isolated fragments via the linear network diminishes with distance from occupied fragments and habitat cover.

Distance effects on White-browed Treecreeper occurrence in linear sites (i.e. demographic and mainland isolation) could not be confidently distinguished from the effects of decreasing habitat cover in the immediate landscape. That is, were isolated sites vacant because they were further than the dispersal distance from the nearest occupied patch, or did the lack of habitat restrict either the supply of immigrants or the routes available to reach isolated sites, thereby decreasing the probability of colonization? This is a subtle distinction but one that has significant management implications for resource allocation and reserve planning. Evidence from hierarchical partitioning suggests that the ratio of Belah woodland to native vegetation in the immediate landscape has a larger independent effect on site occupancy than distance effects (Fig. 3.9b). This implies that White-browed Treecreepers are precluded from occupying some sites due to a lack of habitat in the immediate landscape and / or access routes rather than excessive dispersal distances. Conversely, an increase in the proportion of habitat surrounding unoccupied remote sites may increase the probability of their occupancy. However, loss of habitat cover often impacts on demographic processes by disrupting dispersal (Hansson 1991, Walters et al. 1999) preventing an uncoupling of their impacts. Experimental manipulations are required to further our understanding of the respective effects of demographic isolation and habitat cover at local and regional scales.

**Efficacy of linear vegetation in facilitating White-browed Treecreeper movement**

Many ecologists advocate maintaining or re-establishing habitat corridors between isolated remnants to mitigate the isolation effects of habitat fragmentation (e.g. Noss
1983, Merriam 1991, Hobbs 1992, Lindenmayer 1994, Haas 1995, Fleury & Brown 1997, Beier & Noss 1998, Bennett 1999; but see Simberloff & Cox 1987, Simberloff et al. 1992, Hess 1994). A minor component of this study was a preliminary assessment of the use of linear vegetation as corridors by the White-browed Treecreeper in the fragmented landscape around Yarrara. This is usually accomplished either by comparing occupancy rates or abundance in patches with and without corridors, or by documenting animal movements within corridors (Beier & Noss 1998, Haddad 1999, 2000, Sieving et al. 2000). There was little evidence from the comparative occupancy rates of isolates and connected fragments to suggest that corridors are obligatory for White-browed Treecreeper patch occupancy in this landscape. Once area and/or habitat quality effects were accounted for, it mattered little whether a fragment was physically connected via a linear linkage or not. The only two isolates above the observed critical threshold in fragment area were both occupied. Conversely, connected fragments near or above the fragment area threshold were not invariably occupied. The logical conclusion is that the isolates in this study were not functionally isolated.

Functional isolation may be related to the “gap-distance” – the distance from an isolate to the nearest native vegetation, or the discontinuity in linear vegetation (Desrochers & Hannon 1997, Brooker et al. 1999). This ranged from 150 m to 650 m in the surveyed fragments. The two occupied isolates had gap distances of 150 m and 450 m. However, even if the threshold gap-distance – the distance across open ground a White-browed Treecreeper will not cross – was between 450m and 650m, it would have been obscured by area effects because fragments with a gap distance greater than 450 m were less than 18 ha in area. Moreover, without the network of linear vegetation, the gap distance of many isolates would have been much higher, and by definition, many connected fragments would have been isolates. Therefore, landscape-scale comparisons are required to properly assess the role of linear vegetation in maintaining functional connectivity within the landscape (e.g. Saunders & Ingram 1987, Pither & Taylor 1998, Mech & Hallett 2001).

Some evidence for the use of corridors by White-browed Treecreepers comes from direct observations of animals in linear habitat. The occupied linear sites tended to be close to occupied habitat, and particularly continuous woodland. This may represent habitat supplementation (Dunning et al. 1992), whereby territories anchored in the
nearby patch are expanded to include part of the linear habitat. The detection in each survey of one pair at the same location close to continuous woodland is consistent with this hypothesis.

Some animals may reside permanently in linear habitat (Newbey & Newbey 1987, Arnold & Weeldenburg 1990, Bennett 1990b). The low reporting rate of White-browed Treecreepers in three of the “occupied” linear sites (Fig. 3.2b) may reflect permanent, but elongated, territories in the linear network (e.g. Bennett 1991, Wiens 1994, Clergeau & Burel 1997). Alternately, the low reporting rate may reflect transient use by mature individuals searching for foraging or breeding habitat, or natal dispersers. The latter possibility was supported by one sighting of a colour-banded juvenile female in a linear site that was several kilometres from its natal territory. These alternative explanations illustrate the variation in animal movements across time and space and therefore the multifarious mechanisms by which linear vegetation may increase landscape connectivity (Harris & Scheck 1991, Bennett 1999). Elucidation of the time-frame over which movements are made would afford considerable ecological insights that could be applied to conservation efforts in this and other regions.

Permeability of the landscape to White-browed Treecreeper movement

Recognition that the permeability of the “matrix” to animal movements is central to the functional connectivity of a landscape is fundamental for conservation management and planning in fragmented landscapes (Forman & Godron 1981, Forman 1995, Dunning et al. 1992, Taylor et al. 1993, McIntyre & Hobbs 1999). A vital first step in this process is to appreciate how movement patterns of individuals are affected by the spatial structure of their environment (Ims 1995).

The spatial configuration of remnant vegetation in the Yarrara district provides some degree of permeability to movements of the White-browed Treecreeper. The persistence of the species in isolated fragments and their detection in linear sites indicates they are capable of moving through the landscape. Functional connectivity is a fusion of species’ behaviour with the spatial arrangement of habitat in a landscape (Forman 1995). To this end, White-browed Treecreepers appear willing to cross up to 450 m of open ground to prospect for habitat. Stepping-stone habitat of
small woodlots, or even single trees, is likely to enhance connectivity over moderate distances (perhaps up to 1 km). Fragments that are too small for residence (e.g. 1 – 15 ha) may still provide stop-over points for foraging and roosting on longer movement events or may supplement the foraging habitat of residents in fragmented landscapes. Corridors of linear habitat may be the most effective course of movement through the landscape for White-browed Treecreepers in terms of penetration distance through the matrix, coverage of the landscape and therefore exposure to vacant and suitable habitat. Not all of the linear vegetation in the Yarrara district is Belah woodland. This implies that the White-browed Treecreeper is able to move through mallee or shrubby vegetation in the linear network to reach stands of Belah woodland, whether they are within the linear network or discrete fragments. The extent of use and efficacy of these alternative routes requires quantification. However, conservation planning for this species must heed the requirement for connectivity at the landscape scale.

**Conclusions**

The utility of remnant vegetation as habitat for the White-browed Treecreeper in the fragmented agricultural landscape around Yarrara was largely determined by spatial characteristics. The size of remnant patches was critical: a threshold area of 18.5 ha of Belah woodland was identified for occupancy of fragments. Habitat quality may be reduced by stock grazing, with the effects most keenly felt in patches of marginal utility (estimated to be 15 – 25 ha). There was an indication that isolation effects precluded occupancy of linear sites at the extremity of the study area, but in general, most of the fragments surveyed were accessible. This indicated that the landscape was permeable to movement by the White-browed Treecreeper, facilitated by the extensive network of linear habitat in the landscape, and clusters of small to medium fragments. Therefore, most habitat was close enough to existing populations (i.e. demographic isolation) and native vegetation (i.e. gap distance) to enable some degree of movement through the landscape. However, the persistence of the species in this landscape is undoubtedly due to the extensive tracts of Belah woodland in the reserve system. Further research on demographic processes in the linear network and fragments is required to assess the contribution of habitat outside the reserves to local population persistence.
Chapter 4

Habitat use by the White-browed Treecreeper during the non-breeding season
4.1 Introduction

The choice of a place in which to live is the simplest expression of the concept of habitat selection by animals. This may seem to be straightforward, but in practice, habitat selection is a complex process, influenced by a species’ physiological tolerances, its interactions with other species, resource abundance and distribution, population density of its own and other species, and other biotic and abiotic factors (Block & Brennan 1993). To optimize survival and reproductive success, different species interact with the environment in different permutations of resource utilization, morphological and physiological adaptations, and behavioural responses to environmental stimuli (Cody 1985, Block & Brennan 1993). This results in the disproportionate use of particular parts of the environment – that is, habitat selection.

Studies of habitat selection are scale dependent (Morris 1987, Wiens 1989b, Orians & Wittenberger 1991, MacNally & Quinn 1998, Robinson et al. 2000, Johnson et al. 2001). The work of John Wiens and colleagues on shrubsteppe birds in North America has been especially influential in demonstrating that birds respond to different environmental stimuli at different spatial scales, and that the ecological scale of investigation significantly impacts on the interpretation of habitat preferences (Rotenberry & Wiens 1980, 1998, Wiens & Rotenberry 1981, Wiens et al. 1987, Wiens 1985). Allen and Starr (1982) define two aspects of ecological scale inherent in all habitat selection studies: the extent of a study is defined by the spatial and temporal boundaries within which it is conducted and the grain is the size of the sampling units used to measure habitat use.

This chapter reports on habitat use by the White-browed Treecreeper during the non-breeding season in tracts of woodland that support relatively large local populations. The objective is to determine whether particular vegetation and habitat attributes affect the degree to which various parts of the woodland are used by the White-browed Treecreeper. In essence, the study is operating at the scale of individual territories – which areas are more likely to be included in territories and are there areas within territories that are used more frequently by the occupants? If so, are there habitat attributes that define the areas that are more likely to be used? Habitat use was studied in four distinct tracts of woodland, two each in the Yarrara and Wyperfeld districts, which are about 130 km apart (Fig. 4.1). The grain of this study was constant (i.e. 1-ha plots were used throughout), but the data were analysed on
two levels: within the region as a whole and within each of the districts. Thus, there was variation in spatial extent over which the results were interpreted.

Distribution and habitat occupancy patterns of birds often show a strong correlation with vegetation structure and habitat configuration, particularly when different habitat types are contrasted (Recher 1969, Willson 1974, Rotenberry & Wiens 1980, Morse 1985, Rumble & Anderson 1996). However, as Terborgh (1985) cautions, the correlation between vegetation structure and species diversity or occupancy patterns may reflect collinearity with other aspects of the environment that are not as readily measured or apparent to human observers. Vegetation structure is closely tied to floristic composition, but even within vegetation associations of similar structure, birds commonly exhibit disproportionate use of particular plant species [e.g. grassland (Rotenberry 1985); shrub-steppe (Wiens 1985); mixed deciduous-conifer forest (Sherry & Holmes 1985, Adams & Morrison 1993, McShea et al. 1995, Robichaud & Villard 1999); *Eucalyptus* woodland (Noske 1985, Ford et al. 1986, Recher & Majer 1994, Saunders & Burgin 2001)].

Habitat selection by bark-foraging species is most likely to be influenced by characteristics of the canopy tree layer. North American woodpeckers selectively forage on larger trees, often displaying floristic preferences, and exploit decayed wood and dead trees more than expected from their availability (Morrison et al. 1987, Flemming et al. 1999, Weikel & Hayes 1999, Zwicker & Walters 1999). Likewise, habitat use by the Brown Creeper *Certhia americana* and Red-breasted Nuthatch *Sitta canadensis* is influenced by tree species, tree diameter and bark texture (Adams & Morrison 1993, Weikel & Hayes 1999). In the most detailed single-species study of habitat use by Australian treecreepers to date, Luck (2000) found that territory location of the Rufous Treecreeper *Climacteris rufa* was predicted by the density of hollow-bearing trees and logs, tree size and the quantity of standing dead wood. Luck also noted that in a second study area, treecreeper occurrence was negatively correlated with shrub cover. Noske (1979, 1985) studied habitat use amongst three species of treecreepers and the Varied Sitella *Daphoenositta chrysoptera* and concluded that they were partitioned by tree species and bark type, as well as foraging substrate. The occurrence of hollow-nesting birds, such as treecreepers, has also been correlated with the size and age of trees, and the
density of hollows in forests and woodlands (Saunders et al. 1982, Sedgwick & Knopf 1990, Luck 2000; see Chapter 7).

Most single-species studies of habitat use and selectivity are based on comparisons of sites in which the study animal was located with those in which it was not. This approach assumes that occupied sites represent suitable, or preferred, habitat and conversely, that absence sites are unsuitable, or avoided. However, the mere presence of the study animal provides little information on the site’s habitat value (North & Reynolds 1996) or the relative frequency or intensity of use amongst those sites at which the study animal was observed. The detection of individuals that are temporarily passing through an area may be erroneously construed as an indication of suitable habitat. The classification of sites as ‘absent’ or ‘unused’ is even more troublesome because failure to detect the study animal does not necessarily demonstrate that the habitat is unsuitable. Johnson (1981, in North & Reynolds 1996) suggested that the study species may be absent from a site for reasons other than habitat suitability, such as low population density or biotic interactions, or that the species does use the site but was not detected during the sampling program. It is near impossible to differentiate between the three alternatives (i.e. unsuitable habitat, suitable habitat but not used for other reasons, suitable habitat and used but not detected) using a dichotomous present or absent classification.

The approach used in this study differed from conventional habitat use studies. To explore the relationships between vegetation characteristics and use by the White-browed Treecreeper, I conducted an observational study in a series of 1-ha plots. The starting assumption was that all habitat within the woodlands was accessible to the White-browed Treecreeper and used to some degree. An ordinal measure of habitat use was generated that ranked plots according to the frequency of use by the White-browed Treecreeper. Differential frequency of use of plots was then examined in relation to inter-site variation in habitat and vegetation characteristics.

Based on the existing knowledge of bark-foraging and cavity-nesting birds, I expected the White-browed Treecreeper to preferentially use areas with higher tree density, larger trees and more dead standing timber. Such habitat would provide more foraging substrate (i.e. trunk surface area) per hectare, and reduce the amount of time and energy individuals spend in searching for, and travelling between, foraging substrates. In addition, areas with larger and older trees contain more
Habitat use during the non-breeding season

hollows (Bennett et al. 1994, Soderquist & Lee 1994, Gibbons 1999), a critical resource for nesting. An extensive and healthy shrub community may indicate more productive areas with a rich and abundant arthropod fauna (Recher et al. 1996), and therefore greater food availability. On the other hand, dense shrubs may interfere with the flight trajectories of treecreepers during foraging, which typically involve successive diagonal flights from the higher branches of one tree to the base of the trunk of the next foraging tree. Therefore, areas with very dense shrubs, particularly tall shrubs, may be avoided. Thus, much of this chapter is founded on three hypotheses:

1. That the White-browed Treecreeper will favour areas with high tree density.
2. That the White-browed Treecreeper will favour areas with many dead standing trees.
3. That the White-browed Treecreeper will avoid areas with high density of tall shrubs.

Two supplementary hypotheses were also investigated that related to edge-effects and use of alternative woodland types:

4. That the White-browed Treecreeper will avoid areas adjacent to cultivated agricultural land or open grassland (i.e. there will be a detectable “edge-effect”).
5. That the White-browed Treecreeper will avoid areas of Black Box or mallee in preference to structurally comparable areas of Pine-Buloke or Belah, respectively.

4.2 Methods

Study sites

Habitat use was studied in four tracts of woodland in which White-browed Treecreepers were known to occur. Two tracts were located in the Yarrara district (Yarrara FFR and Mallanbool FFR) and two in the Pine Plains district of Wyperfeld National Park (‘Wyperfeld South-east’ and ‘Wyperfeld North’) in north-west Victoria (Fig. 4.1). Yarrara FFR and Mallanbool FFR are large remnants of native vegetation surrounded by broad-acre cropping agricultural land. Both reserves were
originally gazetted and managed as forestry reserves and have never been extensively grazed by stock. However, large volumes of Slender Cypress-Pine *Callitris gracilis* were extracted from both reserves. Consequently, both reserves now consist of predominantly Belah *Casuarina pauper* woodland with a floristically diverse understorey (Fig. 4.2a). Mallee *Eucalyptus spp.* woodland persists at the margins of both reserves.

In contrast, the tracts of Buloke *Allocasuarina leuhammadii* and Slender Cypress-Pine woodland in the Wyperfeld district exist within a mosaic of different native vegetation types that include mallee communities, Black Box *E. largiflorens* woodland, Scrub Cypress-Pine *C. verrucosa* woodland, saltbush and lakebed herb communities, and grasslands. Trees were felled for fencing and construction by pastoralists but the area was not intensively managed for forestry or cleared for cropping, although extensive grain production occurs east of the National Park. However, this area was grazed by stock until the late 1980s and subsequently large kangaroo and rabbit populations have continued to exert significant grazing pressure on the native vegetation. Accordingly, the woodland now consists largely of widely spaced, mature trees with a grassy understorey and a sparse shrub layer (Fig. 4.2b, 4.2c). In the areas where the shrub layer is relatively undisturbed, it is dominated by larger species, generally over 2m in height (*Acacia spp.* and *Melaleuca lanceolata*). Table 4.1 summarizes the environmental and vegetation characteristics of the four woodland tracts.
Table 4.1 Environmental and vegetation characteristics of the four woodland tracts used to study fine-scale habitat use.

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</tr>
<tr>
<td><strong>Area</strong>&lt;sup&gt;b&lt;/sup&gt; (ha)</td>
<td>838</td>
<td>192</td>
<td>1859</td>
<td>513</td>
</tr>
<tr>
<td><strong>Elevation (m)</strong></td>
<td>30 - 60</td>
<td>40 - 60</td>
<td>80 - 105</td>
<td>100 - 120</td>
</tr>
<tr>
<td><strong>Landform</strong></td>
<td>Floodplain / scattered north – south dunes</td>
<td>Stranded beach ridge (NNW-SSE)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Topography</strong></td>
<td>Undulating dunes ~10m - 30m</td>
<td>Flat</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean annual rainfall (mm)</td>
<td>325 – 350</td>
<td>275 – 300</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Tree density (ha&lt;sup&gt;-1&lt;/sup&gt;)</strong></td>
<td>55.6</td>
<td>23.9</td>
<td>86.9</td>
<td>88.1</td>
</tr>
<tr>
<td><strong>Tree species IV&lt;sup&gt;c&lt;/sup&gt;</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>C. pauper</em></td>
<td>0</td>
<td>0</td>
<td>184.8</td>
<td>182.2</td>
</tr>
<tr>
<td><em>A. leuhmanni</em></td>
<td>145.5</td>
<td>18.0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>C. gracilis</em></td>
<td>38.5</td>
<td>179.5</td>
<td>0</td>
<td>3.5</td>
</tr>
<tr>
<td><em>E. largiflorens</em></td>
<td>8.1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>A. oleifolia</em></td>
<td>0</td>
<td>0</td>
<td>9.1</td>
<td>11.9</td>
</tr>
<tr>
<td><strong>Dead standing tree density (ha&lt;sup&gt;-1&lt;/sup&gt;)</strong></td>
<td>14.6</td>
<td>15.4</td>
<td>11.2</td>
<td>13.7</td>
</tr>
<tr>
<td><strong>Shrub density (ha&lt;sup&gt;-1&lt;/sup&gt;)</strong></td>
<td>79.9</td>
<td>0</td>
<td>1074.4</td>
<td>1784.6</td>
</tr>
<tr>
<td><strong>Physiognomy&lt;sup&gt;d&lt;/sup&gt; (%)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grass/herbs</td>
<td>30.9</td>
<td>72.3</td>
<td>9.2</td>
<td>8.5</td>
</tr>
<tr>
<td>Shrubs (1-3 m)</td>
<td>10.1</td>
<td>0</td>
<td>26.5</td>
<td>32.3</td>
</tr>
<tr>
<td>Shrubs (3-5 m)</td>
<td>3.1</td>
<td>1.4</td>
<td>4.7</td>
<td>4.6</td>
</tr>
</tbody>
</table>

<sup>a</sup> Vegetation data from point-centered quarter-method transects collected during regional surveys (see Chapter 2). Number of transects per patch: Wyp S (4); Wyp N (2); Yarrara (9); Mallanbool (3).

<sup>b</sup> Area of *Casuarina* or *Allocasuarina* – *Callitris* woodland only. Yarrara FFR and Mallanbool FFR also encompass ca. 250 ha and 90 ha of mallee woodland, respectively.

<sup>c</sup> Importance Value (IV) = Relative density (%) + Relative basal area (%)

<sup>d</sup> Horizontal cover estimated in modified Braun-Blanquet scale (see Chapter 2).
Figure 4.1. Location of study areas for investigation of habitat use (Yarrara FFR, Mallanbool FFR, Wyperfeld North and Wyperfeld South-east).
Figure 4.2. Examples of the three main woodland types surveyed.

(a) Belah woodland at Yarrara

(b) Buloke woodland at Wyperfeld SE

(c) Slender Cypress-pine woodland at Wyperfeld N
Placement of habitat plots

Habitat use by the White-browed Treecreeper was examined by measuring the frequency of use across a series of square 1-ha plots (hereafter referred to as habitat plots). Within each woodland tract, there was substantial heterogeneity in habitat structure and to a lesser extent, floristic composition of canopy trees. Habitat plots were selectively placed to sample a gradient of variation in the three habitat components that were the main focus of this study, namely canopy tree density, dead standing tree (DST) density and shrub cover. Because interactions between these components may be significant, an attempt was made to stratify habitat plots amongst three levels (low, intermediate, high) of each component. For example, within the set of habitat plots with low tree density and low shrub cover, plots were sought with low DST density, intermediate DST density and high DST density. However, conditions corresponding to only 12 of the 27 combinations of habitat components were found. It is stressed that because the allocation of habitat plots into density categories was based on a subjective visual assessment, this stratification was used only as a guide for plot placement. All analyses were based on continuous measurements of habitat parameters.

Habitat plots were placed in areas of relatively homogenous habitat in relation to the three major variables of interest, and the corners and mid-points of each side flagged with coloured tape. Habitat plots were usually separated by a minimum of 100 m but it is likely that more than one plot was located within a single White-browed Treecreeper territory in several cases. However, because the response variable is the relative frequency of use, rather than presence/absence or density of birds, this lack of independence does not undermine the sampling strategy.

In total, 96 habitat plots were established in either Belah or Pine-Buloke woodland, with 30 habitat plots located in Wyperfeld S, 15 in Wyperfeld N, 31 in Yarrara FFR and 20 in Mallanbool FFR. Of these, ten were located within 200 m of cropped farmland and designated “hard edge” plots, seven “soft edge” plots bordered open grassland that was not cultivated or grazed by stock, and seven “ecotone” plots were adjacent to another woody vegetation type (e.g. Mallee scrub, Black Box woodland) (Fig 4.3). In addition, six habitat plots were placed in Black Box woodland contiguous with Pine-Buloke woodland at Wyperfeld, and four plots were located in mallee woodland at Yarrara FFR.
Habitat use during the non-breeding season

Censuses of the White-browed Treecreeper

To census White-browed Treecreepers, two perpendicular lines connecting the mid-points of opposite sides of the plot were imagined, dividing the plot into quarters (Fig. 4.2). Fifteen minutes was spent in each habitat plot, consisting of one 3-minute observation period per quarter, plus the time required to move between quarters. The number of White-browed Treecreepers detected within the habitat plot was recorded. Calls were not included unless it could be unequivocally determined the individual was within the plot boundaries.

All censuses were conducted outside of the breeding season in late autumn or winter, minimizing variation in habitat use due to seasonal effects. Each of the 106 habitat plots was censused six times, with three surveys (one survey = 106 habitat plot censuses) in 1998 (20/5-29/5; 24/6-2/7; 4/8-10/8) and three in 1999 (3/5-13/5; 15/6-24/6; 10/8-20/8). The sequence in which plots were censused was not randomized due to logistic practicalities, but varied between surveys. The direction in which I moved around a particular plot alternated between surveys, as did the starting quarter. Censuses were conducted throughout daylight hours because it was anticipated there would be little daily variation in degree of activity at this time of year. This was tested after the 1998 surveys by comparing the frequency of occurrence of White-browed Treecreepers across all 106 plots in censuses conducted between 0600-1000, 1000-1500 and 1500-1900. There was not significant variation between time periods in any of the surveys when considered independently (May: \( \chi^2 = 4.24, \ d.f. = 2, \ P = 0.12 \); June: \( \chi^2 = 0.10, \ d.f. = 2, \ P = 0.99 \); August: \( \chi^2 = 0.52, \ d.f. = 2, \ P = 0.77 \)), nor when combined (\( \chi^2 = 1.69, \ d.f. = 2, \ P = 0.43 \)). Nonetheless, surveys were arranged such that each plot was censused no more than twice during each of the following time periods: 0600-1000, 1000-1200, 1200-1400 and 1400-1800 and there was a maximum of three censuses between 1000 and 1400.

The response variable in all analyses was frequency of use by the White-browed Treecreeper. That is, the number of censuses in which at least one White-browed Treecreeper was detected in a particular habitat plot. This is analogous to reporting rate but because all habitat plots were surveyed six times, it is expressed as a discrete integer rather than a fraction for ease of interpretation. Frequency was chosen because it represents consistency of use for a given hectare of habitat; that is, how often do White-browed Treecreepers use this piece of habitat relative to other areas.
with different habitat characteristics? It is assumed that better quality or preferred habitat will be used more consistently, which will be reflected in a higher frequency count.

**Habitat assessments**

Vegetation composition and structure were sampled using one randomly positioned, 100 m by 10 m, belt transect per habitat plot, which was divided into four 25 m sections (Fig. 4.3). Within each 25 m section, every tree (>8 cm diameter at breast height (DBH)) was counted, including dead trees, and the following measurements recorded: species, DBH (measured with calibrated tape), height (estimated in categories), presence of hollows and extent of lichen cover. Lichen cover on trees was quantified because it was considered an important component of the bark surface (e.g. increase habitat for bark-dwelling invertebrates, change bark texture), which may influence habitat use by bark-foraging species. The number of small dead standing trees (<2 m high) and fallen logs were counted. The number of shrubs in each of three height classes (0.5-1 m, 1-3 m, 3-5 m) was tabulated and the species noted, although species were not enumerated separately. The rest of the habitat plot was searched and shrub species not recorded in the transect were catalogued. The percentage cover of vegetation height categories (physiognomy) and ground layer variables (Table 4.2) within each 25 m section were estimated using a modified Braun-Blanquet scale (see Chapter 2). The properties of the ground layer were measured because treecreepers sometimes forage on the ground, and therefore the characteristics of the ground may influence habitat use. In addition, the composition and complexity of the ground layer (e.g. amount of lichen, mosses, fallen logs, woody debris etc.) is a good indicator of disturbance. Based on the transect data, the vegetation and structural features of each habitat plot were represented by the variables in Table 4.2.
Figure 4.3. 1) Diagram showing placement of habitat plots in an hypothetical patch of Buloke woodland. Density of stippling represents variation in vegetation structure (e.g. tree density) within the Buloke patch. Legend to the different plot types as follows: H – ‘hard edge’; O – ‘soft edge’; E – ‘ecotone’; L – low tree density; I – intermediate tree density; D – high tree density; B – Black Box; M – mallee.

2) Example of belt transect for vegetation sampling, sub-divided into 4 equal sections.

3) Search method employed during bird censuses in habitat plots. Three minutes was spent at each solid dot before progressing to the next quarter. Birds were most likely to be detected within the shaded quarter corresponding to each sample point.
Table 4.2  Vegetation and habitat variables measured in each habitat plot.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Transformation</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Canopy tree layer</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree density (stems ha(^{-1}))</td>
<td>Number of tree stems &gt;8cm DBH.</td>
<td>Natural log</td>
</tr>
<tr>
<td>Mean tree DBH (cm)</td>
<td>Mean tree diameter at breast height.</td>
<td>Natural log</td>
</tr>
<tr>
<td>CV tree DBH</td>
<td>Co-efficient of variation of tree DBH across all trees in the sample.</td>
<td></td>
</tr>
<tr>
<td>Tree dominance (cm(^2)/100m(^2))</td>
<td>Sum of total basal area of all trees, including dead standing trees.</td>
<td></td>
</tr>
<tr>
<td>Mean tree height (m)</td>
<td>Height classes: 0-2, 2-5, 5-10, 10-15 and 15-20 m. Mean height calculated from class midpoint.</td>
<td></td>
</tr>
<tr>
<td>Mean tree lichen cover</td>
<td>Average of tree lichen cover score [0=absent, 1=low (&lt;25% surface covered) or 2=high (&gt;25% surface covered)].</td>
<td></td>
</tr>
<tr>
<td>Hollows (#)</td>
<td>The number of trees with hollows.</td>
<td></td>
</tr>
<tr>
<td>Dead trees (^a)</td>
<td>The density (stems ha(^{-1})) and dominance (cm(^2)/100m(^2)) of dead standing trees &gt;2 m tall.</td>
<td>4(^{th}) square root</td>
</tr>
<tr>
<td>Small dead trees (stems ha(^{-1}))</td>
<td>Number of small dead trees &lt;2 m tall and &lt;8 cm DBH.</td>
<td></td>
</tr>
<tr>
<td><strong>Tree species composition</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Importance Value (score/200)</td>
<td>Sum of relative density and relative dominance for each species, where relative density is the percentage of stems and relative dominance the percentage of total basal area represented by a species. IV calculated for Belah, Buloke, Slender Cypress-pine, Cattlebush, Black Box, Mallee and dead standing trees (irrespective of species).</td>
<td></td>
</tr>
<tr>
<td><strong>Shrub layer</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shrub density (stems ha(^{-1}))</td>
<td>Number of individual stems in 0.5-1m, 1-3 m, 3-5 m height classes, plus total density summed across all three classes.</td>
<td></td>
</tr>
<tr>
<td>Shrub richness (#)</td>
<td>Total number of woody shrub species counted in entire habitat plot.</td>
<td></td>
</tr>
<tr>
<td><strong>Physiognomy</strong>(^b)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vegetation cover (%)</td>
<td>Percent coverage by vertical projection of grass/herbs, woody shrubs &lt;1 m, woody shrubs 1-3 m, woody shrubs or small trees 3-5 m, and canopy trees &gt;5 m. All classes were summed to give total vegetation cover.</td>
<td>Arcsine (^c)</td>
</tr>
</tbody>
</table>
### Ground layer

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Transformation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bare ground (%)</td>
<td>Proportion of ground with exposed soil.</td>
<td>Arcsine</td>
</tr>
<tr>
<td>Coarse litter (%)</td>
<td>Proportion of ground covered by fallen branches, sticks and bark (&lt;8cm diameter, &gt;1cm diameter).</td>
<td>Arcsine</td>
</tr>
<tr>
<td>Fine litter (%)</td>
<td>Proportion of ground covered by branchlets, leaves, seed pods and cones and other small (&lt;1cm) detritus.</td>
<td>Arcsine</td>
</tr>
<tr>
<td>Fallen logs (%)</td>
<td>Proportion of ground covered by fallen logs (&gt;8cm diameter).</td>
<td>Arcsine</td>
</tr>
<tr>
<td>Fallen log density (# ha(^{-1}))</td>
<td>Count of fallen logs with some part of log inside the transect.</td>
<td>Natural log</td>
</tr>
<tr>
<td>Lichen (%)</td>
<td>Proportion of ground covered by lichen.</td>
<td>Arcsine + Sqrt</td>
</tr>
<tr>
<td>Moss (%)</td>
<td>Proportion of ground covered by moss and bryophytes.</td>
<td>Arcsine</td>
</tr>
</tbody>
</table>

\(^{a}\) All dead standing trees taller than 2 m were counted, irrespective of diameter. This was because many dead trees had lost or shed their bark or were decaying, which made it impossible to accurately measure their true DBH over bark.

\(^{b}\) The plot estimate was derived from the mean of the mid-point of the % cover estimates for the physiognomy height classes and ground cover variables in each of the four sections per belt transect.

\(^{c}\) Some cover variables required further transformation (grass/herb cover – Natural log; shrub <1 m – Square root; shrubs & trees 3-5 m – Natural log).
Habitat plots were placed in areas that appeared homogeneous at a one-hectare scale, with respect to tree density and shrub cover. However, to assess homogeneity within habitat plots quantitatively, the coefficient of variation among the 25 m sections was calculated for the following variables: tree density, mean tree DBH, tree dominance and total shrub density. The mean physiognomic cover values for the entire transect were also used to quantify vertical heterogeneity (D) (after Wiens et al. 1987) using Hill’s (1973) diversity index:

\[ D = \frac{1}{\sum p_i^2}, \]

where \( p_i \) is the proportion of the \( i^{th} \) structural class.

An index of horizontal heterogeneity (HH) within each habitat plot was developed (following Freemark & Merriam 1986), using an index derived from the Shannon information function:

\[ HH = \sum_{i=1}^{r} \sum_{j=1}^{c} x_{ij} \ln(x_{ij}/X_i) \]

where \( r \) is the total number of variables used to characterize \( c \) transect sections, \( x_{ij} \) is the value for the \( i^{th} \) variable in the \( j^{th} \) transect section and \( X_i \) is the mean for variable \( i \).

For all habitat plots, \( c = 4 \). Horizontal heterogeneity was calculated for the tree layer (\( HH_{\text{tree}} \)), using mean tree density and mean tree DBH (\( r = 2 \)), and for the shrub/ground layer (\( HH_{\text{shrub}} \)), incorporating the physiognomic cover categories and percentage cover of bare ground, coarse litter, fine litter and fallen logs (\( r = 9 \)).

**Data analysis**

**Paired comparisons**

The frequency with which White-browed Treecreepers used ‘hard edge’, ‘soft edge’ and ‘ecotone’ habitat plots, and Black Box and mallee plots, was assessed by firstly matching each ‘test’ plot with a ‘control’ plot, using hierarchical clustering. For example, to find interior habitat plots that were structurally and floristically similar to edge plots, I entered all habitat variables in Table 4.2 (except for the ground layer variables) plus D, \( HH_{\text{tree}} \) and \( HH_{\text{shrub}} \) as standardized z-scores in an hierarchical cluster analysis of the 96 Belah or Pine-Buloke habitat plots. From the resulting dendrogram, I selected the closest ‘reasonable’ interior plot as the control for each edge plot. One ‘hard edge’ and two ‘ecotone’ test plots could not be matched with
control plots and were excluded from comparisons. I repeated this procedure with a second cluster analysis to match Black Box and mallee plots with similarly structured control plots, but excluded the floristic variables and all edge plots from the analysis. The control plot in a matched pair was selected from the same region as the test plot (i.e. Wyperfeld – Wyperfeld and Yarrara – Yarrara). Frequency of use in the test plot was then compared with the control plot using the marginal homogeneity test for paired samples of categorical data (SPSS v.10).

**Principal components analysis**

Principal Components Analysis (PCA) was conducted to examine the relationship between habitat plots in environmental space. First, the distribution of all habitat parameters was checked (histograms, probability-plots, Kolmogorov-Smirnov test for normality) and transformations were applied to those variables that were not normally distributed (see Table 4.2). The bimodal distribution of ‘trees with hollows’ and ‘small DST density’ could not be improved by transformation, and both variables were excluded from the analysis. A Pearson correlation matrix was then constructed for the remaining 29 variables. Pairs or complexes of variables with $|r| > 0.7$ were represented in the PCA by a single variable. This reduced the matrix to 20 variables by 96 habitat plots. All components with eigenvalues $>1$ were extracted and a Varimax rotation was applied to the final solution to aid interpretation of the extracted components.

Frequency of use by White-browed Treecreepers was examined in relation to the PCA ordination of habitat plots. PCA scores were also used as dependent variables in one-way ANOVA between frequency of use response categories.

**Multivariate modelling of habitat use**

The general approach to modelling was to construct the most parsimonious model from a set of candidate explanatory variables to identify the habitat features to which White-browed Treecreepers were responding in their choice of habitat. Frequency of habitat plot use was modelled using ordinal logistic regression (OLR) (McCullagh & Nelder 1989, Hosmer & Lemeshow 2000) because the response variable was restricted to one of seven ordinal categories (0, 1, 2, 3, 4, 5 or 6). Ordinal logistic
regression models the probability that a plot belongs to each frequency-of-use category as a function of the habitat properties of that plot, retaining the information inherent in the ordinal rank of the response variable (North & Reynolds 1996). The logit link function is used to derive category probabilities as a linear function of the significant explanatory variables, and model constants and parameter estimates are based on maximum likelihood estimation. North and Reynolds (1996) provide a detailed discussion and example of the application of OLR to habitat selection by the Northern Spotted Owl *Strix occidentalis caurina*.

Two types of habitat use models were developed. First, I used components 1 to 6 from the PCA analysis as the explanatory variables of frequency of habitat plot use (the *PCA model*). The second model focused on habitat features that were originally identified as potential determinants of habitat selectivity by White-browed Treecreepers, namely tree density, tree dominance, HH\textsubscript{tree}, dead standing tree (DST) dominance, and horizontal vegetation cover in the 0-1 m, 1-3 m and 3-5 m height categories. This model was called the *direct model* because habitat variables were entered directly into the model. Habitat use models were developed at a “regional” scale, using all 96 habitat plots, and at a sub-regional or “district” scale for the Yarrara district (51 plots) and Wyperfeld district (45 plots), respectively.

As the population of habitat plots was not truly random, but drawn from a limited population of woodland tracts (i.e. Yarrara FFR, Mallanbool FFR, Wyperfeld SE and Wyperfeld N), there was potential for dependency in habitat use by White-browed Treecreepers within tracts. Before constructing the OLR models, I tested for dependency within the data by including ‘tract’ as a random effect in a generalized linear mixed model that included the explanatory variables from the PCA model and direct model, respectively, as co-variates (Bennington & Thayne 1994). To examine the significance of ‘tract’ in influencing habitat use, I used the residual maximum likelihood (REML) procedure in GenStat 5 (VSN 2000) to assess the change in deviance when ‘tract’ was excluded from the full model (e.g. Legge 2000). The residuals from the mixed model were checked to ensure they were approximately normally distributed (Neave et al. 1996). If there was no evidence of dependency within patches, OLR proceeded with ‘tract’ excluded from the analysis.

Ordinal logistic regression models were fitted manually using both backwards elimination and forward stepwise selection of terms. The significance of explanatory
variables was assessed by examining the change in the model log-likelihood statistic when terms were either removed or added to the model. Polynomial quadratic expressions (i.e. \( x + x^2 \)) for tree density, tree dominance and vegetation cover were examined by comparing the change in deviance of models when linear terms were replaced by their quadratic expression.

A final model was constructed for each scenario (i.e. model type by spatial scale) and interactions between significant parameters were examined. The planes of the frequency of use categories versus the final model parameters were tested for parallel slopes (North & Reynolds 1996). For the regional scale models, the fitted models were again subject to the REML procedure (i.e. generalized linear mixed model with ‘tract’ as the random effect), to check that there was not dependency within the data when the statistical noise created by non-significant model co-variates was removed. The probability of the frequency of use in each plot being in each ordinal category was then determined (logit link function) as a function of the significant parameters in the final models. The PLUM procedure in SPSS v.10 was used for all ordinal logistic regressions.

The performance of the final models was assessed by their classification error (i.e. the proportion of plots that are erroneously classified given the final model parameters). Classification error derived from the same data used to construct the model will bias the results. To assess the extent of this bias in the current modelling, I used the jack-knifing technique suggested by North and Reynolds (1996). In brief, this involves removing a single observation (habitat plot) from the data, re-estimating the model parameters and applying the re-fitted model to the excluded observation. The predicted ordinal category is then compared to the observed category. This is repeated for each observation in the dataset, building up an unbiased estimate of classification error (North & Reynolds 1996). As SPSS does not have any facility to automate this process, the jack-knifing procedure was highly repetitive and time-consuming. Therefore, it was only applied to one model, and the ‘jack-knifed’ classification error was compared to the ‘raw’ classification error.
4.3 Results

Occurrence of White-browed Treecreepers

White-browed Treecreepers were detected at least once in 68 of the 96 (71%) habitat plots. However, treecreepers were detected on significantly more plots in the Yarrara district (92%) than at Wyperfeld (47%) (Yates $\chi^2 = 25.7$, $P < 0.001$; Fig. 4.4a). Moreover, at Yarrara, White-browed Treecreepers were detected on an average of $33.3 \pm 2.8\%$ of plots per survey, compared with $13.3 \pm 1.3\%$ of plots per survey at Wyperfeld.

White-browed Treecreepers were detected only once in the six surveys at 27 habitat plots, twice at 18 plots, three times at 16 plots, four times at six plots and five times at one plot. For all analyses, frequency categories 4 and 5 were combined. The distribution of the detection frequency categories differed between the districts ($\chi^2 = 29.6$, $d.f. = 4$, $P < 0.001$). At Wyperfeld, White-browed Treecreepers were not detected in the majority of plots, and the detection frequency followed a negative exponential distribution (Fig. 4.4b). In contrast, many habitat plots at Yarrara had multiple detections of White-browed Treecreepers (Fig. 4.4b).
Figure 4.4a. Number of habitat plots in which White-browed Treecreepers were detected at least once during the six survey rounds, in the Wyperfeld and Yarrara districts, respectively.

Figure 4.4b. Frequency of detection of White-browed Treecreepers in habitat plots at Wyperfeld and Yarrara.
Use of edge plots

White-browed Treecreepers used habitat plots adjacent to cultivated paddocks (hard edge), open grassland (soft edge) and other woody vegetation types (ecotone) at the same frequency as interior control plots (Table 4.3).

Table 4.3 Frequency of habitat plot use by White-browed Treecreepers in edge and control plots. Marginal homogeneity tests were used to compare frequency of use in edge and control plots.

<table>
<thead>
<tr>
<th></th>
<th>Hard Edge</th>
<th>Soft Edge</th>
<th>Ecotone</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Edge</td>
<td>Control</td>
<td>Edge</td>
</tr>
<tr>
<td>n</td>
<td>9 pairs</td>
<td>7 pairs</td>
<td>5 pairs</td>
</tr>
<tr>
<td>Range in detection frequency</td>
<td>0 - 3</td>
<td>0 - 3</td>
<td>0 - 4</td>
</tr>
<tr>
<td>Median detection frequency</td>
<td>2.0</td>
<td>1.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Std. MH statistic</td>
<td>-0.775</td>
<td>-0.180</td>
<td>0.577</td>
</tr>
<tr>
<td>Significance</td>
<td>0.439</td>
<td>0.857</td>
<td>0.564</td>
</tr>
</tbody>
</table>

Use of Black Box and mallee

At Wyperfeld, habitat use by White-browed Treecreepers showed a strong trend towards plots in Buloke or Cypress-pine in preference to habitat plots in Black Box (Table 4.4). White-browed Treecreepers were not detected in any of the six Black Box plots in any of the six surveys. Similarly, at Yarrara FFR, the four mallee plots were not used as frequently as the control Belah woodland plots, although White-browed Treecreepers were detected in each of three mallee plots on one occasion (Table 4.4). The biological significance of these results is probably greater than indicated by the statistical significance of the tests, given the small number of comparisons and correspondingly, the high risk of Type II errors. The test plots were in vegetation contiguous with the control woodland, and given that White-browed Treecreepers did not actively avoid edge habitat, it is unlikely that the lower detection frequencies result from spatial segregation of the contrasting vegetation types.
Table 4.4. Frequency of habitat plot use by White-browed Treecreepers in Black Box and Mallee plots and the respective control plots. Marginal homogeneity tests were used to compare frequency of use in test and control plots.

<table>
<thead>
<tr>
<th></th>
<th>Wyperfeld</th>
<th>Yarrara</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Black Box</td>
<td>Control</td>
</tr>
<tr>
<td>( n )</td>
<td>6 pairs</td>
<td>4 pairs</td>
</tr>
<tr>
<td>Range in detection frequency</td>
<td>0 - 0</td>
<td>0 - 2</td>
</tr>
<tr>
<td>Median detection frequency</td>
<td>0.0</td>
<td>1.0</td>
</tr>
<tr>
<td>Std. MH statistic</td>
<td>1.897</td>
<td>1.886</td>
</tr>
<tr>
<td>Significance</td>
<td>0.058</td>
<td>0.059</td>
</tr>
</tbody>
</table>

**Relationships among habitat plots**

**Summary of habitat variables**

The vegetation and habitat characteristics varied greatly among the habitat plots within each of the districts, but there were also consistent dissimilarities between the habitat at Wyperfeld and Yarrara (Table 4.5). Tree density ranged over two orders of magnitude, from a low of 10 trees ha\(^{-1}\) at Wyperfeld, to very dense stands of nearly 1000 trees ha\(^{-1}\) in Yarrara FFR. Tree density was generally lower at Wyperfeld, but tree dominance was higher because mean tree diameter was greater at Wyperfeld. There was less variation in size among individual trees (CV tree DBH) in the Wyperfeld habitat plots, but the Yarrara plots were more homogeneous in terms of the spacing of trees as reflected by lower HH\(_{\text{tree}}\) values. The dominance of dead trees was greater at Wyperfeld, where stands of dead Cypress were common. However, the prevalence of trees with hollows was higher at Yarrara, where there were up to 90 trees with hollows per plot, although most plots had less than 10 hollow-bearing trees.

The extent of grass or herb cover varied from virtually absent to greater than 50% vertical projection. Habitat plots at Wyperfeld had more grass cover than those at Yarrara, although the variation in the proportion of bare ground was similar between the two districts. Woody shrub cover ranged from zero (several Wyperfeld plots) to approximately 50% (many Yarrara plots). The maximum cover of 52% in the 1-3 m
height range corresponds to a shrub stem density of 3740 ha$^{-1}$ and 20 species within the habitat plot. In contrast, there was relatively little variation in cover in the 3-5 m class, although plots at Yarrara were consistently shrubbier. Variation in canopy cover (>5 m) reflects variation in tree density, ranging from zero to above 40%, with little difference in the extent of variation between Wyperfeld and Yarrara. Habitat plots at Yarrara generally had greater vertical structural diversity, due to greater woody shrub cover in the 0-3 m height range. Horizontal heterogeneity within the different physiognomic height classes (HH$_{shrub}$) varied considerably amongst the 96 habitat plots, but the degree of variation was consistent between the two districts.

**Principal components analysis**

The seven PCA components with eigenvalues greater than one accounted for 78% of the variation in the full data matrix (Table 4.6). Fifteen of the 20 variables have their strongest correlation with one of the first three components. The first component represents a gradient from woodlands characterized by large trees that are widely, but patchily spaced, with a grassy understorey, through to woodlands comprised of several shrub layers and smaller trees that are more closely and uniformly spaced. Component 2 represents the tree layer, and is positively associated with tree density, tree dominance, canopy cover and dead standing tree dominance. Ground layer variables are most closely aligned with the third component, representing a gradient from a relatively undisturbed ground layer with high moss cover and many fallen logs through to a more disturbed environment with high exposure of bare ground.

Components 4 to 7 tend to be dominated by one or two variables, for which the component loadings are much higher than for all other variables. Component 4 differentiates between plots with low and high lichen cover, which is usually positively associated with canopy cover. Component 5 contrasts habitat plots with low horizontal heterogeneity of shrubs and low vertical structural diversity to those with a more patchy and complex vegetation structure. The sixth component represents the volume of fallen timber, being positively correlated with coarse woody debris cover and fallen log density. The final component represents total vegetation cover, and is largely redundant because each of its constituent elements is strongly associated with one of the earlier components.
Table 4.5. Values of selected vegetation and structural variables in habitat plots [mean ± s.d.; (range)]. Significant differences between districts are designated by superscript (A, B: lower case \( P < 0.05 \), upper case \( P < 0.01 \)).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Wyperfeld (( n = 45 ))</th>
<th>Yarrara (( n = 51 ))</th>
<th>Total (( n = 96 ))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree density (stems ha(^{-1}))</td>
<td>141.6 ± 103.9 (^{A}) (10 – 500)</td>
<td>218.2 ± 145.7 (^{B}) (20 – 980)</td>
<td>182.3 ± 132.9 (10 – 980)</td>
</tr>
<tr>
<td>Tree dominance (cm(^2)/100m(^2))</td>
<td>802.9 ± 298.4 (^{A}) (169.5 – 1456.8)</td>
<td>534.2 ± 307.7 (^{B}) (41.1 – 1289.3)</td>
<td>660.1 ± 330.5 (41.1 – 1456.8)</td>
</tr>
<tr>
<td>Mean tree DBH (cm)</td>
<td>30.2 ± 9.1 (^{A}) (14.4 – 53.3)</td>
<td>16.8 ± 4.2 (^{B}) (8.6 – 27.4)</td>
<td>23.1 ± 9.6 (8.6 – 53.3)</td>
</tr>
<tr>
<td>CV tree DBH</td>
<td>33.3 ± 15.6 (^{A}) (0 – 75.4)</td>
<td>57.6 ± 18.3 (^{B}) (30.0 – 111.9)</td>
<td>46.2 ± 20.9 (0 – 111.9)</td>
</tr>
<tr>
<td>Mean tree lichen cover (cm(^2)/100m(^2))</td>
<td>0.96 ± 0.28 (^{a}) (0 – 1.5)</td>
<td>1.12 ± 0.32 (^{b}) (0.3 – 1.9)</td>
<td>1.05 ± 0.31 (0 – 1.9)</td>
</tr>
<tr>
<td>Number of trees with hollows (ha(^{-1}))</td>
<td>3.3 ± 7.4 (0 – 30)</td>
<td>8.2 ± 20.1 (0 – 90)</td>
<td>5.9 ± 15.6 (0 – 90)</td>
</tr>
<tr>
<td>DST dominance (cm(^2)/100m(^2))</td>
<td>224.3 ± 183.4 (^{A}) (0 – 741.5)</td>
<td>47.7 ± 183.4 (^{B}) (0 – 194.8)</td>
<td>130.5 ± 155.9 (0 – 741.5)</td>
</tr>
<tr>
<td>Fellon log density (ha(^{-1}))</td>
<td>229 ± 178 (^{a}) (0 – 800)</td>
<td>162 ± 127 (^{b}) (0 – 700)</td>
<td>194 ± 156 (0 – 700)</td>
</tr>
<tr>
<td>Bare ground cover (%)</td>
<td>49.3 ± 10.9 (28.8 – 75.0)</td>
<td>46.0 ± 16.7 (12.5 – 87.5)</td>
<td>47.6 ± 14.3 (12.5 – 87.5)</td>
</tr>
<tr>
<td>Coarse litter cover (%)</td>
<td>4.5 ± 1.9 (1.1 – 8.3)</td>
<td>4.3 ± 2.0 (1.8 – 10.0)</td>
<td>4.4 ± 1.9 (1.1 – 10.0)</td>
</tr>
<tr>
<td>Ground lichen cover (%)</td>
<td>0.7 ± 1.1 (^{a}) (0 – 5.0)</td>
<td>3.8 ± 2.0 (^{b}) (0.3 – 10.8)</td>
<td>2.3 ± 2.2 (0 – 10.8)</td>
</tr>
<tr>
<td>Moss cover (%)</td>
<td>5.9 ± 4.7 (0 – 17.6)</td>
<td>3.3 ± 5.1 (0 – 24.4)</td>
<td>4.5 ± 5.1 (0 – 24.4)</td>
</tr>
<tr>
<td>Grass/herb cover (%)</td>
<td>25.2 ± 16.3 (^{A}) (1.8 – 62.5)</td>
<td>4.6 ± 5.5 (^{B}) (0.1 – 26.3)</td>
<td>14.2 ± 15.7 (0.1 – 62.5)</td>
</tr>
<tr>
<td>Woody shrub 0-1m cover (%)</td>
<td>1.7 ± 2.8 (^{A}) (0 – 16.9)</td>
<td>14.3 ± 8.9 (^{B}) (2.4 – 39.4)</td>
<td>8.4 ± 9.2 (2.4 – 39.4)</td>
</tr>
<tr>
<td>Woody shrub 1-3m cover (%)</td>
<td>4.8 ± 7.9 (^{A}) (0 – 30.6)</td>
<td>14.8 ± 10.1 (^{B}) (0.3 – 51.9)</td>
<td>10.1 ± 10.4 (0 – 51.9)</td>
</tr>
<tr>
<td>Woody vegetation 3-5m (%)</td>
<td>1.2 ± 2.5 (^{A}) (0 – 14.4)</td>
<td>2.1 ± 2.1 (^{B}) (0 – 11.5)</td>
<td>1.7 ± 2.3 (0 – 14.4)</td>
</tr>
<tr>
<td>Canopy &gt;5m cover (%)</td>
<td>12.1 ± 8.7 (0.8 – 35.0)</td>
<td>13.6 ± 10.1 (0.8 – 43.8)</td>
<td>12.9 ± 9.5 (0.8 – 43.8)</td>
</tr>
<tr>
<td>Total vegetation cover (%)</td>
<td>45.0 ± 10.3 (26.8 – 68.8)</td>
<td>49.4 ± 16.8 (16.5 – 83.8)</td>
<td>47.3 ± 14.2 (16.5 – 83.8)</td>
</tr>
<tr>
<td>Vertical diversity (D)</td>
<td>2.12 ± 0.85 (^{A}) (1.02 – 3.88)</td>
<td>3.06 ± 0.55 (^{B}) (2.13 – 4.57)</td>
<td>2.62 ± 0.85 (1.02 – 4.57)</td>
</tr>
<tr>
<td>HH shrub</td>
<td>61.1 ± 25.8 (19.4 – 113.2)</td>
<td>60.5 ± 24.0 (16.7 – 125.6)</td>
<td>60.8 ± 24.8 (16.7 – 125.6)</td>
</tr>
</tbody>
</table>
Table 4.6. Principal components analysis of the variation in vegetation and habitat characteristics in the 96 habitat plots. Variables are listed in decreasing order of factor loadings. Underscoring designates the principal component with which each variable has the highest loading.

<table>
<thead>
<tr>
<th>Component</th>
<th>Component 1</th>
<th>Component 2</th>
<th>Component 3</th>
<th>Component 4</th>
<th>Component 5</th>
<th>Component 6</th>
<th>Component 7</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eigenvalue</td>
<td>4.716</td>
<td>2.704</td>
<td>1.752</td>
<td>1.671</td>
<td>1.615</td>
<td>1.610</td>
<td>1.605</td>
</tr>
<tr>
<td>% variation explained</td>
<td>23.6</td>
<td>13.5</td>
<td>8.8</td>
<td>8.4</td>
<td>8.1</td>
<td>8.1</td>
<td>8.1</td>
</tr>
<tr>
<td>Cumulative %</td>
<td>37.1</td>
<td>45.9</td>
<td>54.2</td>
<td>62.3</td>
<td>70.3</td>
<td>78.4</td>
<td></td>
</tr>
</tbody>
</table>

**Positive**

CV tree DBH***

Ground lichen cover***

Woody shrub cover 0-1m***

Vertical diversity***

Woody shrub cover 1-3m***

Tree density***

Woody veg. cover 3-5m***

**Negative**

Mean tree DBH***

HH_tree***

Moss cover***

Grass/herb cover***

Grass/herb cover 1-3m*

HH_tree***

Tree dominance**

Mean tree DBH***

HH_tree***

Moss cover***

Grass/herb cover***

Grass/herb cover 1-3m*

HH_tree***

Tree dominance**

* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$
An ordination of the 96 habitat plots defined by components 1 and 3 clearly differentiates between the Wyperfeld and Yarrara districts on component 1 (Fig. 4.3). This reflects the woodland structure at Wyperfeld, characterized by large trees at relatively low density and a grassy understorey, in contrast to the higher tree density and extensive shrub cover, and therefore vertical structural diversity at Yarrara. Within each district, the tracts separate along component 3, with higher moss cover and more fallen logs, and less bare ground and sparser low shrub (1-3 m) cover found at Yarrara and Wyp N than at Mallanbool and Wyp SE, respectively.

Figure 4.5. Distribution of habitat plots in environmental space defined by PCA component 1 and PCA component 3.
Habitat use by the White-browed Treecreeper

Univariate analysis

Habitat use was initially examined using Spearman’s rank correlation. At the regional extent, frequency of plot use was positively correlated with tree density and negatively correlated with patchiness in tree spacing (HH\textsubscript{tree}) (Table 4.8). In those habitat plots with higher tree density, mean tree size was generally smaller but there was more variation in size between trees (CV tree DBH), which accounts for the significant negative and positive associations between plot use and these variables, respectively. Plots with high grass and herb cover were visited less frequently, and consistency of plot use increased with increasing shrub cover and structural diversity, and decreasing horizontal patchiness in shrub cover (Table 4.8). There was a positive association between lichen cover (ground and tree) and White-browed Treecreeper habitat use (Table 4.8).

Many of the significant relationships at the regional scale did not hold at the district scale (i.e. extent) of investigation (Table 4.8). Within the 45 habitat plots at Wyperfeld, none of the measured variables were significantly correlated with frequency of plot use by White-browed Treecreepers. At Yarrara, some of the associations evident at the regional scale were maintained, such as the positive correlation with tree density and negative correlation with grass and herb cover. However, most of the significant relationships were not sustained. Tree dominance and canopy cover were not correlated with habitat use at the regional scale but emerged as significant variables at Yarrara. The direction of the significant correlation between vertical diversity (D) and frequency of plot use changed from positive at a regional scale to negative at a district scale. This indicates that amongst all 96 plots, White-browed Treecreepers favour those with greater vertical structural diversity but within Yarrara, where vertical diversity is generally complex, they use plots with less complex vertical structure more frequently.
Table 4.8. Spearman rank correlations between frequency of detection of White-browed Treecreepers and characteristics of habitat plots. Only significant ($P < 0.05$) correlations are shown.

<table>
<thead>
<tr>
<th></th>
<th>Region</th>
<th>Wyperfeld</th>
<th>Yarrara</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>96</td>
<td>45</td>
<td>51</td>
</tr>
<tr>
<td><strong>Woodland structure</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree density</td>
<td>0.341**</td>
<td></td>
<td>0.331*</td>
</tr>
<tr>
<td>Tree dominance</td>
<td></td>
<td></td>
<td>0.281*</td>
</tr>
<tr>
<td>Mean tree DBH</td>
<td>-0.378***</td>
<td></td>
<td></td>
</tr>
<tr>
<td>CV tree DBH</td>
<td>0.332**</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$HH_{tree}$</td>
<td></td>
<td></td>
<td>-0.350***</td>
</tr>
<tr>
<td><strong>Physiognomy</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grass/herb cover</td>
<td>-0.501***</td>
<td></td>
<td>-0.394**</td>
</tr>
<tr>
<td>Woody shrub 0-1m</td>
<td>0.444***</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Woody shrub 1-3m</td>
<td>0.278**</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Canopy cover</td>
<td></td>
<td></td>
<td>0.322*</td>
</tr>
<tr>
<td>Vertical diversity D</td>
<td>0.223*</td>
<td></td>
<td>-0.372**</td>
</tr>
<tr>
<td>$HH_{shrub}$</td>
<td>-0.207*</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Habitat condition</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree lichen cover</td>
<td>0.239*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ground lichen cover</td>
<td>0.528***</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$

Habitat plots were categorized according to their frequency of use by White-browed Treecreepers as ‘not detected’, ‘low use’ (detected on 1 or 2 surveys) or ‘high use’ (detected on 3 or more surveys), and habitat variables summarized for each category (Table 4.9). Differences between the fixed main effects of ‘district’ and ‘frequency of use’ were initially tested using two-way ANOVA. However, this analysis was confounded by a sampling anomaly that stemmed from two important differences between the districts: significant differences in vegetation and habitat characteristics (Table 4.5) and unequal distribution of plots amongst the frequency of use categories (Fig.4.4b). This resulted in biased weighting of the ‘not detected’ sample with Wyperfeld plots and, conversely, Yarrara plots dominated the ‘high use’ sample. This anomaly produced ambiguous results, masking several important trends in some instances and generating ‘artificial’ differences in other variables. Thus, one-way
ANOVA were used to examine differences between frequency of use categories for the region, and separately for each district.

At the regional extent, tree density, variation in tree size, ground lichen cover, woody shrub cover 0-3 m, tree canopy cover and vertical structural diversity were significantly higher in ‘high use’ plots than ‘not detected’ plots. Most of these variables were also significantly higher in the ‘low use’ plots than plots in which treecreepers were not detected (Table 4.9). Conversely, mean tree size, patchiness in tree spacing, and grass and herb cover were significantly higher in ‘not detected’ plots (Table 4.9).

At Wyperfeld, habitat plots in which treecreepers were not detected had significantly less cover of ground lichen than either ‘low use’ or ‘high use’ plots. There were no other significant differences detected at Wyperfeld (Table 4.9).

At Yarrara, ‘high use’ and ‘low use’ plots had significantly less grass and herb, and woody shrub 3-5 m cover than ‘not detected’ plots. ‘High use’ plots also had significantly greater canopy cover than ‘not detected’ plots (Table 4.9).

Of the 21 variables examined, only tree dominance, tree lichen cover and ground lichen cover showed consistent trends with frequency of use categories at both Wyperfeld and Yarrara (Table 4.9). All three variables increased with frequency of use by White-browed Treecreepers.
Table 4.9. Vegetation and habitat characteristics (mean ± s.e.) of habitat plots categorized by frequency of use by the White-browed Treecreeper. Variables in red text showed consistent trends with frequency of use at both Wyperfeld and Yarrara.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Extent 1</th>
<th>Not detected 2</th>
<th>Low use 3</th>
<th>High use 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree density (stems ha⁻¹)</td>
<td>Wyp</td>
<td>145.4 ± 25.8</td>
<td>133.1 ± 20.7</td>
<td>150.0 ± 10.5</td>
</tr>
<tr>
<td></td>
<td>Yar</td>
<td>145.0 ± 44.1</td>
<td>194.5 ± 18.6</td>
<td>272.8 ± 46.6</td>
</tr>
<tr>
<td></td>
<td>Region**</td>
<td>145.4 ± 22.8ᵃ</td>
<td>172.7 ± 14.6ᵇ</td>
<td>246.1 ± 37.9ᵇ</td>
</tr>
<tr>
<td>Tree dominance (cm³/100m²)</td>
<td>Wyp</td>
<td>776.0 ± 67.2</td>
<td>801.6 ± 71.4</td>
<td>936.0 ± 67.8</td>
</tr>
<tr>
<td></td>
<td>Yar</td>
<td>387.5 ± 264.1</td>
<td>488.7 ± 41.9</td>
<td>639.9 ± 83.3</td>
</tr>
<tr>
<td></td>
<td>Region</td>
<td>720.5 ± 71.4</td>
<td>600.0 ± 43.0</td>
<td>704.3 ± 71.1</td>
</tr>
<tr>
<td>Mean tree DBH (cm)</td>
<td>Wyp</td>
<td>31.2 ± 2.3</td>
<td>29.7 ± 1.8</td>
<td>27.1 ± 1.1</td>
</tr>
<tr>
<td></td>
<td>Yar</td>
<td>13.9 ± 3.2</td>
<td>17.0 ± 0.7</td>
<td>17.2 ± 0.9</td>
</tr>
<tr>
<td></td>
<td>Region**</td>
<td>28.7 ± 2.3ᵃ</td>
<td>21.5 ± 1.2ᵇ</td>
<td>19.3 ± 1.2ᵇ</td>
</tr>
<tr>
<td>CV tree DBH</td>
<td>Wyp</td>
<td>33.4 ± 3.5</td>
<td>30.7 ± 3.2</td>
<td>41.2 ± 6.7</td>
</tr>
<tr>
<td></td>
<td>Yar</td>
<td>55.7 ± 12.3</td>
<td>61.3 ± 3.6</td>
<td>51.9 ± 3.4</td>
</tr>
<tr>
<td></td>
<td>Region*</td>
<td>36.6 ± 3.7ᵃ</td>
<td>50.4 ± 3.4ᵇ</td>
<td>49.6 ± 3.1ᵇ</td>
</tr>
<tr>
<td>Mean tree lichen cover (score of 0, 1, or 2)</td>
<td>Wyp</td>
<td>0.95 ± 0.06</td>
<td>0.95 ± 0.06</td>
<td>1.1 ± 0.07</td>
</tr>
<tr>
<td></td>
<td>Yar</td>
<td>0.95 ± 0.26</td>
<td>1.1 ± 0.06</td>
<td>1.2 ± 0.05</td>
</tr>
<tr>
<td></td>
<td>Region</td>
<td>0.95 ± 0.06</td>
<td>1.0 ± 0.05</td>
<td>1.2 ± 0.04</td>
</tr>
<tr>
<td>Number of trees with hollows (ha⁻¹)</td>
<td>Wyp</td>
<td>2.1 ± 0.08</td>
<td>5.0 ± 2.7</td>
<td>4.0 ± 2.4</td>
</tr>
<tr>
<td></td>
<td>Yar</td>
<td>7.5 ± 7.5</td>
<td>5.9 ± 2.4</td>
<td>12.2 ± 6.8</td>
</tr>
<tr>
<td></td>
<td>Region</td>
<td>2.9 ± 1.2</td>
<td>5.6 ± 1.8</td>
<td>10.4 ± 5.4</td>
</tr>
<tr>
<td>DST dominance (cm³/100m²)</td>
<td>Wyp</td>
<td>206.5 ± 31.7</td>
<td>261.9 ± 56.2</td>
<td>189.0 ± 80.6</td>
</tr>
<tr>
<td></td>
<td>Yar</td>
<td>31.1 ± 11.4</td>
<td>44.8 ± 7.0</td>
<td>56.0 ± 11.3</td>
</tr>
<tr>
<td></td>
<td>Region</td>
<td>181.5 ± 29.6</td>
<td>122.0 ± 25.5</td>
<td>84.9 ± 21.7</td>
</tr>
<tr>
<td>HHₜree</td>
<td>Wyp</td>
<td>25.4 ± 4.9</td>
<td>17.4 ± 4.3</td>
<td>8.9 ± 6.9</td>
</tr>
<tr>
<td></td>
<td>Yar</td>
<td>3.6 ± 2.0</td>
<td>5.6 ± 1.3</td>
<td>4.2 ± 1.5</td>
</tr>
<tr>
<td></td>
<td>Region**</td>
<td>22.3 ± 4.4ᵃ</td>
<td>9.8 ± 1.9ᵇ</td>
<td>5.3 ± 1.9ᵇ</td>
</tr>
<tr>
<td>Fallen log density (ha⁻¹)</td>
<td>Wyp</td>
<td>237 ± 37</td>
<td>167 ± 31</td>
<td>390 ± 103</td>
</tr>
<tr>
<td></td>
<td>Yar</td>
<td>50 ± 16</td>
<td>171 ± 26</td>
<td>173 ± 24</td>
</tr>
<tr>
<td></td>
<td>Region</td>
<td>210 ± 34</td>
<td>170 ± 20</td>
<td>220 ± 34</td>
</tr>
<tr>
<td>Bare ground cover (%)</td>
<td>Wyp</td>
<td>48.5 ± 1.7</td>
<td>50.6 ± 3.3</td>
<td>49.1 ± 7.0</td>
</tr>
<tr>
<td></td>
<td>Yar</td>
<td>42.0 ± 3.2</td>
<td>46.6 ± 3.3</td>
<td>45.8 ± 3.9</td>
</tr>
<tr>
<td></td>
<td>Region</td>
<td>47.6 ± 1.6</td>
<td>48.0 ± 2.4</td>
<td>46.5 ± 3.4</td>
</tr>
<tr>
<td>Coarse litter cover (%)</td>
<td>Wyp</td>
<td>4.6 ± 0.4</td>
<td>4.3 ± 0.4</td>
<td>4.6 ± 1.2</td>
</tr>
<tr>
<td></td>
<td>Yar</td>
<td>3.8 ± 1.1</td>
<td>4.4 ± 0.4</td>
<td>4.3 ± 0.4</td>
</tr>
<tr>
<td></td>
<td>Region</td>
<td>4.5 ± 0.4</td>
<td>4.4 ± 0.3</td>
<td>4.3 ± 0.4</td>
</tr>
<tr>
<td>Ground lichen cover (%)</td>
<td>Wyp*</td>
<td>0.4 ± 0.1ᵃ</td>
<td>1.1 ± 0.3ᵇ</td>
<td>1.1 ± 1.0ᵇ</td>
</tr>
<tr>
<td></td>
<td>Yar</td>
<td>2.1 ± 0.7</td>
<td>3.8 ± 0.3ᵇ</td>
<td>4.2 ± 0.5</td>
</tr>
<tr>
<td></td>
<td>Region***</td>
<td>0.6 ± 0.2ᵃ</td>
<td>2.8 ± 0.3ᵇ</td>
<td>3.5 ± 0.5ᵇ</td>
</tr>
<tr>
<td>Moss cover (%)</td>
<td>Wyp</td>
<td>5.4 ± 1.0</td>
<td>6.4 ± 1.2</td>
<td>6.5 ± 1.5</td>
</tr>
<tr>
<td></td>
<td>Yar</td>
<td>6.0 ± 2.7</td>
<td>3.3 ± 1.1</td>
<td>2.6 ± 0.9</td>
</tr>
<tr>
<td></td>
<td>Region</td>
<td>5.5 ± 0.9</td>
<td>4.4 ± 0.8</td>
<td>3.5 ± 0.8</td>
</tr>
</tbody>
</table>
Multi-variate analysis

A multi-variate approach to describing habitat use patterns may account for co-variation in habitat characteristics more clearly. The principal components ordination of habitat plot characteristics, differentiated by the frequency of White-browed Treecreeper detection (Fig. 4.6), illustrates three key points. First, increasing detection with component 1 indicates White-browed Treecreepers used habitat plots in relatively dense woodland, associated with a complex and vigorous shrub layer, more consistently than plots containing widely and irregularly spaced trees that were...
coupled with a sparse and structurally simple grassy understorey. The highest frequencies were attained in plots with high, but not extreme, scores for component 1, indicative of a decline in habitat use when shrub density exceeds a comfortable limit. Second, there was a tendency for White-browed Treecreepers to favour plots in the mid to upper range of component 4, which are characterized by abundant ground and tree lichen. Third, there was a clear trend for frequency of use to decrease in plots in the upper range of component 5. This suggests White-browed Treecreepers were less inclined to use areas with a very patchy shrub layer brought about by relatively high cover in the 3-5 m height class. The most distinct separation of habitat plots with respect to frequency of use is achieved by an ordination of components 1 and 5. Plots with high frequency of use are clustered in the lower right portion of this ordination, which represents woodland with a high density of evenly spaced, relatively small trees and a moderate to high density shrub community that is low in stature (<3m), consistent in its horizontal cover and undisturbed.

One-way analysis of variance of component scores in relation to frequency of use categories supported the graphical ordinations (Fig. 4.7). The response of the White-browed Treecreeper to variables incorporated in components 1, 4 and 5 was reiterated. In contrast, frequency of plot use did not vary significantly with respect to components 2, 3 and 6. Thus, at a regional scale, neither the characteristics of the tree layer in isolation from the shrub strata (component 2), nor the ground layer variables (components 3 and 6) appear to exert a significant influence on habitat utilization by White-browed Treecreepers.

Each of the woodland tracts surveyed occupies a different portion of the ordination of components 1 and 5 (Fig. 4.8). The positive association between component 1 and frequency of detection that was evident at the regional scale is discernible only at Wyperfeld SE when each tract is examined separately. There were no conspicuous trends between habitat use and component 1 at Yarrara FFR, Mallanbool FFR or Wyperfeld N (Fig. 4.8). The negative association between component 5 and frequency of detection is also obscured when the extent of examination is reduced. Whilst the pattern appears to hold at Wyperfeld SE and to a lesser extent at Yarrara FFR, the frequency of use of habitat plots at Wyperfeld N and Mallanbool FFR does not appear to be related to component 5 (Fig. 4.8).
Figure 4.6. Principal components ordination of habitat plots, differentiated by frequency of detection of White-browed Treecreepers.
Figure 4.7. Comparison of principal component scores between frequency of detection categories. P-values refer to one-way ANOVA.
Figure 4.8. Frequency of detection of White-browed Treecreepers in each patch in relation to environmental space as defined by PC 1 and PC 5. Size of circles indicates frequency of detection (see Fig 4.6).
**Multivariate modelling of habitat use**

**Regional models**

There was no change in model deviance when the random effect of ‘tract’ was removed from the full regional *PCA model*, and negligible change when removed from the *direct model* ($\chi^2 = 0.04$). Thus, there was no evidence of dependency within woodland tracts for either model, and ordinal logistic regression proceeded without ‘tract’ as an explanatory variable.

**PCA model**

Forward selection and backward elimination of the principal components produced the same final model (Table 4.10). At the regional scale, the probability of a plot belonging to a high frequency of use category was positively related to both component 1 and component 4 (Table 4.11). Habitat plots with low values of both component 1 and component 4 (low density woodland with grassy understorey) were unlikely to be used at all by White-browed Treecreepers. In contrast, there was a better than 50% probability of consistent use of plots (detected on $\geq 50\%$ of surveys) in the upper range of the observed values for both PCA components, which reflects high tree density, high shrub cover, complex vertical structure and abundant lichen cover (Fig. 4.9).

This model correctly allocated 43% of habitat plots to their observed frequency of use response category (i.e. classification error = 57%). However, given that there are five response categories, this is a stringent test of model accuracy. Only 21% of plots were misclassified by more than one response category, analogous to 79% accuracy in allocation of plots to low, moderate and high frequency of use categories. The model underestimated frequency of habitat use in 75% of the plots that were misclassified by more than one response group. The performance of the model was not improved by including an interaction term and the slope co-efficients for each parameter did not differ significantly across the response categories (i.e. null hypothesis test of parallel planes was not rejected). The fitted model was subjected to the REML procedure, and again there was no change in deviance when the random effect of “tract” was removed from a model that also included components 1 and 4.
Table 4.10.  Forward selection and backward elimination of principal components for the ordinal logistic regression model of habitat plot use at a regional scale ($n = 96$ plots).

<table>
<thead>
<tr>
<th>Current model</th>
<th>PC 1</th>
<th>PC 2</th>
<th>PC 3</th>
<th>PC 4</th>
<th>PC 5</th>
<th>PC 6</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forward selection</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept only +</td>
<td>24.89***</td>
<td>0.10</td>
<td>0.01</td>
<td>8.07**</td>
<td>2.32</td>
<td>0.03</td>
</tr>
<tr>
<td>Intercept + C1 +</td>
<td>1.54</td>
<td>0.00</td>
<td>9.93**</td>
<td>1.84</td>
<td>0.29</td>
<td></td>
</tr>
<tr>
<td>Intercept + C1 + C4 +</td>
<td>2.23</td>
<td>0.05</td>
<td>1.97</td>
<td>0.35</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Backward elimination</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Full model -</td>
<td>27.16***</td>
<td>2.16</td>
<td>0.04</td>
<td>10.75**</td>
<td>2.03</td>
<td>0.03</td>
</tr>
</tbody>
</table>

* Change in deviance follows a $\chi^2$ distribution with 1 d.f.
  *** = $P < 0.001$, ** = $P < 0.01$.

Table 4.11.  Final ordinal logistic regression model of habitat plot use at the regional scale, as determined from principal components.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>s.e.</th>
<th>Wald</th>
<th>$P$</th>
<th>95% CI: lower</th>
<th>95% CI: upper</th>
</tr>
</thead>
<tbody>
<tr>
<td>Threshold</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Frequency of use = 0</td>
<td>-1.101</td>
<td>0.257</td>
<td>18.321</td>
<td>&lt;0.001</td>
<td>-1.606</td>
<td>-0.597</td>
</tr>
<tr>
<td>Frequency of use = 1</td>
<td>0.521</td>
<td>0.237</td>
<td>4.843</td>
<td>0.028</td>
<td>0.057</td>
<td>0.984</td>
</tr>
<tr>
<td>Frequency of use = 2</td>
<td>1.597</td>
<td>0.280</td>
<td>32.576</td>
<td>&lt;0.001</td>
<td>1.049</td>
<td>2.145</td>
</tr>
<tr>
<td>Frequency of use = 3</td>
<td>3.109</td>
<td>0.430</td>
<td>52.195</td>
<td>&lt;0.001</td>
<td>2.266</td>
<td>3.953</td>
</tr>
<tr>
<td>Variables</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Component 1</td>
<td>1.052</td>
<td>0.219</td>
<td>23.127</td>
<td>&lt;0.001</td>
<td>0.623</td>
<td>1.480</td>
</tr>
<tr>
<td>Component 4</td>
<td>0.617</td>
<td>0.198</td>
<td>9.714</td>
<td>0.002</td>
<td>0.229</td>
<td>1.005</td>
</tr>
</tbody>
</table>
Figure 4.9. Predictions of the fitted ordinal logistic regression ‘PCA model’ for the probability of frequency of use of habitat plots by the White-browed Treecreeper at the regional extent. In (a), component 4 is held constant at its mean value, and in (b) component 1 is held at its mean value. Confidence intervals are omitted for simplicity (but see Table 4.11)
Direct model

Preliminary assessments showed that quadratic expressions for shrub cover in the 1-3 m and 3-5 m height classes explained slightly more variation in habitat use than their respective linear expressions, and hence were used in model fitting procedures. The method of model fitting affected the selection of parameters, with shrub cover (0-1 m) and horizontal heterogeneity of the tree layer significant in forward selection, and shrub cover (1-3 m) and tree density fitted by backward elimination (Table 4.12). The performance of the backward elimination model was marginally superior in terms of classification accuracy (exact response group: 38% vs. 36% correct; within one response group: 82% vs. 78% correct) and was therefore the preferred model (Table 4.13).

The probability of regular use by the White-browed Treecreeper increased with shrub cover (1-3 m) and tree density (Fig. 4.10). A plot with approximately 170 trees had a 75% chance of being used at least once but only a 20% probability of being used consistently (≥ 50% of surveys) (Fig. 4.10b). In comparison, a plot with 350 trees had a 90% chance of being used at least once and nearly 40% probability of being used regularly (Fig. 4.10b). The model tended to be conservative in its predictions, with the frequency of habitat use underestimated in 14 of the 17 plots that were misclassified by more than one response group. Once again, the inclusion of an interaction term did not significantly improve the model; the null hypothesis for the test of parallel planes was not rejected; and the random effect of “tract” in the fitted model was not significant ($\chi^2 = 1.71$).
Table 4.12. Forward selection and backward elimination of parameters in ordinal logistic regression of the direct model of habitat plot use at a regional scale (n = 96 habitat plots).

<table>
<thead>
<tr>
<th>Current model</th>
<th>Tree density&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Tree dominance</th>
<th>HH&lt;sub&gt;tree&lt;/sub&gt;&lt;sup&gt;b&lt;/sup&gt;</th>
<th>DST dominance&lt;sup&gt;c&lt;/sup&gt;</th>
<th>Cover 0-1 m&lt;sup&gt;d&lt;/sup&gt;</th>
<th>Cover 1-3 m&lt;sup&gt;e&lt;/sup&gt;</th>
<th>Cover 3-5 m&lt;sup&gt;b,e&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Forward selection</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept only</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>11.62***</td>
<td>0.14</td>
<td>15.14***</td>
<td>1.63</td>
<td>19.99***</td>
<td>*</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td>Intercept + Cover 0-1m</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4.68*</td>
<td>0.34</td>
<td>5.09*</td>
<td>0.04</td>
<td>1.70</td>
<td>0.33</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept + Cover 0-1m + HH&lt;sub&gt;tree&lt;/sub&gt;</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.13</td>
<td>0.09</td>
<td>1.46</td>
<td>2.27</td>
<td>0.44</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Backward elimination</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Full model</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3.66†</td>
<td>0.01</td>
<td>1.47</td>
<td>1.36</td>
<td>1.47</td>
<td>4.85*</td>
<td>2.45</td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> Change in deviance follows a χ² distribution with 1 d.f.

*** = P < 0.001, ** = P < 0.01, * = P < 0.05, † = P < 0.1.

<sup>b</sup> Natural log transformation

<sup>c</sup> 4<sup>th</sup> square root transformation

<sup>d</sup> Square root transformation

<sup>e</sup> Quadratic expression (x + x²) used

---

Table 4.13. Final ordinal logistic regression model of habitat plot use at the regional scale (direct model).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>s.e.</th>
<th>Wald</th>
<th>P</th>
<th>95% CI: lower</th>
<th>95% CI: upper</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Threshold</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Frequency of use = 0</td>
<td>1.342</td>
<td>0.569</td>
<td>5.559</td>
<td>0.018</td>
<td>0.226</td>
<td>2.458</td>
</tr>
<tr>
<td>Frequency of use = 1</td>
<td>2.762</td>
<td>0.619</td>
<td>19.935</td>
<td>&lt;0.001</td>
<td>1.550</td>
<td>3.974</td>
</tr>
<tr>
<td>Frequency of use = 2</td>
<td>3.772</td>
<td>0.666</td>
<td>21.124</td>
<td>&lt;0.001</td>
<td>2.468</td>
<td>5.076</td>
</tr>
<tr>
<td>Frequency of use = 3</td>
<td>5.304</td>
<td>0.775</td>
<td>46.866</td>
<td>&lt;0.001</td>
<td>3.785</td>
<td>6.823</td>
</tr>
<tr>
<td><strong>Variables</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree density</td>
<td>1.664</td>
<td>0.490</td>
<td>11.534</td>
<td>0.001</td>
<td>0.704</td>
<td>2.625</td>
</tr>
<tr>
<td>Shrub cover 1-3 m + (Shrub cover 1-3 m)&lt;sup&gt;2&lt;/sup&gt;</td>
<td>2.125</td>
<td>0.635</td>
<td>11.205</td>
<td>0.001</td>
<td>0.881</td>
<td>3.369</td>
</tr>
</tbody>
</table>
Figure 4.10. Predictions of the fitted ordinal logistic regression ‘direct model’ for the probability of frequency of use of habitat plots by the White-browed Treecreeper at the regional extent. In (a), tree density is held constant at its mean value, and in (b) shrub cover (1-3 m) is held at its mean value. Confidence intervals are omitted for simplicity (but see Table 4.13).

Values relate to the quadratic expression of the arcsine transformation of % shrub cover.
District models

Wyperfeld

The null model could not be significantly improved by the inclusion of any of the principal components (Table 4.14). Component 1 was closest to inclusion in the fitted model in both backward elimination ($P = 0.179$) and forward selection ($P = 0.075$). Similarly, none of the variables included in the direct model significantly improved the null model (Table 4.15). Removal ($P = 0.119$) or addition ($P = 0.095$) of HHtree caused the largest change in model deviance, and was negatively associated with frequency of use. However, it appears that neither the principal components nor any of the habitat parameters included in the direct model significantly affect the frequency of use of habitat plots by the White-browed Treecreeper at Wyperfeld.

Table 4.14 Forward selection and backward elimination of principal components for the ordinal logistic regression model of habitat plot use at Wyperfeld ($n = 45$ plots).

<table>
<thead>
<tr>
<th>Current model</th>
<th>Change in deviance$^a$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PC 1</td>
</tr>
<tr>
<td>Forward selection</td>
<td></td>
</tr>
<tr>
<td>Intercept only +</td>
<td>3.17†</td>
</tr>
<tr>
<td>Backward elimination</td>
<td></td>
</tr>
<tr>
<td>Full model -</td>
<td>1.81</td>
</tr>
</tbody>
</table>

$^a$ Change in deviance follows a $\chi^2$ distribution with 1 d.f. † = $P < 0.1$.

Table 4.15 Forward selection and backward elimination of parameters in ordinal logistic regression of the direct model of habitat plot use at Wyperfeld ($n = 45$ plots).

<table>
<thead>
<tr>
<th>Current model</th>
<th>Change in deviance$^{a,b}$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Tree density</td>
</tr>
<tr>
<td>Forward selection</td>
<td></td>
</tr>
<tr>
<td>Intercept only +</td>
<td>0.27</td>
</tr>
<tr>
<td>Backward elimination</td>
<td></td>
</tr>
<tr>
<td>Full model -</td>
<td>0.45</td>
</tr>
</tbody>
</table>

$^a$ Change in deviance follows a $\chi^2$ distribution with 1 d.f. † = $P < 0.1$.

$^b$ See Table 4.12 for transformations used for habitat variables.
The effect of lichen cover was not envisaged to be significant at the outset of this study and hence was not included as a potential parameter in the direct model. However, subsequent to the univariate analysis, ground lichen cover was considered worthy of closer examination. It significantly improved the null model in forward selection \((\chi^2 = 3.85, P = 0.05)\), and its removal from the full model also caused a significant change in model deviance \((\chi^2 = 5.74, P = 0.017)\). Frequency of plot use was positively associated with lichen cover. A model that included only ground lichen cover correctly assigned 60% of plots to their exact frequency of use, and 82% of plots within one response group.

**Yarrara**

Components 2 and 4 were selected as significant parameters in the PCA model at Yarrara by both forward selection and backward elimination (Table 4.16). Component 2 is strongly associated with the tree layer, being positively correlated with tree density, tree dominance, canopy cover and dominance of dead trees. Frequency of plot use was positively related to both components (Table 4.17). At low values of component 2 (relatively sparse woodland), frequency of plot use was predicted to be low, with a 50% chance that White-browed Treecreepers would be present on only one of the six surveys (Fig. 4.11a). Plots in the mid-range of component 2 were predicted to be occupied on two surveys, and plots in the upper range (highest tree density, canopy cover) were most likely to be occupied on 50% of surveys (Fig. 4.11a). A similar pattern is predicted for component 4, which is related to the abundance of ground and tree lichen, and the amount of canopy cover. Within the range of scores for component 4 observed at Yarrara, the predicted frequency of use shifts from one out of every six surveys at low values to two surveys in the mid-range to three surveys for high values (Fig. 4.11b).

The model was not improved by inclusion of an interaction term and the test for parallel slopes was not significant. The exact classification error of the model was high (73%). However, 80% of plots were classified correctly within one response group. In the remaining 20% of plots that were misclassified by more than one response group, there was an equal number of over- and under-estimates of frequency of habitat use.
Table 4.16. Forward selection and backward elimination of principal components for the ordinal logistic regression model of habitat plot use at Yarrara (n = 51 plots).

<table>
<thead>
<tr>
<th>Current model</th>
<th>PC 1</th>
<th>PC 2</th>
<th>PC 3</th>
<th>PC 4</th>
<th>PC 5</th>
<th>PC 6</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Forward selection</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept only +</td>
<td>0.21</td>
<td>5.49*</td>
<td>0.13</td>
<td>7.18**</td>
<td>2.05</td>
<td>0.98</td>
</tr>
<tr>
<td>Intercept + C4 +</td>
<td>1.80</td>
<td>5.22*</td>
<td>0.70</td>
<td>3.89*</td>
<td>0.65</td>
<td></td>
</tr>
<tr>
<td>Intercept + C4 + C2 +</td>
<td>2.41</td>
<td>1.11</td>
<td>3.77†</td>
<td>1.94</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Backward elimination</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Full model -</td>
<td>0.22</td>
<td>6.21*</td>
<td>0.68</td>
<td>6.11*</td>
<td>1.28</td>
<td>0.44</td>
</tr>
</tbody>
</table>

* Change in deviance follows a \( \chi^2 \) distribution with 1 d.f.
*** = \( P < 0.001 \), ** = \( P < 0.01 \), * = \( P < 0.05 \), † = \( P < 0.1 \).

Table 4.17. Final ordinal logistic regression model of habitat plot use in the Yarrara district, as determined from principal components.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>s.e.</th>
<th>Wald</th>
<th>( P )</th>
<th>95% CI: lower</th>
<th>95% CI: upper</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Threshold</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Frequency of use = 0</td>
<td>-2.808</td>
<td>0.578</td>
<td>23.612</td>
<td>&lt;0.001</td>
<td>-3.940</td>
<td>-1.675</td>
</tr>
<tr>
<td>Frequency of use = 1</td>
<td>-0.612</td>
<td>0.331</td>
<td>3.419</td>
<td>0.064</td>
<td>-1.262</td>
<td>0.037</td>
</tr>
<tr>
<td>Frequency of use = 2</td>
<td>0.766</td>
<td>0.332</td>
<td>5.332</td>
<td>0.021</td>
<td>0.115</td>
<td>1.418</td>
</tr>
<tr>
<td>Frequency of use = 3</td>
<td>2.591</td>
<td>0.507</td>
<td>26.105</td>
<td>&lt;0.001</td>
<td>1.597</td>
<td>3.585</td>
</tr>
<tr>
<td><strong>Variables</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Component 2</td>
<td>0.672</td>
<td>0.293</td>
<td>5.255</td>
<td>0.022</td>
<td>0.097</td>
<td>1.246</td>
</tr>
<tr>
<td>Component 4</td>
<td>0.657</td>
<td>0.262</td>
<td>6.260</td>
<td>0.012</td>
<td>0.142</td>
<td>1.171</td>
</tr>
</tbody>
</table>
Figure 4.11. Predictions of the fitted ordinal logistic regression ‘PCA model’ for the probability of frequency of use of habitat plots by the White-browed Treecreeper in the Yarrara district. In (a), component 4 is held constant at its mean value, and in (b) component 2 is held at its mean value. Confidence intervals are omitted for simplicity (but see Table 4.17).
There were differences in the parameters selected by forward selection and backward elimination for the direct model of habitat use at Yarrara. Tree dominance was the first parameter fitted in forward selection, followed by vegetation cover (3-5 m) (Table 4.18). However, although the removal of vegetation cover (3-5 m) from the full model resulted in a significant change in model deviance, tree dominance was not significant (Table 4.18). However, the change in deviance and goodness-of-fit statistics were superior for the two-parameter model, which was chosen as the final model (Table 4.19).

The predicted probability of use increased with tree dominance (Fig. 4.12a). However, White-browed Treecreepers were so prevalent at Yarrara that even in plots with very low tree cover (~100 cm² / 100 m²), the model predicted an 85% probability of treecreepers being present on at least one of the six surveys (Fig. 4.12a). Plots at Yarrara with a tree dominance of 700 cm² / 100 m² had a 95% probability of being used to some degree by White-browed Treecreepers. As the level of tree dominance increased, the probability of more frequent use increased, with a better than 70% chance that plots with high tree dominance (>1200 cm² / 100 m²) would be occupied on three or more of the six survey rounds.

It was surprising that vegetation cover (3-5m) was a significant explanatory parameter because the range of values recorded was limited (raw values: 0% – 11.5%). Nonetheless, treecreepers were less inclined to forage in areas with comparatively high cover of tall shrubs (Fig. 4.12b). That the quadratic expression explained slightly more of the variation in habitat use than the linear term suggests that the intensity of the behavioural response increased as vegetation cover increased.

The classification error of this model was 71%. However, only 16% of plots were misclassified by more than one response group, suggesting the model is reasonably good at allocating plots to broad habitat use categories. Habitat use was underestimated in seven of the eight plots that were misclassified by more than one response group.
### Table 4.18. Forward selection and backward elimination of parameters in ordinal logistic regression of the direct model of habitat plot use at Yarrara (n = 51 plots).

<table>
<thead>
<tr>
<th>Current model</th>
<th>Tree density</th>
<th>Tree dominance</th>
<th>( HH_{tree} )</th>
<th>DST dominance</th>
<th>Cover 0-1 m</th>
<th>Cover 1-3 m</th>
<th>Cover 3-5 m</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Forward selection</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept only +</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4.48*</td>
<td>5.12*</td>
<td>0.83</td>
<td>1.23</td>
<td>0.30</td>
<td>0.10</td>
<td>3.51†</td>
<td></td>
</tr>
<tr>
<td>Intercept + Tree dominance +</td>
<td>0.90</td>
<td>0.08</td>
<td>0.03</td>
<td>0.01</td>
<td>0.65</td>
<td>4.98*</td>
<td></td>
</tr>
<tr>
<td>Intercept + Tree dominance +</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cover 3-5m +</td>
<td>1.00</td>
<td>0.07</td>
<td>0.27</td>
<td>0.21</td>
<td>0.73</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Backward elimination</strong></td>
<td>1.77</td>
<td>2.55</td>
<td>0.38</td>
<td>0.01</td>
<td>0.20</td>
<td>1.60</td>
<td>5.45*</td>
</tr>
</tbody>
</table>

\( ^{a} \) Change in deviance follows a \( \chi^2 \) distribution with 1 d.f.

\( ^{b} \) See Table 4.12 for transformations used for habitat variables

### Table 4.19. Final ordinal logistic regression model of habitat plot use in the Yarrara district (direct model).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>s.e.</th>
<th>Wald</th>
<th>( P )</th>
<th>95% CI: lower</th>
<th>95% CI: upper</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Threshold</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Frequency of use = 0</td>
<td>-2.569</td>
<td>0.788</td>
<td>10.621</td>
<td>0.001</td>
<td>-4.114</td>
<td>-1.024</td>
</tr>
<tr>
<td>Frequency of use = 1</td>
<td>-0.456</td>
<td>0.650</td>
<td>0.492</td>
<td>0.483</td>
<td>-1.731</td>
<td>0.819</td>
</tr>
<tr>
<td>Frequency of use = 2</td>
<td>0.942</td>
<td>0.659</td>
<td>2.043</td>
<td>0.153</td>
<td>-0.350</td>
<td>2.233</td>
</tr>
<tr>
<td>Frequency of use = 3</td>
<td>2.680</td>
<td>0.779</td>
<td>11.833</td>
<td>0.001</td>
<td>1.153</td>
<td>4.207</td>
</tr>
<tr>
<td><strong>Variables</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vegetation cover (3-5 m) +</td>
<td>-8.263</td>
<td>3.626</td>
<td>5.195</td>
<td>0.023</td>
<td>-15.369</td>
<td>-1.157</td>
</tr>
<tr>
<td>Vegetation cover (3-5 m)²</td>
<td>-0.0024</td>
<td>0.001</td>
<td>6.858</td>
<td>0.009</td>
<td>0.0006</td>
<td>0.0042</td>
</tr>
<tr>
<td>Tree dominance</td>
<td>0.0024</td>
<td>0.001</td>
<td>6.858</td>
<td>0.009</td>
<td>0.0006</td>
<td>0.0042</td>
</tr>
</tbody>
</table>
Figure 4.12. Predictions of the fitted ordinal logistic regression ‘direct model’ for the probability of frequency of use of habitat plots by the White-browed Treecreeper in the Yarrara district. In (a), vegetation cover (3-5m) is held constant at its mean value, and in (b) tree dominance is held at its mean. Confidence intervals are omitted for simplicity (but see Table 4.19).

*Values relate to the quadratic expression of the arcsine transformation of % vegetation cover.
**Model Assessment**

The direct model at Yarrara (i.e. Table 4.19) was subjected to formal model assessment via the jack-knife procedure. Overall, 78% of habitat plots were misclassified with respect to their observed frequency of use category. This compares with the classification error of 71% derived from the ‘raw’, or biased, estimation. Using the more liberal interpretation of correct classification (i.e. within one response group), the jack-knifed classification error of 20% compares favourably with the raw estimate of 16%. These comparisons suggest that although the raw classification error overestimates model performance, the difference is small, particularly when broad categories of frequency of habitat use are used.

A partition of the error within the model indicates that the model is better at predicting which plots will be used at low and moderate levels than identifying plots that will be used repeatedly by treecreepers (Table 4.20). That is, the model tends to be conservative in its predictions of frequency of use. Further, the model does not cope well with extremes of habitat use, as it did not allocate any plots to the zero or 4+ frequency of use categories. This implies that the model could be improved by the inclusion of a parameter that ‘fine-tunes’ the model predictions at the extremes of frequency of use.

**Table 4.20.** The percentage of habitat plots classified into each frequency of use category by the jack-knife procedure for the direct ordinal logistic regression model of habitat use at Yarrara. Dark shading indicates percentage of plots correctly classified to the exact category of observed use; light shading indicates percentage of plots correctly classified within one response category.

<table>
<thead>
<tr>
<th>Observed use</th>
<th>Total (n)</th>
<th>Predicted use: 0</th>
<th>Predicted use: 1</th>
<th>Predicted use: 2</th>
<th>Predicted use: 3</th>
<th>Predicted use: 4+</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>4</td>
<td>0%</td>
<td>75%</td>
<td>0%</td>
<td>25%</td>
<td>0%</td>
</tr>
<tr>
<td>1</td>
<td>14</td>
<td>0%</td>
<td>35.7%</td>
<td>50%</td>
<td>14.3%</td>
<td>0%</td>
</tr>
<tr>
<td>2</td>
<td>15</td>
<td>0%</td>
<td>53.3%</td>
<td>6.7%</td>
<td>40%</td>
<td>0%</td>
</tr>
<tr>
<td>3</td>
<td>13</td>
<td>0%</td>
<td>23.1%</td>
<td>38.5%</td>
<td>38.5%</td>
<td>0%</td>
</tr>
<tr>
<td>4+</td>
<td>5</td>
<td>0%</td>
<td>20%</td>
<td>60%</td>
<td>20%</td>
<td>0%</td>
</tr>
</tbody>
</table>
4.4 Discussion

Factors affecting habitat use by the White-browed Treecreeper

It is critical to determine the spatial scale at which processes of habitat selection are operating (Sherry & Holmes 1985, Wiens 1989b, MacNally & Quinn 1998). The geographic extent over which White-browed Treecreepers appeared to be selecting areas with greater tree density, low-stature shrub cover, abundance of lichen and vertical structural diversity, and lower mean tree diameter, grass and herb cover, and patchiness of the shrub layer. For brevity, I shall refer to this collection of variables as the regional syndrome.

However, the regional extent (sensu Allen & Starr 1982) was greater than the lifetime home range of an individual White-browed Treecreeper, and therefore beyond the universe of experience for individual birds. Thus, it is inappropriate, and potentially misleading, to interpret the results of the regional analysis in terms of the processes of habitat selection by individual birds. Moreover, much of the variation between habitat plots at Wyperfeld and Yarrara is captured by the regional syndrome. It was also clear that the population density of the White-browed Treecreeper was higher in the Yarrara district than at Wyperfeld. Thus, the regional syndrome may reflect the discrepancy in population density between districts rather than the habitat preferences of individual birds per se.

Analysis of habitat use at the district scale produced a different outcome. At Yarrara, habitat use by the White-browed Treecreeper was predominantly influenced by the tree component of the habitat, reflected in the positive association with tree density, tree dominance, canopy cover and quantity of dead wood. The sub-canopy stratum was also important, with habitat use curtailed in areas with a relatively high density of tall shrubs and saplings. White-browed Treecreepers tended to avoid areas with high grass and herb cover, which may have been a surrogate for low tree density. Few habitat variables adequately described habitat use of the White-browed Treecreepers at Wyperfeld. The most consistent bird-habitat relationship was a positive association with the abundance of ground lichen, with less convincing trends for tree dominance and variation in tree spacing and size (HHtree).
How do these findings compare with my original expectations that White-browed Treecreepers would preferentially select areas with higher tree density, larger trees, more hollows and more dead timber? In a regional context, White-browed Treecreepers were detected more often in areas with greater tree density. Further, the effect of tree density is largely responsible for the significant positive association of habitat use with tree dominance that was evident in both districts. Contrary to expectations, and most other studies of bark-foraging and cavity-nesting birds (e.g. Noske 1985, Adams & Morrison 1993, Newton 1994, Weikel & Hayes 1999, Luck 2000), habitat use at the regional scale was negatively correlated with tree size, and no significant relationship with the abundance of hollow-bearing trees or dead timber was detected. However, it is probably more informative to examine habitat use at a local scale to determine how birds relate to the habitat they occupy.

At Yarrara, frequency of plot use was higher in areas with greater tree dominance, due to increases in both tree density and mean tree size (Table 4.9). However, mean tree diameter was not a significant explanatory variable of frequency of use. At Wyperfeld, mean tree size was not significantly related with habitat use but the direction of the association was negative, contrary to expectations. Thus, the spacing or density of trees in a stand appears to influence habitat use by the White-browed Treecreeper more than the size of trees. The dominance of dead standing trees was not a significant factor in either district, although the positive association between dead tree dominance and habitat use was in the direction anticipated.

Hollows are a critical resource for the reproductive success of the White-browed Treecreeper and the availability of suitable hollows for nesting must direct habitat selection by White-browed Treecreepers to some degree. The absence of a consistent relationship between habitat use and the abundance of hollow-bearing trees in this study may be because the grain of investigation was too coarse to detect nest-site selection. However, it is more likely that because this study was conducted during the non-breeding season, nest-site characteristics were less influential in determining habitat use. Habitat use often tracks seasonal variation in resource requirements, resulting in seasonal shifts in habitat selectivity (e.g. Hutto 1985a, Ford & Paton 1985, Robinson 1992, Cale 1994, Keane & Morrison 1999). Thus, a different view of habitat use may have been obtained during the breeding season. Even so, the plots at Wyperfeld in which no treecreepers were detected invariably had few hollow-bearing
trees, suggesting that such areas were less likely to regularly attract White-browed Treecreepers.

Statistical models of habitat selection inevitably over-simplify the response of animals to variation in the spatial and temporal distribution of resources. In this study, considerable variation in habitat use could not be explained by the parameters included in the modelling process. Moreover, the models were inclined to underestimate frequency of habitat use, suggesting that White-browed Treecreepers were exploiting a wider range of resources than could be accounted for in the models. Thus, whilst the models are adequate for an overview of habitat use, they fail to encompass the subtleties or diversity of resource use exhibited by the White-browed Treecreeper. However, I am unable to distinguish whether this study has overlooked key variables pertinent to habitat use by the White-browed Treecreeper (i.e. the models lack subtlety), or whether their habitat use is too diverse to be accurately described by a handful of vegetation characteristics.

**Spatial variation in habitat use**

The degree of heterogeneity in habitat parameters, as measured by the coefficient of variation, was similar between habitat plots at Wyperfeld and Yarrara. However, the bird-habitat relationships were generally stronger, and White-browed Treecreepers appeared to be using different habitat features as proximate environmental cues for habitat use at Yarrara. What might be causing this spatial variation in the patterns of habitat use?

One possible explanation might lie in the difference between the districts in absolute values of many of the habitat parameters, coupled with non-linear relationships between behavioural responses and habitat parameters (Meents *et al.* 1983). Consider the shape of a curve representing frequency of use versus a hypothetical habitat variable (Fig. 4.13). Suppose that an animal infrequently uses habitat with low values of the variable, and that the response of the animal is relatively insensitive to increases in the variable up to a given level. The slope of the curve representing this behavioural response will be less than one. Once a threshold level of the habitat variable is reached, frequency of use increases rapidly in relation to changes in the variable, such that the slope is now greater than one. It is likely that beyond a second
threshold the animal’s response plateaus because frequency of use has an upper limit (i.e. all the time) whereas the habitat variable may theoretically be infinite. The animal’s response to changes in the habitat variable could be defined as selective when the slope of the response curve is greater than one (Fig. 4.13).

Given the large differences in habitat structure between Wyperfeld and Yarrara, it is feasible that the range of values for several habitat characteristics (e.g. tree density, tree dominance) in the respective districts may occupy different parts of the response curve (Fig. 4.13). Thus, White-browed Treecreepers may respond selectively to the habitat variable at one location but not another, even though the grain of investigation and the degree of heterogeneity (reflected in the distance occupied along the x-axis) is equivalent in the two study areas. The inclusion of quadratic terms in some of the ordinal regression models (e.g. vegetation cover (3-5 m)) supports the existence of non-linear responses.

Spatial variation in habitat use may also be amplified by abiotic or biotic factors that render otherwise suitable resources unavailable in one location but not at another (Block & Brennan 1993, McShea et al. 1995). Interspecific constraints on habitat use have been demonstrated for closely related species in a variety of habitats (Cody 1985, but see Wiens 1989a). At Wyperfeld, the abundance of the Brown Treecreeper seemed to be greater and they were dispersed throughout the woodland, compared with Yarrara where they were primarily confined to plots around the edge of woodland tracts. Thus, competitive exclusion by Brown Treecreepers may have limited White-browed Treecreepers from using suitable habitat at Wyperfeld, a constraint that was not as apparent at Yarrara. Consequently, differences between habitat that was used frequently and habitat that was under-utilized at Wyperfeld were minimal, obscuring habitat selectivity.

The geographic variation in habitat selectivity may also be related to the differences in population density between the districts (Svärdson 1949, Fretwell & Lucas 1969, Rosenzweig 1985). Under Fretwell and Lucas’ "ideal-free" model, habitat use is most selective at low population densities because individuals have unrestricted access to the range of habitats available and should use the most suitable habitat preferentially (Wiens et al. 1987, Rosenzweig 1991). The results of this study are inconsistent with this model because White-browed Treecreepers appeared to be more selective at higher densities. However, the flip-side of the “ideal-free” model is
that habitat which is intrinsically less suitable (e.g. Wyperfeld) may be adequate if the population density is lower than in superior habitat (e.g. Yarrara) (Cody 1985). A primary assumption here is that there is a trade-off between low intraspecific competition and low "quality" habitat. Thus, individuals inhabiting lower quality habitat at lower densities may be less selective in their habitat use because they must exploit a wider range of resources to fulfill their basic requirements.

Figure 4.13. Non-linear relationship between frequency of use and a hypothetical environmental variable. Habitat selection is only apparent between threshold 1 and threshold 2, when the slope (r) of the behavioural response is greater than 1. A hypothetical situation is depicted whereby the range of values for the environmental variable at Wyperfeld span the section of the response curve that does not show habitat selection, whereas selection is apparent for the range of values at Yarrara.

Adaptive significance of habitat use

Whilst the correlative approach used in most studies of habitat use (including this one) is informative for describing and predicting where animals live, explanations of
the underlying causal mechanisms of habitat selection remain speculative. It is widely assumed that because habitat selection impacts strongly on key determinants of individual fitness, it has been subject to intense natural selection pressure and therefore patterns observed in nature approach the optimum expression of habitat selection (Cody 1974, Partridge 1978, Wiens 1985, Martin 1998). The challenge for ecologists is to move beyond description of animal - habitat associations and the identification of selectivity or preferential use of certain habitat features to derive, and ideally test experimentally, adaptive explanations of the mechanisms for the observed patterns (e.g. Sherry & Holmes 1985, Parrish 1995, Martin 1998, Whelan 2001).

In attempting to determine why vegetation structure is important to White-browed Treecreepers and the selective agents that shape habitat use, it is important to recognize that the patterns of habitat use observed in this study relate principally to the choice of foraging habitat during winter. Therefore, attributes of vegetation structure that impinge on the availability of food (i.e. arthropods), efficiency of obtaining food at a foraging site and costs of moving between foraging sites were likely to influence individual fitness and hence habitat use (MacArthur & Pianka 1966, Schoener 1971, Robinson & Holmes 1984, Whelan 2001). This differs from many studies of habitat selection that focus on breeding birds (e.g. Recher et al. 1985, Erckmann et al. 1990, Orians & Wittenberger 1991, Pribil & Picman 1997, Burkhardt et al. 1998), in which nest site requirements may exert more influence on habitat selection than foraging resources (Steele 1993, Matsuoka et al. 1997).

The grain of investigation in this study was the response of White-browed Treecreepers to heterogeneity between stands of trees (i.e. habitat plots). Thus, adaptive explanations of habitat use must involve behavioural processes that operate at the scale of stands of trees.

Lichen cover was associated with frequency of use of habitat plots in both districts, suggesting it may play an important role in habitat selectivity. However, it is unclear whether lichen cover itself was the proximate cue used by individual birds for habitat selection. It may be that lichen cover co-varies with the particular woodland structure that White-browed Treecreepers prefer, or that areas with low disturbance are characterized by both an abundance of lichen (Nilsson et al. 1995, Yates et al. 2000) and repeated use by White-browed Treecreepers.
White-browed Treecreepers appeared to select foraging habitat based on the configuration (density, dominance, canopy cover) and floristic composition of canopy trees present in a stand. The positive correlation with tree dominance probably represents selection of stands with the largest surface area of prime foraging substrate (i.e. trunk surface). This not only maximizes access to foraging resources but may also increase foraging efficiency, by maximizing the time required to deplete the foraging resources within a stand, thereby reducing the relative time and energy spent on longer, less profitable flights in search of foraging sites. If this reasoning is extended to foraging decisions within stands, it is expected that stands with larger diameter trees would be preferred, optimizing the ratio between time spent actively foraging on trunks and tree-to-tree flights. There was little evidence in support of this hypothesis: mean tree diameter within plots was not an influential variable in habitat selectivity. Individuals probably incur negligible energetic costs during tree-to-tree flights within a stand of trees, although detailed foraging observations of individuals, which have yet to be analysed (JQR raw data), may reveal that larger trees are used selectively within stands.

This raises a puzzling aspect of habitat use by the White-browed Treecreeper: why did they respond to variation in tree density of habitat plots, in contrast to their indifference to the mean size of trees in the plots? I propose that it would be energetically beneficial for individuals to make a preliminary assessment of the amount of foraging substrate in an area before moving into it. The White-browed Treecreeper may achieve this by using tree density as the proximate environmental stimulus. It may be that treecreepers are able to assess gross structural traits such as tree density (or canopy cover) from afar, but are unable to resolve more detailed characters such as tree diameter – that is, they can’t see the trees for the forest!

Why do White-browed Treecreepers selectively occupy Belah and Pine-Buloke woodlands in north-west Victoria? Compared with other dryland (non-floodplain) vegetation communities in the region (e.g. mallee woodland, Scrub-pine woodland), Belah, Buloke and Slender Cypress-pine trees are relatively tall, offering a greater surface area for foraging for an equivalent tree basal area (i.e. dominance). In addition, all three species are single-stemmed, have sparse foliage and few lateral branches low on the trunk, structural attributes which enable their trunks to be easily accessed by incoming treecreepers. The distance over which treecreepers can detect
prey may also be greater compared with trees that have dense foliage and many branches. Riverine woodlands (e.g. Black Box, River Red Gum *E. Camaldulensis*) have a similar structure and tree morphology but Brown Treecreepers are abundant in riverine woodlands (LCC 1987, Emison & Bren 1989, Major *et al.* 2001), thus limiting the opportunity for settlement by the smaller and presumably subordinate White-browed Treecreeper.

I propose that the fissured, craggy bark of all three species underpins the preference of White-browed Treecreepers for Belah, Buloke and Slender Cypress-pine. This differs markedly from the smooth or decorticating bark found on the trunks of mallee or gum trees, or the more finely textured bark of box trees. The foraging technique and morphology of White-browed Treecreepers may have evolved in response to the coarse tessellation and ridges of Cypress-pine, Belah and Buloke bark and its associated arthropod community. The White-throated Treecreeper and Red-browed Treecreeper partition resources in eucalypt woodland based on bark texture, with each species employing different foraging techniques to exploit different bark types (Noske 1979). This highlights the potential for treecreepers to adjust their foraging behaviour and habitat use in response to bark texture.

Bark texture may also influence food availability. Adams and Morrison (1993) found that arthropod density was positively correlated with bark 'roughness' in conifer-hardwood forests in California. If a similar relationship exists in northwest Victoria, White-browed Treecreepers may be favouring those tree species with the highest density of bark-dwelling arthropods. The potential for arthropod specialization, and therefore diversity, would be expected to increase with surface heterogeneity and availability of micro-habitats. The association between habitat use and lichen cover may be explained along similar lines. Lichen further increases surface heterogeneity and micro-habitat diversity for arthropods, as well as providing food for invertebrate grazers such as beetles. Therefore, arthropod diversity and abundance may be positively correlated with lichen abundance, encouraging White-browed Treecreepers to forage for longer in stands with extensive lichen cover. Finally, White-browed Treecreepers may be able to gain more secure footholds on the rough bark, increasing the efficiency with which they move over the bark surface. Clearly, these ideas need to be further developed with comparative morphological studies,
and an intensive survey of arthropod availability on contrasting bark types with different lichen abundance.

The influence of shrubs on foraging behaviour and habitat use by the White-browed Treecreeper depends on the height profile of the shrub layer and the scale of reference. In a regional context, White-browed Treecreepers were detected more frequently in woodlands with a relatively high cover of low-stature shrubs (0-3 m). Woodlands with a diverse and abundant shrub component are likely to support a more prolific arthropod community (Zack & Ligon 1985a, Abensperg-Traun et al. 1996, Recher et al. 1996) and hence, a larger population of higher-order consumers, such as the White-browed Treecreeper. In addition, a ground layer mosaic of low shrubs, bare ground, fine and coarse litter, logs and cryptophytes is often found in ‘low-disturbance’ woodlands that have an extensive cover of low shrubs. White-browed Treecreepers regularly foraged on the ground at Yarrara, feeding on ants, beetles, grubs and other terrestrial invertebrates that cannot be captured using purely arboreal foraging techniques. The dense foliage of the low shrubs concealed the birds from predators, yet the open spaces between shrubs were suitable for hunting ground invertebrates.

However, low-shrub cover did not account for much variation in habitat use between stands of trees within a woodland. This suggests the extent of low-shrub cover is not a proximate environmental cue for individual White-browed Treecreepers. Thus, the scale at which low-shrub cover influences the distribution of the White-browed Treecreeper appears to be above the scale at which the processes of individual habitat selection operate. On the other hand, individuals at Yarrara tended to avoid stands of trees with relatively high cover of tall shrubs (3-5 m). Tall shrubs may interfere with the flight trajectories of treecreepers, and may obscure the view of individuals as they scan their immediate environment before flying to their next foraging tree. It may also reflect low tree density in those areas with high cover of tall shrubs. However, there was not a significant correlation between tall shrub cover and tree density ($r = 0.08$) or tree dominance ($r = 0.23$) at Yarrara, suggesting that the relationship is more than a statistical artefact. The existence of such mechanisms remains speculative until manipulative field experiments on the effects of shrub cover are conducted. Whilst the design of such experiments is straightforward, the
administrative and ethical impediments to conducting them in conservation reserves are substantial.

Finally, frequency of use may not be a true indication of the fitness consequences of habitat selection or of habitat quality (van Horne 1983). However, White-browed Treecreepers do not possess the three life-history characteristics that are most likely to be associated with decoupling the animal density – habitat quality relationship (van Horne 1983), namely strong social dominance interactions (Chapter 6), high reproductive capacity (Chapter 9) and habitat generalists (Chapter 2, this chapter). Furthermore, White-browed Treecreepers do not occupy different habitat types during different seasons, an environmental characteristic identified by Van Horne (1983) as instrumental in the decoupling of density with habitat quality. Therefore, frequency of habitat use was probably a fair indicator of habitat selection and habitat quality. The next step is to measure the reproductive success of individuals in relation to their habitat choices (Martin 1998). If those individuals that use the ‘preferred’ habitat have greater reproductive success, it indicates that the habitat preferences identified in the frequency of use study are indeed adaptive and are indicative of habitat quality.

Conclusions

Different environmental factors influenced habitat selectivity by the White-browed Treecreeper at different spatial scales. Analysis at the regional level suggests that population density may be determined, at least in part, by the habitat attributes encapsulated in the *regional syndrome*. Thus, tracts of woodland that have high values for tree density, low-stature shrub cover, abundance of lichen and vertical structural diversity, and low values for grass and herb cover, and patchiness of the shrub layer are likely to support larger populations of the White-browed Treecreeper. However, the processes underlying these patterns operate at a larger spatial scale than habitat selection by individuals, which are more likely to be revealed from analyses at the district scale.

The strength and nature of the bird-habitat associations differed between Wyperfeld and Yarrara. This may be related to the distinct differences between districts in vegetation structure and population density of White-browed Treecreepers.
Nonetheless, some general principles of habitat selectivity were evident. As predicted, individuals preferentially foraged in woodland stands with higher tree density and fewer tall shrubs. The density of standing dead trees was not a significant factor, contrary to expectations. The cover of ground lichen, which probably reflects the level of disturbance and structural complexity of the ground layer, was a reliable indicator of habitat use. Predictive models of the influence of significant vegetation parameters on habitat use by the White-browed Treecreeper were developed for the region, and for the Yarrara, which could be used to plan management actions for the White-browed Treecreeper (see Chapter 11).
Chapter 5

Habitat use at multiple spatial scales
5.1 Introduction

The distribution and abundance of a species is the realization of ecological processes that operate across a range of spatial and temporal scales (Morris 1987, Wiens 1989b, Bellamy et al. 1998). For example, at the continental scale, climate, altitude and gross topographical features are likely to define the physical or biogeographic limits of a species (Keast 1981). Inter-specific competition may determine the type of habitat in which a species is found (Sherry & Holmes 1988, Wiens 1989a). Landscape structure and total amount of habitat may be important for the regional persistence of a species (Andrén 1994, Hinsley et al. 1996b, Villard et al. 1999). In turn, the viability of local populations may depend on the configuration of habitat in the landscape (Opdam et al. 1994, Brooker et al. 1999). At finer scales of habitat selection, individuals are able to directly explore and assess alternative habitats and base their settlement patterns and foraging behaviour on factors that act directly on the fitness of individuals, such as food availability, nest sites or protection from predators (Hutto 1985b). Thus, to identify the environmental factors that influence these processes, and in so doing determine the distribution of a species, a multi-scale approach to habitat selection must be adopted (e.g. Johnson 1980, Wiens et al. 1986).

The preceding chapters have identified factors that influence the distribution of the White-browed Treecreeper at the regional scale (Chapter 2), at the district scale (Chapter 3) and within occupied patches (Chapter 4). The aim of this chapter is to draw these results together into a cohesive overview of habitat use in a multi-scale framework. I will demonstrate that the scale of investigation affects the environmental factors identified as important in patterns of habitat use, and consider the consequences of scale dependence for the management of this species.

5.2 Extent and grain

While most ecologists recognize the importance of scale, many refer to the scale of their study ambiguously, failing to explicitly make the distinction between extent and grain (sensu Allen & Starr 1982; see Chapter 4). This is worrisome given the recent proliferation of ‘hierarchical’ or ‘multi-scale’ studies of habitat selection (e.g. Burkhardt et al. 1998, Huhta et al. 1998, Michaels & Cully 1998, Saab 1999, Beck & George 2000). Typically, these studies measure ‘microhabitat’ variables based on a
specific reference point (e.g. territory, nest site, foraging site, perch, singing post) and ‘meso’ or ‘macrohabitat’ variables in one or more larger frames of reference (e.g. sample plots of increasing size, patch characteristics, habitat type). Thus, the grain of the sampling unit varies for different explanatory variables, but the sampling unit for the response variable (i.e. grain) and the spatial domain over which data is collected (i.e. extent) remain constant. This is not problematic per se, as long as the grain is appropriate for the ecological question under study, and the results are not applied to processes operating at scales greater than the extent of the study (MacNally & Quinn 1998). However, the response of a species to a particular environmental factor may depend on the spatial (or temporal) extent over which data is collected and interpreted (Wiens et al. 1987), and the grain of the response variable may influence the predictor variables that are identified as important (Pribil & Picman 1997, Robichaud & Villard 1999).

The multi-scale approach taken in this research included variation in both extent and grain (Table 5.1). Distribution of the White-browed Treecreeper (the response variable) was sampled in discrete patches (Chapters 2 and 3) and 1-ha plots within patches (Chapter 4): that is, variation in grain. The spatial extent over which data was collected also varied, from regional (Chapters 2 and 4) to district (Chapters 3 and 4). In addition, Chapters 2 and 3 included patch-specific (e.g. vegetation structure and floristics, patch size) and landscape (e.g. isolation, woodland cover, landscape context) explanatory variables, conforming to the more liberal interpretation of a multi-scale investigation.

### Table 5.1 Variation in the scale of investigation of habitat use in this study.

<table>
<thead>
<tr>
<th>Chapter</th>
<th>Extent</th>
<th>Grain</th>
<th>Significant Variables</th>
<th>Relevant Processes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chapter 2</td>
<td>Regional</td>
<td>Patch &gt; 50 ha</td>
<td>Demographic Isolation; Woodland floristics</td>
<td>Dispersal behaviour; Metapopulation dynamics; Macro-habitat selection</td>
</tr>
<tr>
<td>Chapter 3</td>
<td>District</td>
<td>Patch &gt; 1 ha</td>
<td>Patch Size; Habitat quality (grazing)</td>
<td>Resource availability; Competitive interactions?</td>
</tr>
<tr>
<td>Chapter 4</td>
<td>Regional</td>
<td>1-ha plot</td>
<td>Tree Density; Low Shrub Cover; Grass/herb Cover; Lichen Cover</td>
<td>Resource availability</td>
</tr>
<tr>
<td>Chapter 4</td>
<td>District</td>
<td>1-ha plot</td>
<td>Woodland floristics; Tree Dominance; Tall Shrub Cover</td>
<td>Foraging behaviour</td>
</tr>
</tbody>
</table>
5.3 **Contrasting effects at contrasting scales**

The description of an animal’s ‘ecological niche’ in terms of the multi-dimensional environmental space it occupies (Hutchinson 1957) is the cornerstone of modern habitat-suitability models (e.g. James 1971, Collins *et al.* 1982, Kikkawa 1982, Verner *et al.* 1986, Lindenmayer *et al.* 1990a, Neave *et al.* 1996, Rettie & Messier 2000). These models commonly emphasize the importance of vegetation characteristics as proximate environmental cues for habitat use during foraging, nesting or resting. The ecological niche of the White-browed Treecreeper is described by the finest scale of investigation in this study – frequency of use of 1-ha plots at the ‘district’ scale. A model of ‘foraging-habitat suitability’ was constructed for the Yarrara district, based on woodland floristics, tree dominance and tall shrub cover (Table 5.1). However, the dangers of extrapolating the results from one area of a species’ range to another (Collins 1983) are illustrated by comparing habitat use between Yarrara and Wyperfeld. The significant factors at Yarrara did not accurately describe habitat use at Wyperfeld.

The marked differences in vegetation structure between Yarrara and Wyperfeld were assumed to contribute to the higher reporting rate of White-browed Treecreepers at Yarrara. Thus, when the extent of inference was extended to the regional scale but the grain was held constant (i.e. 1-ha plots), habitat attributes encapsulated in the *regional syndrome*, which differed from those identified in the district analysis, emerged as significant explanatory variables of habitat use (Chapter 4; Table 5.1). The reasons for the differences in the significant factors at different scales of extent relate to the ecological processes that are relevant at the respective scales. The district analysis focused on proximate cues used by individuals for habitat use while foraging. These differed from the factors that determine the carrying capacity of occupied habitat (i.e. resource availability) that were detected in the regional analysis.

The habitat-use study was restricted to relatively large tracts of woodland. Therefore, it was not able to account for other factors that may influence habitat use by the White-browed Treecreeper, such as landscape factors (Hinsley *et al.* 1995, Howell *et al.* 2000), history of habitat change (Knick & Rotenberry 2000, Pidgeon *et al.* 2001), species interactions (Rosenzweig 1985, Sherry & Holmes 1988) or biotic invasions (Hobbs 2001). In a fragmented agricultural landscape (Chapter 3), distribution of the
White-browed Treecreeper was predominantly determined by patch size (Table 5.1). Habitat quality, in terms of grazing intensity and history, was of secondary importance, but fine-scale habitat factors such as tree density were not influential. These factors probably reflect the minimum area requirements, or the minimum resource requirements, for a pair of treecreepers. Complementarity in abundance of the White-browed Treecreeper with the Brown Treecreeper and several species of parrots in the smaller fragments suggests competitive interactions may also influence distribution at the district scale.

This contrasts with the regional-scale study in which demographic isolation was of paramount importance in determining distribution, presumably due to its effect on dispersal success and metapopulation persistence (Chapter 2; Table 5.1). However, isolation was not an important determinant of patch occupancy at the district scale, apparently because the amount and configuration of habitat in relation to the movement ability of the White-browed Treecreeper rendered the landscape relatively permeable. Thus, individuals were able to reach most patches of remnant habitat in the landscape. This is not to say that isolation will never be an important factor at the district or landscape scale, but rather it was not significant in this specific case.

Conversely, patch size was not a significant predictor of patch occupancy in a regional context. This is not surprising given that patches less than 50 ha were not surveyed in the regional study. It is significant that the districts in which White-browed Treecreepers were present contained at least one very large tract (> 500 ha) of suitable woodland, whereas the districts without White-browed Treecreepers did not contain such a patch. The extensive tracts of woodland may act as source habitat from which individuals can emigrate into the surrounding landscape (Pulliam 1988, Harrison et al. 1988). However, the pattern of patch occupancy at the regional extent suggests that local populations persist only in landscapes with a network of patches in relatively close proximity. I propose that White-browed Treecreepers were not detected in several districts that had large patches of suitable woodland because of the absence of a network of patches below the demographic isolation threshold. Clearly, local persistence will be prolonged (i.e. local population size will be larger) in landscapes with greater overall habitat cover due to the associated increase patch size and decrease in isolation. Furthermore, access to and occupancy of remote
Habitat use at multiple scales

habitat depends on functional routes for dispersal through the landscape, which in turn will be correlated with the overall amount of habitat in the landscape.

Thus, the scale of investigation, in terms of both extent and grain, had a significant bearing on the interpretation of patterns of habitat use. Different vegetation attributes were identified as important determinants of the distribution of the White-browed Treecreeper within occupied patches, contingent on the spatial extent of inference, and consequently, the ecological process under investigation. At a larger grain of sampling, landscape factors tended to be better predictors of habitat use than within-patch attributes. At a regional extent, isolation was the most important factor in describing the distribution of the species. In fragmented landscapes with low connectivity, populations in small patches are vulnerable to extinction from stochastic events and isolation effects reduce the likelihood of re-colonization. Extinction in a succession of fragments without successful re-colonization will culminate in extinction at the district scale. The effects of these processes are amplified in landscapes without extensive tracts of habitat. However, in districts in which sufficient habitat remains and the configuration of habitat enables movement through the landscape, distribution is explained by patch-specific attributes such as patch size and quality.

5.4 Framework for scale dependence

The scale dependence of habitat use can be interpreted in terms of a multi-scale, hierarchical model of patch structure (Kotliar & Wiens 1990). In this framework, a “patch” is defined as an area differing from its surrounding, and can be applied across a range of absolute spatial scales. The basic premise is that a patch at any given scale has an internal structure that is determined by the heterogeneity at lower levels in the hierarchy. Organisms may respond to heterogeneity at several levels, and therefore the environmental factors that best describe the responses of animals will vary at different levels within the hierarchy of patch structure (Wiens 1989b).

This framework can be applied to the patterns of habitat use observed in the White-browed Treecreeper. I suggest that different parts of a tree (i.e. trunk, limb, branch, outer branch, foliage) are internally homogeneous from a treecreeper’s perspective
and therefore constitute the smallest discrete patch in the hierarchy [first-order patch, *sensu* Kotliar & Wiens (1990)]. Contrast between first-order patches produces heterogeneity within a single tree. As the spatial scale of the hierarchy increases, heterogeneity is contrasted between trees (second-order patches) on the basis of tree species, size and health; between stands of trees (third-order patches) based on the density, distribution and mean size of trees within the stand and the shrub component; and between aggregations of stands of trees (fourth-order patches) which vary in the distance between stands, habitat between stands and quality of stands. Fourth-order patches equate to the conventional definition of a patch used throughout this thesis: an area delimited by the dominant canopy tree species and a general similarity in vegetation structure.

Above this scale, White-browed Treecreepers may respond to heterogeneity between different vegetation types within a mosaic of natural vegetation or between remnants within an agricultural landscape. Spatial scales greater than this are beyond the lifetime home range of individuals and therefore outside the limits of the hierarchical model as applied to habitat selection by individuals. However, the patch-structure model can be extended to ecological processes operating at larger spatial scales, such that local networks of habitat (analogous to district-level in this study) represent fifth-order patches with heterogeneity determined by spatial configuration of habitat. The entire study area of north-west Victoria is the highest order patch in this study (sixth-order).

The important point is that a species distribution at a particular order in the hierarchy depends on the internal patch-structure of that order, which in turn, is described by the heterogeneity of the lower levels in the hierarchy. Accordingly, the variables that influence the distribution of a species are determined by the order at which the hierarchy is investigated. For example, the configuration of habitat at the district scale (fifth-order patch) influences local population persistence of the White-browed Treecreeper and therefore, distribution at the regional scale (sixth-order patch). Thus, factors that discriminate between districts (e.g. degree of isolation of woodland remnants, amount of habitat cover) determine the internal heterogeneity of the regional ‘patch’, and consequently the distribution of the species in a regional context. Similarly, the distribution of the White-browed Treecreeper within occupied
woodland (fourth-order patches) is best described by factors that discriminate between stands of trees (third-order patches): tree dominance and shrub cover.

### 5.5 Management implications of scale dependence

It is tempting for multi-scale studies to partition the variation in a species distribution or abundance among factors operating at different scales. There is an intuitive appeal in being able to claim, for example, that a species is responding to landscape factors more than within-patch vegetation attributes. Such an assertion would greatly simplify management priorities and actions. However, as I have demonstrated for the White-browed Treecreeper, animals respond to factors and processes operating at many scales, each of which is likely to contribute to the fitness of individuals, and collectively, the survival of the species. The challenge for conservation biologists is to identify which factors are operating at which scales and advise land managers accordingly.

Although some general principles hold across several spatial scales [e.g. ‘connectivity’ is important at regional and landscape scales (Taylor et al. 1993)], some factors may have a critical influence at only one scale. Failure to recognize a critical environmental factor for population persistence, or to consider factors in isolation from higher and lower scales may result in ineffective or counter-productive management. For example, patches of suitable vegetation (within-patch attributes) may not be occupied because of factors operating at the landscape scale (e.g. isolation effects, patch size, landscape context) (James et al. 1984, Opdam et al. 1994, Dunning et al. 1995, Bellamy et al. 1998). Thus, habitat restoration actions (e.g. restoring shrub layer, increasing tree density) that do not take landscape issues (e.g. patch size, landscape context) into account are unlikely to increase the survival of the target species. Conversely, increasing patch size and re-vegetating corridors without attention to specific habitat requirements will not be sufficient to conserve the White-browed Treecreeper in many agricultural landscapes. Thus, conservation of the White-browed Treecreeper requires integrated and coordinated habitat management across multiple scales. To this end, guidelines for habitat management at the regional, landscape and patch scale are presented in Chapter 11.
Chapter 6

Social organization, survival and breeding strategy of the White-browed Treecreeper at Yarrara Flora and Fauna Reserve, north-west Victoria
6.1 Introduction

Birds employ a wide range of breeding strategies to maximize their lifetime reproductive success (Newton 1989). The most common system involves a single monogamous pair in which both parents contribute to the care of their offspring (Ford 1989). Variations in which the male, female or both, mate with additional partners are numerous but care of the offspring usually remains the responsibility of the parents (Brown 1987). An uncommon exception to this is cooperative breeding, practiced by only 3% of bird species in the world (Brown 1987, Arnold & Owens 1998). It is characterized by the presence of individuals who provide alloparental care to the young but are not their genetic parents (Brown 1978). The extra-parental carers are frequently, but not exclusively, offspring of the genetic parents from previous broods that have delayed dispersal and assist in caring for their siblings.

Cooperative breeding was first recognized by Australasian ornithologists in the 19th century (Boland & Cockburn 2002) although Alexander Skutch (1935) is generally attributed with coining the term “helpers-at-the-nest” and “discovering” cooperative breeding. However, interest in cooperative breeding remained stagnant until the 1960s, when Skutch (1961) published the first review of helping behaviour in birds. Shortly after that, Hamilton (1963, 1964) developed the theory of kin selection (now known as inclusive fitness theory) to explain the evolution of eusociality in insects. Williams (1966) recognized that the challenge to Darwinian natural selection presented by the apparently altruistic helping behaviour of some birds could be reconciled within the context of Hamilton’s theory (Brown 1978). With the concurrent maturing of the study of bird behaviour as a predictive science, avian helping behaviour was used to test predictions of kin selection theory, stimulating much research on cooperative breeding (Emlen 1999).

Cooperatively breeding species are disproportionately frequent in the Australian avifauna compared to their incidence worldwide (Dow 1980a, Brown 1987, Clarke 1995). The reasons for this are not clear, but the high proportion of Australian ‘old endemic’ species that breed cooperatively suggest it evolved independently, early in the radiation of Australian passerines (Russell 1989). Initially, cooperative breeding was proposed as an adaptive response to fluctuations in resource availability associated with a variable environment (Rowley 1965, Harrison 1969b). However, more recent explanations have focused on aseasonality and low annual variation in
food resources, producing conditions favourable to sedentariness and territoriality (Ford et al. 1988, Geffen & Yom-Tov 2000). A phylogenetic pre-disposition for increased longevity and small clutch sizes also appears to be correlated with a propensity for cooperative breeding (Emlen 1978, Brown 1987, Poiani & Jermiin 1994, Arnold & Owens 1998) and Australian birds tend to be more long-lived (Rowley & Russell 1991, Yom-Tov et al. 1992) and have smaller clutches (Woinarski 1985, Yom-Tov 1987) than northern hemisphere birds. However, a causal relationship between these factors has not been established, and the alternative hypothesis of long-lived birds breeding exclusively as simple pairs is true of many species (Clarke 1995). Nonetheless, sedentariness and longevity are likely to promote habitat saturation and delayed dispersal, increasing opportunities for social contact and eventually the evolution of cooperative breeding (Dow 1980b, Ford et al. 1988, Arnold & Owens 1998).

The breeding biology of Australo-Papuan treecreepers (Climacteridae) is of particular interest because cooperative and non-cooperative breeding strategies occur within the same family (Noske 1980). For five of the six Australian species, breeding has been sufficiently studied to allow classification of their breeding strategy (Dow 1980a, Schodde & Tidemann 1986, Clarke 1995). Facultative cooperative breeding has been confirmed in the Red-browed Treecreeper (Noske 1991), Brown Treecreeper (Noske 1991), Rufous Treecreeper (Rose 1996, Luck 2000), and Black-tailed Treecreeper (Noske 1980). In contrast, the White-throated Treecreeper breeds exclusively in simple pairs (Noske 1980, 1991). However, the breeding biology of the White-browed Treecreeper has, hitherto, not been investigated and hence its breeding strategy has not been clarified. Speculation varies from ‘may breed cooperatively’ (Noske 1980) to ‘apparently’ non-cooperative (Skutch 1999). Certainly, there have been no reports of helpers at the nests of White-browed Treecreepers (Schodde & Tidemann 1986).

Although breeding strategy cannot be definitively predicted from ecological or life-history traits (Dow 1980a, Clarke 1995), White-browed Treecreepers possess many characteristics commonly associated with cooperative breeding. For example, they inhabit semi-arid woodlands that have mild winters and relatively low seasonal fluctuation in resources but great unpredictability of rainfall between years (Ford et al. 1988, Rowley & Russell 1990a, Arnold & Owens 1999). They are sedentary,
territorial, insectivorous and actively pursue their prey, attributes prevalent amongst cooperative breeders (Grimes 1976, Ford et al. 1988, Ford 1989). Perhaps the strongest clue to their breeding strategy comes from phylogeny (Ligon 1993, Cockburn 1996), with all four congeners of the White-browed Treecreeper breeding cooperatively to some extent. Thus, based on habitat, ecology and phylogeny, White-browed Treecreepers were predicted to breed cooperatively.

A colour-banded population of White-browed Treecreepers was established at Yarrara Flora and Fauna Reserve to study their demography, territoriality, nesting behaviour, breeding biology and reproductive success. The results of this body of research are presented in the next four chapters (Chapters 6 – 9) with a synthesis of the theoretical implications of the results in Chapter 10. An understanding of the breeding system employed by White-browed Treecreepers is pivotal to the interpretation of this data. Accordingly, social composition and breeding strategy are described at the outset of this chapter, providing the socio-biological context for much of the subsequent analysis, even though the methodology used to confirm breeding strategy (i.e. nest watches) is not detailed until Chapter 8. This chapter also presents the first accounts of adult survival, sex ratio, territory size and territory dispersion for this species. Characteristics of nest sites used by White-browed Treecreepers and a model of hollow use are presented in Chapter 7. Chapter 8 deals with nesting behaviour, including courtship, nest construction, egg laying, incubation, brooding and nestling provisioning. In addition, Chapter 9 provides the first estimates for this species of the duration of the incubation and nestling periods. Finally, reproductive success and post-fledging dispersal are considered in Chapter 9, with particular emphasis on the effect of breeding strategy (group size) on reproductive output.

6.2 Methods

Study area

This research was conducted primarily¹ at Yarrara Flora and Fauna Reserve (FFR) (34° 25' S, 141° 25' E) in north-west Victoria, south-eastern Australia (Fig. 6.1). The

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¹ Some aspects of nesting biology were supplemented with records from nearby locations (see Ch. 3).
climate in this region is semi-arid with an average annual rainfall of less than 300mm, falling predominantly in winter, but summer thunderstorms are common and rainfall is highly variable among months and years. Winter temperatures are mild and summers are very hot with daytime maxima often exceeding 40˚C. Yarrara FFR is ca. 2,200 ha in total, of which 1,870 ha is Belah woodland and the remainder is mallee woodland. Yarrara FFR is the largest continuous tract of Belah woodland in Victoria and the largest block of native vegetation between the Murray-Sunset National Park and the Murray River in a landscape primarily devoted to wheat cultivation.

The study was conducted within a study plot of ca. 100 ha in the southern block of Yarrara FFR (Fig. 6.1). Vegetation structure and species composition were relatively homogeneous throughout the study plot (Fig. 6.2). It consisted of an open woodland canopy (5-15m high), dominated by mature Belah trees with occasional Sugarwood Myoporum platycarpum and mallee Eucalyptus spp. trees. The mid-storey (2-5m) was composed of scattered Cattlebush Alectryon oleifolia, Small Cooba Acacia ligulata and Leafless Ballart Exocarpus aphyllus, with patchy aggregations of Twin-leaf Emu-bush Eremophila oppositifolia, Narrow-leaf Hopbush Dodonaea angustissima or Sweet Quandong Santalum acuminatum and regenerating Slender Cypress-pine along the disused irrigation channels. Vigorous understorey (<2m) growth was dominated by Chenopodiaceae, particularly Spiny Fan-flower Scavola spinescens, Hedge Saltbush Rhagodium spinescens and Barrier Saltbush Enchylaena tomentosa, with patches of abundant Desert Cassia Senna artemisioides and Comb Grevillea Grevillea huegelii. Olearia Daisy-bush Olearia pimeleoides, Common Emu-bush Eromophila glabra, Wait-a-while Acacia nyssophylla, Pale Turpentine Beyaria lechenaultii and Weeping Pittosporum Pittosporum phylliraeoides were common and widespread. Yarrara FFR was originally proclaimed as a forestry reserve, and virtually every mature Slender Cypress-pine has been removed. Yarrara FFR has never been intensively grazed by stock. Thus, the ground layer is relatively undisturbed with a mosaic of lichen, moss, herbs, fine litter, woody debris, logs, low shrubs and bare soil. Dead timber is abundant, either as standing dead trees or fallen logs and coarse woody debris.
Social organization, survival and breeding strategy

Figure 6.1. Location of Yarrara Flora and Fauna Reserve in north-west Victoria, and position of the study plot within the reserve.
Figure 6.2. Typical Belah woodland with shrubby understory at Yarrara FFR.

**Trapping and colour-banding**

White-browed Treecreepers were studied at Yarrara FFR during the 1998/99 and 1999/2000 breeding seasons (referred to hereafter as 1998 and 1999, respectively). Over the course of the study, 48 adults and 12 fledglings were trapped in mist-nets. Each bird was banded with a numbered aluminium band supplied by the Australian Bird and Bat Banding Scheme on its right leg, as well as a unique combination of three colour bands, one on its right leg and two on its left leg. Basic morphometric, moult and plumage data were recorded for each bird trapped. Mist-netting was most intensive prior to the first breeding season, but continued throughout the study to trap fledglings and unbanded adults. Approximately 73% in 1998, and 93% in 1999, of the adults in the study plot had been captured and banded by the peak nesting period.

**Group composition**

Group membership was determined from nest watches at active nests (see Chapter 8). Thus, individuals that participated in one of the following activities were deemed to belong to that breeding unit for that nesting attempt: nest construction and maintenance, incubation, feeding the incubating bird, brooding, feeding nestlings or brooding bird, nest cleaning, “sweeping” (see Chapter 8), feeding or shepherding fledglings. Theoretically, individuals could belong to more than one breeding unit simultaneously or change breeding units within or between breeding seasons.
Social organization, survival and breeding strategy

Survival

The banded population was censused in August (pre-breeding) and February (post-breeding) in each breeding season to calculate survival rates of adult birds, using the following equation (modified from Nicholls & Woinarski 1988, Noske 1991):

\[
\text{Mean % annual survival} = 100 \times \left( \frac{\Sigma b}{\Sigma a} \right)^2
\]

where \(a\) is the number of banded birds present initially and \(b\) is the number present six months later. The fraction was squared because the population was censused every six months rather than annually.

Territoriality

The entire study plot was marked out in a 100m x 100m grid by colour-coded flagging tape. Territory\(^2\) size was determined by recording the position coordinates of colour-banded birds that were encountered during habitat use censuses (see Chapter 4), foraging observations (unpublished data), systematic traverses of the study plot (three conducted) or incidental observations. The distance and direction from the point at which the bird was first sighted to the nearest grid marker was measured. Thus, a ‘longitude’ and ‘latitude’ pertaining to the reference grid was obtained for each position ‘fix’. The location of territorial disputes between neighbours was recorded in the same way. The error associated with these position fixes was estimated at 5 – 10 m, considerably less than the precision of hand-held GPS units, which had an estimated error of 15 – 100 m, depending on the number and location of satellites within their receiving range (personal observation).

Individuals were retrospectively allocated to territories based on their participation in breeding activities. Position fixes of individuals from the same breeding unit were pooled to determine territory size per breeding unit. Thus, individuals that switched breeding units between, or within, breeding seasons contributed to two territory size estimates but no individual simultaneously contributed to two territory size estimates. The territory size of each group was estimated using a (i) bivariate normal ellipse

\(^2\) For simplicity, ‘territory’ is preferred to ‘home-range’ throughout this thesis because areas of occupancy were actively defended, and occupied more or less exclusively. However, it is acknowledged that some references to ‘territory’ may more accurately be described as ‘home-range’ because they include areas that were used for foraging and/or exploring but were probably outside the boundaries of the defended area.
(Jennrich & Turner 1969) and (ii) minimum convex polygon (MCP) (Mohr 1947) in RANGES V (Kenward & Hodder 1996). Ellipse calculations assume an arithmetic centre of activity and a normally distributed fix density on two axes (Harris et al. 1990). Although these assumptions are violated in most real populations, ellipses provide a useful initial estimate of territory size with as few as 10 position fixes (Kenward & Hodder 1996). Ellipse calculations also assume consecutive fixes are independent in time. Thus, successive fixes for an individual were at least one hour apart, which was a conservative estimate of the time required for an individual to move from one side of its territory to the other, and therefore be effectively independent (White & Garrott 1990).

Minimum convex polygons are the most common method used to estimate territory size (Harris et al. 1990) but require more fixes to produce stable area estimates. The adequacy of the sample size for each breeding unit was evaluated by visual assessment of sequential plots of territory size versus the cumulative number of position fixes. Territory size estimates were considered stable if an asymptote was reached.

Minimum convex polygons supplement the ellipse analysis as they provide more information on the shape of territories and are immune to autocorrelation of locational data (Harris et al. 1990). However, MCPs are strongly influenced by peripheral fixes and outlying fixes that are well beyond the normal range, leading to over-estimates of territory size. Thus, minimum convex polygons that progressively reduced the proportion of fixes included in the polygon (100%, 99%, 95% and 50%) were calculated to assess the influence of outlying fixes. Fixes were excluded in order of their distance from the arithmetic ‘centre of activity’, which was re-calculated after excluding each furthest fix (Kenward & Hodder 1996).

6.3 Results

Group composition and cohesion

Eleven breeding units in 1998 and 15 breeding units in 1999 were monitored. Extra-parental adult attendants were present in nine of the 26 (34.6%) breeding unit-years, with the remaining 17 (65.4%) breeding unit-years consisting of unassisted pairs (Fig. 6.3a). Two to five adults (mean of 2.4 ± 0.1) were observed attending the same
brood but more than one extra-parental attendant was rare (Fig. 6.3b). There was no significant difference in the incidence of cooperative breeding between years (1998: 27%, 1999: 40%; Yates $\chi^2 = 0.063, P = 0.8$) (Fig. 6.3). It is possible that four pairs that were detected breeding only in 1999 did, in fact, attempt to breed in 1998 but were not noticed because they failed early in the season and did not re-nest. However, this seems unlikely, as breeding units that failed in their first nesting attempt before the end of October generally re-nested (see Chapter 8). Even if the four “non-breeding units” were included as pairs, the proportion of cooperatively breeding units would not differ significantly between years (Yates $\chi^2 = 0.64, P = 0.43$).

![Figure 6.3. Composition of White-browed Treecreeper breeding units at Yarrara FFR 1998 – 1999 (n = 26 breeding unit-years).](image-url)
The extra-parental attendants assisted in provisioning the incubating female and nestlings, nest maintenance, nest cleaning and post-fledging care (see Chapter 8) and were thus deemed *helpers* at *cooperative* nests (*sensu* Skutch 1961, Brown 1978). The eight individuals that were observed helping were all males. Of those eight, the natal nest of three was known and they all helped in their natal territory in the next breeding season. This observation provides sound evidence that helpers were the progeny of the breeding pair. Throughout this thesis, I shall distinguish between cooperative and non-cooperative breeding strategies by using ‘pair’ to refer to a breeding pair without helpers and ‘group’ to refer to a primary breeding pair with one or more helpers. ‘Breeding unit’ is a generic term for both pairs and cooperative groups.

Members of a breeding unit kept in vocal contact whilst foraging, during both the breeding and non-breeding seasons. At longer distances, birds initiated contact with a shrill chirruping call. Their partner frequently replied with a series of staccato notes that gradually built into a continuous rolling chirrup. When individuals were in close proximity, a soft, short call that was reminiscent of a cat purring (*prrr prrr*) call was used to maintain contact. Birds on the same tree emitted a very soft *seep seep* contact call. Such antiphonal calling has been described in both the Red-browed Treecreeper and Brown Treecreeper (Noske 1979). A harsh cackle was infrequently heard. The precise context of this call is unclear but it was used in territorial disputes.

Members of the same breeding unit often foraged together in loose aggregations of 3 to 5 birds during the non-breeding season. Yet, immature females in their first year that partially delayed dispersal (Chapter 9) tended to forage independently, had little overt communication with other group members and were generally confined to a small portion of the group’s territory. Paradoxically, non-breeding adult females were intermittently tolerated on several territories, although they never assisted the breeding effort in any detectable way and tended to be aggressively excluded from the vicinity of active nests. These “floating” females often foraged in close proximity with other group members, particularly non-breeding male helpers. The genetic relationship between these females and the breeding pair was not known.

The composition and size of breeding units differed between breeding seasons (Fig. 6.4). The retention of male offspring from 1998 increased the group size in three territories in 1999 (e.g. T11). Consequently, the breeding strategy of these three
breeding units changed from pairs in 1998 to cooperative groups in 1999. Mortality and/or emigration reduced the largest group (T2) that consisted of five adults in 1998 to three in 1999. The female (WB) moved to an adjacent territory following the disappearance of her putative partner (WU), evicting the incumbent female (YY), pairing with the resident male (OB) and inheriting the offspring of YY from 1998 as a helper in 1999. A “floating” female (WR) assumed the vacant breeding position in the first territory (T2). The displaced female (YY) remained in the study area for the duration of the 1999 breeding season but did not re-partner. More routine compositional changes were observed on two occasions whereby a widowed bird formed a new partnership, between breeding seasons in the first case (T4) and during a nesting cycle in the second (T13).

**Sex ratio**

The sex ratio of adults banded in the study plot was approximately equal (25 ♂♂: 23 ♀♀). The sex ratio of nest attendants (breeding birds and helpers) was skewed towards males (1998: 16 ♂♂:11 ♀♀; 1999: 21 ♂♂:15 ♀♀), but not significantly (1998: $\chi^2 = 0.93$, $P = 0.34$; 1999: $\chi^2 = 1.00$, $P = 0.32$), nor was there any difference in the sex ratio between years (Yates $\chi^2 = 0.03$, $P = 0.85$). Fledgling sex ratios were close to parity (21 ♂♂: 18 ♀♀; $\chi^2 = 0.23$, $P = 0.63$) reflecting the wider adult community.
Figure 6.4. History of selected White-browed Treecreeper individuals at Yarrara 1998 – 1999, showing variation in group composition and cohesion.
Survival

Survival calculations were confounded by uncertain results from the last census period. Breeding birds were presumed to have died or emigrated if other birds had assumed their social position. However, three males and four females were not sighted during fieldwork in January or February 2000, but the vacancies in their respective social groups had not been filled. Thus, their status remained equivocal. Therefore, a range of annual survival estimates was calculated, with the missing birds considered deceased in the lower estimate and alive but ‘missed’ in the higher estimate. Given the rate of disappearance of individuals from the study plot in the preceding intervals (Table 6.1), the lower survival rates probably under-estimate true survival.

Table 6.1. Number of banded, adult White-browed Treecreepers surviving in the Yarrara study area\(^1\) in six-month intervals, from August 1998 to February 2000.

<table>
<thead>
<tr>
<th>No. of survivors after six months</th>
<th>Aug 98 – Feb 99</th>
<th>Feb 99 – Aug 99</th>
<th>Aug 99 – Feb 00 (lower estimate)(^2)</th>
<th>Aug 99 – Feb 00 (upper estimate)(^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male (%</td>
<td>11/11 (100%)</td>
<td>14/15 (93%)</td>
<td>14/19 (74%)</td>
<td>17/19 (89%)</td>
</tr>
<tr>
<td>Female (%)</td>
<td>11/12 (92%)</td>
<td>15/15 (100%)</td>
<td>13/20 (65%)</td>
<td>17/20 (85%)</td>
</tr>
<tr>
<td>Total (%)</td>
<td>22/23 (96%)</td>
<td>29/30 (97%)</td>
<td>27/39 (69%)</td>
<td>34/39 (87%)</td>
</tr>
</tbody>
</table>

1 6 adult birds (4 ♂♂, 2 ♀♀) that were banded but never or rarely re-sighted and one male that accidentally died in a mist-net were not included in the survival analysis.

2 See text for justification of upper and lower estimates.

Mean annual adult survival was 71.7% - 85.4% (n = 41). Annual survival of males (75.1% - 87.1%, n = 20) was slightly higher than for females (68.9% - 83.7%, n = 21) but there was considerable overlap in the range of estimates and this difference was negligible relative to the error in survival calculations.

A comparison of the annual survival rate of adults in pairs and groups was limited by (i) differences in the time of banding of individuals and (ii) variation in breeding strategy between seasons in three territories. However, 21 individuals were banded by August 1998 in breeding units that did not change strategy during the course of the study. Ten birds were disbursed among three cooperative groups, there were five pairs and one accidentally died in a mist net. By February 2000, 9 of the 10 individuals originally in groups were still in the study area, although two had
changed territories. The sole disappearance was a male helper that was not seen after the 1998 breeding season. In contrast, 3 of the 10 individuals that were in pairs disappeared, with one female disappearing prior to the 1999 breeding season, a second female not sighted since mid-November 1999 and a male disappearing during the first nesting attempt of 1999. In addition, of a further four pairs that were banded before the 1999 breeding season, two individuals (one male, one female) disappeared from the study plot before the end of the study. Thus, of 18 adults holding a breeding position in a pair, five disappeared, whilst the only adult, of a possible 10, to disappear from a cooperative group during the study, was a helper. To balance this, the six individuals that were in pairs in 1998 and groups in 1999 all survived to February 2000, although one female was displaced from her breeding position and may have departed towards the end of the 1999 breeding season.

**Territoriality**

White-browed Treecreepers occupied all-purpose territories in which foraging, courtship and nesting took place. Discrete territories were vigorously maintained throughout the year. However, habitat use was not entirely exclusive, with some overlap between adjacent territories (Fig. 6.5). Territory defence involved complex displays, in which competing birds faced each other on a trunk or branch, separated by 50 cm to several metres. The participants advanced towards each other with their crown and neck feathers ruffled, heads bobbing up and down, tails fanned and elevated and wings repeatedly opening and closing in a flicking motion. The combatants would then jump up and down the trunk (or along a limb) in this formation, flicking their wings and keeping a relatively constant distance between them. Occasionally one bird might attempt to ‘dive-bomb’ the other. Disputes were usually resolved without physical contact but aerial ‘dogfights’ were observed on several occasions. Disputes were often prolonged, frequently consisting of successive displays at various points along the territory boundary or repeated duels on a conspicuous landmark. Eventually, one bird would concede and depart, often with the victor chasing in pursuit. In nearly all disputes observed, bouts were between birds of the same sex although both birds in a pair were observed to duel, simultaneously, with their counterpart from an adjacent territory. Territorial disputes were observed between neighbouring breeding units and between territory holders and birds from outside the study area.
Figure 6.5. Territory mapping of breeding units in the Yarrara study plot, 1998 - 1999. Black polygons are drawn around outer position fixes (minimum convex polygons of 100% of fixes) for those breeding groups with detailed locational data. Red polygons are estimates of territory range for breeding groups without detailed data. Territory number (e.g. T2) is indicated by red text; the locations of nests are indicated by black text. Refer to Table 7.5 for nest ownership.
**Territory size**

In total, 470 position fixes of 34 individuals in 12 discrete territories, taken from September 1998 to February 2000, were included in the analyses of territory size. Stable territory size estimates were readily obtained from the bivariate normal ellipse method and ranged from 8.3 ha to 27.2 ha (using 95% fix density distribution) with an average territory size of 18 ha (Table 6.2). This method obviously over-estimates actual territory size, as the study area could not accommodate 12 exclusive territories of this size. Territory size estimates derived from ellipses using 90% of the fix density distribution ranged from 6.4 ha to 20.9 ha with a mean of 13.8 ha (Table 6.2).

Mean territory size of the 12 breeding units derived from minimum convex polygon (MCP) calculations decreased from 10.1 ± 1.7 ha when 100% of fixes were included to 9.4 ± 1.3 ha for 99% of fixes and 7.4 ± 0.9 ha for 95% of fixes (Table 6.2). However, analyses of sample size revealed that for a majority of breeding units, territory size was probably under-estimated using MCP. In visual assessments of plots of territory size versus number of position fixes, asymptotes were discernible in 9 of 12 territories for MCP 99% and in 10 of 12 territories for MCP 95% (Fig. 6.6). This suggests sample size was adequate for most territories. However, step-functions were evident in the plots that contained 50 or more fixes, and often occurred after territory size had initially stabilized at between 20 – 30 fixes (Fig. 6.6). That is, periods of no increase in territory size with the addition of 10 to 20 fixes were followed by sharp rises as new fixes were added. Thus, for the 5 territories with fewer than 20 fixes, it is impossible to assess whether the apparent stabilization in territory size would be sustained with a larger sample. Mean territory size of breeding units with more than 20 fixes that appeared to reach asymptotes were 12.2 ± 0.9 ha and 10.1 ± 0.8 ha for MCP 99% and MCP 95% respectively (Table 6.2).
Table 6.2. Estimates of the territory size of 12 breeding units of White-browed Treecreeper at Yarrara FFR, 1998 - 1999. Territory sizes are derived from normal bivariate ellipses (95% and 90% of the fix density distribution) and peeled minimum convex polygons (MCP) that incorporated 100%, 99% and 95% of position fixes.

<table>
<thead>
<tr>
<th>Territory</th>
<th>n (adults)(^1)</th>
<th>n (fixes)</th>
<th>Ellipse 95%</th>
<th>Ellipse 90%</th>
<th>MCP 100%</th>
<th>MCP 99%</th>
<th>MCP 95%</th>
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<tr>
<td>2</td>
<td>4.0</td>
<td>113</td>
<td>21.72</td>
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<tr>
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<td>13.01</td>
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<tr>
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<td><strong>10.17</strong></td>
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</tr>
<tr>
<td>6</td>
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<td>4.06</td>
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<td>Mean</td>
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<td>17.99</td>
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<td>10.11</td>
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<thead>
<tr>
<th></th>
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<th>95%CI–high</th>
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<td>1.66</td>
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<td></td>
<td><strong>0.87</strong></td>
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<td><strong>0.82</strong></td>
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<tr>
<td></td>
<td>2.06</td>
<td>21.24</td>
<td>14.29</td>
</tr>
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<td>6.51</td>
<td>8.44</td>
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<td><strong>14.98</strong></td>
<td><strong>12.36</strong></td>
<td><strong>12.36</strong></td>
</tr>
</tbody>
</table>

\(^1\) Calculated as the mean of adults present in 1998 and 1999.

\(^2\) Bold type designates breeding units with >20 position fixes in which territory size reached an asymptote, according to visual inspection of cumulative plots (see Fig. 6.5).
Figure 6.6. Assessment of territory size asymptotes for White-browed Treecreeper breeding units. Plots represent minimum convex polygon estimates of territory size (99% of fixes ——; 95% of fixes —— ) with position fixes added sequentially. Stars denote the point at which curves were considered to flatten, indicative of an asymptote.
However, the visual assessments of asymptotes (i.e. Fig. 6.6) were not supported by statistical tests (i.e. linear regression). That is, in a majority of cases, the slope of the curve from the estimated point of the asymptote to the end of the curve was significantly greater than zero (results not presented). The consequence of this is a sampling bias in which the number of position fixes per breeding unit is correlated with the estimate of territory size. The problem now becomes how to generate the best estimate of territory size in the absence of asymptotic data, given the limitations of the data.

One solution is to examine the increase in territory size with the number of position fixes at a population scale; that is, consider all breeding units concurrently. When 95% of fixes are included in minimum convex polygon estimations (MCP 95%), 30 to 35 position fixes are required before mean territory size stabilizes across the population, at which point six breeding units are contributing to mean territory size (Fig. 6.7). Considering only the first 30 position fixes of these six breeding units, territories ranged from 6.6 ha to 11.2 ha with an average size of 8.4 ± 0.8 ha (95% CI 6.4 – 10.4 ha).

Figure 6.7. Mean territory size (MCP 95%) of White-browed Treecreeper breeding units versus number of position fixes. Error bars are 95% confidence intervals. The number of breeding units that contribute to each point is indicated at top of graph.
Relationship between group size and territory size

The territory size of White-browed Treecreeper breeding units varied significantly with group size in simple correlation (Table 6.3). However, the MCP estimates of territory size were also dependent on the number of position fixes, which in turn was correlated with group size (Table 6.3). To control for this confounding sampling bias, the residuals of a linear regression of territory size versus the number of fixes were used as an index of territory size, independent of the number of fixes. The residuals of the MCP 95% regression were significantly correlated with the original MCP 95% estimate \( (r = 0.64, P = 0.025) \), indicating that the relative size of breeding unit territories was maintained during the regression procedure. When the sampling bias was controlled for in this way, there was no significant effect of group size on territory size (Table 6.3). Thus, the relationship between territory size and group size apparent in the simple correlation was an artifact of the sampling bias, rather than actual variation in territory size due to variation in group size.

Table 6.3. Relationship between number of position fixes, number of adults (group size) and territory size estimates of White-browed Treecreeper breeding units at Yarrara FFR, 1998 - 1999. The residuals from a regression of the MCP estimates against the number of position fixes were used to control for the sampling bias. Spearman’s rho was used for all comparisons involving group size. Significant correlations in bold type. \( (n = 12 \) in all comparisons)

<table>
<thead>
<tr>
<th>Sampling bias not controlled</th>
<th>Group size</th>
<th>Ellipse 90%</th>
<th>MCP 100%</th>
<th>MCP 95%</th>
</tr>
</thead>
<tbody>
<tr>
<td># of fixes</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( r )</td>
<td>0.665</td>
<td>0.471</td>
<td>0.904</td>
<td>0.775</td>
</tr>
<tr>
<td>( P )</td>
<td>0.018</td>
<td>0.123</td>
<td>&lt;0.000</td>
<td>0.003</td>
</tr>
<tr>
<td>Group size</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( r_s )</td>
<td>0.603</td>
<td>0.653</td>
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<tr>
<td>( P )</td>
<td>0.038</td>
<td>0.021</td>
<td>0.002</td>
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<tr>
<td>Sampling bias controlled</td>
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<tr>
<td># of fixes</td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>( r )</td>
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<tr>
<td>( P )</td>
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<td>0.902</td>
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</tr>
<tr>
<td>( r_s )</td>
<td>0.087</td>
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<tr>
<td>( P )</td>
<td>0.789</td>
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</table>
6.4 Discussion

Breeding strategy

The White-browed Treecreeper is a facultative cooperatively breeding species, in that a moderate fraction (35%) of breeding units contained non-breeding auxiliaries (i.e. helpers) that assisted in rearing non-descendent young. Under Brown’s (1987) hierarchical classification of avian communal breeding systems, they would be categorized as group-territorial, singular-breeding, with male helpers and a (putatively) monogamous mating system. Thus, the White-browed Treecreeper can be added to the growing list of Australian species for which cooperative breeding has been confirmed in some portion of the breeding population. Since Harrison’s (1969b) first inventory, which included 18 passerines, the number of Australian bird species (including non-passerines) for which cooperative breeding has been recorded has grown to 39 in 1976 (Rowley 1976), 65 in 1980 (Dow 1980a) to 80 in the most recent review (Clarke 1995). This reflects the increasing interest in cooperative breeding systems over the last 30 years, which is partly responsible for the bias in breeding biology studies towards cooperative and sedentary species (Clarke 1997). However, it also underlines the prevalence of cooperative breeding in old endemic families of the Australian avifauna (Russell 1989), and suggests that the list of cooperative species will continue to increase as more species are studied in detail [e.g. Black-faced Woodswallow Artamus cinereus (Rowley 1999), Pale Yellow Robin Tregellasia capito (Male 2000)].

The proportion of units breeding cooperatively within the study population of White-browed Treecreepers is at the lower end of a continuum from species consisting entirely of unassisted pairs [i.e. non-cooperative breeders, e.g. Rufous Whistler Pachycephala rufiventris (Bridges 1994), White-fronted Chat Ephthianura albifrons (Major 1991)] to obligate cooperative breeding species in which pairs must be assisted by helpers to fledge offspring [e.g. White-winged Chough Corcorax melanorhamphos (Rowley 1978, Heinsohn 1991, 1995)]. Furthermore, the incidence of cooperative breeding varies between breeding units within the same population (Brown 1987, Stacey & Koenig 1990), between populations of the same species [e.g. Australian Magpie Gymnorhina tibicen (Hughes et al. 1996), Bicolored Wren Campylorhynchus griseus (Austad & Rabenold 1986), Splendid Fairy-wren Malurus splendens (Rowley et al. 1991 cf. Van Bael & Pruett-Jones 2000)], between species
within the same genus or family [e.g. *Acanthiza* (Bell & Ford 1986), North American Jays *Aphelocoma spp.* (Atwood 1980, Woolfenden & Fitzpatrick 1990, Koenig et al. 1992] and between higher taxonomic clades (Russell 1989, Edwards & Naeem 1993, Cockburn 1996). In this study, helpers were present in a smaller proportion of breeding units than in other *Climacteris* species [e.g. Red-browed Treecreeper 65%, Brown Treecreeper 59% (Noske 1991) and Rufous Treecreeper 60% (Luck 2000)].

The relatively low incidence of cooperative breeding, combined with the small size of the complement at cooperative nests (usually only one helper), resulted in a smaller mean group size for the White-browed Treecreeper (2.4 adults) than reported for most cooperatively breeding species. For example, the mean group size of 27 species reviewed by Hatchwell (1999) was 3.3, almost one helper per breeding unit greater than in the Yarrara population of White-browed Treecreepers. This may reflect a bias in early and current studies towards conspicuously cooperative species with many helpers. As more cooperatively breeding species are studied in detail, small group size may be revealed as typical of many species [e.g. mean group size was 2.3 adults in the Purple-crowned Fairy-wren *Malurus coronatus* (Rowley & Russell 1993)]. Nonetheless, the mean group size of White-browed Treecreepers in this study was lower than that reported for the Red-browed Treecreeper [2.8 adults (Noske 1991)], Brown Treecreeper [2.9 adults (Noske 1991); 3.0 adults (Walters et al. 1999)] or Rufous Treecreeper [3.0 adults (Luck 2000)]. However, group size in the Red-browed Treecreeper only varied from 2 to 4 in 20 group-years, which was similar to the extent of variation in group size observed in the White-browed Treecreeper.

The incidence of cooperative breeding in the study population was stable over the two breeding seasons. More cooperatively breeding groups were detected in 1999 than 1998 but this reflects an overall increase in the size of the breeding population rather than a significant rise in the proportion of cooperative groups. The composition of breeding units was also relatively stable, with the pair-bonds of the putative breeding pair maintained for the duration of the study in most territories. This study was too short to determine the duration that helpers remain in their natal territory. However, only one helper disappeared between breeding seasons, whereas three individuals were observed helping in the same territory in both seasons. This indicates males may remain in their natal territory for several seasons, once
established as helpers, before dispersing or inheriting breeding status. Conversely, males raised in territories with helpers already present tended to disperse as soon as they matured (see Chapter 9) rather than remain as additional helpers. This suggests some of the benefits of philopatry and helping may be dependent on an individual’s position in the dominance hierarchy within a breeding unit and hence, the probability of territory inheritance.

Two primary agents of variation in breeding unit composition were discernible. First, in three territories, male offspring remained in their natal territory for the subsequent breeding season, altering the breeding strategy from non-cooperative in 1998 to cooperative in 1999. Second, the disappearance of a breeding individual often led to a complete change in the composition of the breeding pair. The most informative example of the latter occurred in territory T2. Following the death of the putative male breeder after the 1998 season, the widowed female was either evicted by the remaining males, or emigrated on her own volition. This indicates a reluctance to mate with one of the helpers (or vice-versa), presumably all her sons, and is consistent with the incest taboo hypothesis that mother-son matings are avoided at all costs, presumably to reduce inbreeding (Brown 1987, Pusey & Wolf 1996, Cockburn 1998). One of the helpers assumed the male breeding position in T2 and attracted a new partner, who had been ‘floating’ in the territory for some time and was familiar to the new male breeder. This was the only case of male territory inheritance observed but given the short duration of the study was sufficient to suggest that one advantage of philopatry may be to secure a breeding position in a high quality territory. It also reveals the value of “floating” as a strategy for females to secure a breeding position (observed in one other territory) as they are nearby when breeding vacancies arise. Thus, floating females may be tolerated under normal circumstances because they are perceived by male group members as potential mates or step-mothers should the incumbent female disappear.

**Survival**

The annual adult survival of between 70% to 85% for the White-browed Treecreeper is high, but typical for a small Australian passerine (Ford 1989). For example, annual survival ranged from 55% to 87%, with a median of 72%, for 15 species of small to medium temperate Australian passerines (Rowley & Russell 1991). Survival of
southern hemisphere passerines is generally higher than for passerines in the northern hemisphere (Rowley & Russell 1991, Yom-Tov et al. 1992, 1994). Birds in temperate southern continents generally have adequate food availability throughout the year and do not need to endure extremely harsh winters. Certainly, this is true for the White-browed Treecreeper in north-west Victoria, although populations in the interior of Australia experience extreme environmental stresses of heat and aridity that may reduce survival.

The maximum time elapsed from banding to recovery of the Red-browed Treecreeper has been 8 years and an individual Brown Treecreeper has survived for at least 13 years (Baker et al. 1999). Therefore, the maximum longevity of the White-browed Treecreeper could conservatively be estimated at 8 to 10 years. Thus, the short duration of this study relative to the probable longevity of individuals, together with the uncertainty associated with the survival estimates in the last census period, make specific comparisons of annual survival with other species hazardous. However, if the mid-point of the range is accepted as an indicative figure, the annual survival of 78.5% was virtually identical to that of the Red-browed Treecreeper (79%) and Brown Treecreeper (78.2%) and slightly higher than the White-throated Treecreeper (72.6%) (Noske 1991). Similarly, the mid-point of the estimate for male (81.1%) and female (76.3%) White-browed Treecreepers was close to the 77% and 75% for male and female Rufous Treecreepers, respectively (Luck 2000).

Survival often varies with the age and gender of individuals (Clutton-Brock 1988, Newton 1989). Juveniles suffer higher mortality than adults because they may be less efficient foragers, more vulnerable to predators or more likely to disperse, which is generally a risky process. In cooperatively breeding species, there is often a gender-bias in juvenile dispersal as one sex is more inclined to be philopatric (Stacey & Koenig 1990). Consequently, a bias in the adult sex ratio may be expected that favours the philopatric sex. The sex ratio of White-browed Treecreeper fledglings was equal and all philopatric individuals were male; therefore, dispersal was obviously female biased. However, contrary to expectations, the sex ratio in the general adult population (i.e. all adults banded) was also even, which suggests that mortality amongst juvenile males and females was similar despite their different dispersal strategies.
Social organization, survival and breeding strategy

There was a slight (non-significant) male bias in the breeding population, including helpers. This bias would have been more pronounced in a larger sample, assuming helpers are universally male. The disparity between the sex ratio in the breeding population and that of the general population was due to several “floating” females who were resident in the study plot but not involved in any breeding efforts. In addition, several transient adults (equal number of males and females) that were never or rarely detected after banding were included in the overall sex ratio. These transient individuals may have been “roaming” females seeking a breeding vacancy or males that had delayed dispersal for one or more years but were now searching for an opportunity to breed independently. Thus, a variety of strategies may be employed by individuals seeking a breeding position. No comment can be offered on the relative survival of individuals engaged in the respective strategies. However, amongst the breeding population of White-browed Treecreepers resident in the study plot (including helpers), there was no discernible difference in the annual survival of males and females. There was insufficient data in this study to differentiate between survival during the breeding and non-breeding seasons but longer-term studies may be able to clarify and distinguish between sources of mortality.

**Territoriality**

The territorial system of the White-browed Treecreeper was characterized by slightly overlapping, but well-defined, territories that were occupied by a single breeding unit and maintained throughout the year. There was no evidence that territory borders were relaxed during the non-breeding season allowing breeding units to amalgamate into winter-foraging clans, as occurs in several other cooperatively breeding bark-foraging species, such as the Buff-rumped Thornbill *Acanthiza reguloides* (Bell & Ford 1986) and the Varied Sitella *Daphoenositta chrysoptera* (Noske 1998). Alternatively, some cooperatively breeding treecreepers (Noske 1991, Luck 2000) and Manorina honeyeaters (Dow 1979, Clarke 1984, Clarke & FitzGerald 1994) show the reverse trend, with the relaxation of territory boundaries during the breeding season. In these systems, breeders and/or helpers provision young in more than one territory. However, territorial disputes between White-browed Treecreepers were frequent and breeders were particularly resolute in repelling intruders during the breeding season. Furthermore, cross-territorial provisioning of young was not observed (Chapter 8). Thus, the conventional group territorial, singular-breeding
system of the White-browed Treecreeper resembles that of the Red-browed Treecreeper (Noske 1991) and many other cooperatively breeding species (Brown 1987).

One of the consequences of the development of molecular techniques in recent decades has been the acknowledgement that extra-pair fertilization is far more widespread than previously believed (Hughes 1998). However, a recent spate of genetic studies has also confirmed predominantly monogamous mating systems in several species in which extra-pair fertilizations were presumed to be rare on the basis of behavioural observations (Haydock et al. 1996, Conrad et al. 1998, Lundy et al. 1998, Quinn et al. 1999, Legge & Cockburn 2000). In the absence of molecular information, the likelihood of extra-pair fertilization in the White-browed Treecreeper population remains speculative. However, several aspects of their social organization suggest their mating system is monogamous and that extra-pair fertilization is atypical.

First, territory boundaries were vigorously maintained and individuals were seldom sighted outside their territory, reducing the opportunity for extra-pair copulations. Second, courtship displays (Chapter 8) were only observed between established pairs. Third, mate-guarding behaviour, common in species in which extra-pair fertilization occurs (Davies 1990), was not detected. Fourth, copulations were only observed between an established pair (albeit only one pair). Fifth, itinerant or “philandering” males (sensu Rowley & Russell 1990b, 1995) were rarely observed and males contributed to the breeding effort of only one breeding unit. Finally, mother-son matings appeared to be actively avoided, as described above. However, none of these observations authoritatively dismisses the possibility of extra-pair fertilizations, particularly those arising from within a breeding unit (Cockburn 1998). For instance, a subordinate male helper may attempt to mate with the incumbent female, in circumstances in which the female is unrelated to the helper following the death or eviction of the previous female (e.g. Magrath & Whittingham 1997).

**Territory size**

The variety of methods available for calculating territory size and the limitations inherent in their estimation complicate the analysis of territory size. The most
consistent and reliable results in this study were achieved from minimum convex polygons encompassing 95% of position fixes. Radio-telemetry studies often use harmonic mean methods to calculate territory size (Dixon & Chapman 1980), which provide a more accurate description of variation in intensity of habitat use and effective territory size than minimum convex polygons. However, harmonic mean analysis was not appropriate in this study (it was tested in preliminary analyses) because it is sensitive to skewed distributions of position fixes and therefore requires more data than were collected here (Harris et al. 1990).

The mean size of territories with an adequate number of fixes (30) was 8.4 ha, with individual territories ranging from 6.6 ha to 11.2 ha. It is stressed that the territory size estimates refer to the entire breeding unit and not necessarily individual birds. However, there was almost complete overlap of position fixes for members of the same breeding unit and partitioning of the territory was not apparent in the field. Minimum convex polygons are often criticized as they may include habitat not used by individuals (Harris et al. 1990). In this study, position fixes were collected within relatively homogeneous Belah woodland habitat and did not include areas that are avoided by White-browed Treecreepers (e.g. agricultural land, mallee scrub). Further, during continuous tracking, individuals were observed to forage over the entire range of their territory. Thus, it is unlikely that areas not used by White-browed Treecreepers were included in their territory estimates. A second criticism of minimum convex polygons is that they are heavily influenced by peripheral fixes (Harris et al. 1990). This was addressed by using peeled polygons of 100%, 99% and 95% of fixes to assess the influence of outlying fixes (Kenward & Hodder 1996). The substantial decrease in estimated territory size in successive peeled polygons indicated that outlying fixes were exerting a disproportionate influence on territory size calculations when 100% or 99% of fixes were included. This was probably causing an over-estimation of territory size in several breeding units (e.g. T2, T4, T12 and T11; Table 2).

Territory boundaries may gradually shift over time without an appreciable increase or decrease in territory size. Subtle changes in the main foraging areas used by individuals, either seasonally or annually, may result in territory expansion in one direction with simultaneous reductions in other parts of the territory. Position fixes of White-browed Treecreepers were collected over a relatively long period (September
1998 to February 2000) but were not differentiated by date. Thus, small shifts in territory boundaries that may occur over time will increase the area bounded by the minimum convex polygons. The step-functions in the cumulative plots of territory size versus sample size of position fixes (Fig. 5) probably reflect such shifts, especially in those territories with a large sample (e.g. T2, T3, and T12). This reaffirms the selection of the more conservative MCP 95% as the most reliable measure of territory size.

Noske (1986, 1998) has argued that food may be relatively scarce for bark-foragers in Australian eucalypt woodlands and forests. Thus, to gain access to sufficient foraging resources, treecreepers and sitellas must maintain large territories for birds of their size. This study supports this contention. Territories of the White-browed Treecreeper are larger than those of similar-sized birds with different foraging niches, such as the Rufous Whistler (Bridges 1994), Helmeted Honeyeater *Lichenostomus melanops cassidix* (Moysey 1997), Crescent Honeyeater *Phylidonyris pyrrhoptera* (Clarke & Clarke 1999) and Bell Miner *Manorina melanophrys* (Clarke & Fitz-Gerald 1994). The mean territory size of White-browed Treecreepers at Yarrara was 25% smaller than the average of 11.2 ha for the Red-browed Treecreeper in eucalypt forest in northern NSW (Noske 1991) but more than three times larger than for the Rufous Treecreeper (mean = 2.6 ± 0.18 ha) in eucalypt woodland in south-west WA (Luck 2000). Rose (1996) reported larger territories for the Rufous Treecreeper (mean of 7.8 ha) in more heterogeneous habitat that included woodland and areas of human habitation. The only data on the size of Brown Treecreeper territories comes from open farmland with scattered trees in northern NSW, where pairs occupied *ca.* 7 ha and groups of four occupied *ca.* 20 ha (Noske 1991). White-throated Treecreepers appear to maintain smaller territories than cooperatively breeding treecreepers, averaging 3.9 ha in continuous eucalypt forest (Noske 1991).

Considerable variation in territory size exists among breeding units of White-browed Treecreepers (Table 2). Territory size is often related to group size in cooperatively breeding or group territorial species. For example, larger groups of the Laughing Kookaburra *Dacelo novaeguineae* (Legge 2000), Brown Treecreeper (Noske 1991), Chowchilla *Orthonyx spaldingii* (Jansen 1999), Old World Babblers *Turdoides spp.* (Gaston 1978a, Monadjem *et al.* 1995, Shaw & Shewry 2000), Florida Scrub Jay
Aphelocoma c. coerulescens (Woolfenden & Fitzpatrick 1991) and White-throated Magpie-Jay Calocitta formosa (Langen & Vehrencamp 1998) all possess significantly larger territories than smaller groups. In this study, there was no evidence of a significant relationship between group size and territory size, after controlling for the sampling bias. Furthermore, there was no evidence of territory contraction or expansion after changes in group size. For example, the breeding units in territories T1, T11 and T12 continued to occupy similar sized territories after they grew from pairs to trios. The pairs in T11 and T12 in particular, had occupied large territories prior to their increase in group size, although these territories may have been established by larger breeding units before this study commenced. Nonetheless, it appeared that a pair was capable of successfully defending a territory of 8 – 10 ha.

The absence of a significant correlation between the number of occupants and territory size implies that it is probably access to resources (e.g. Stacey & Ligon 1987, Ligon & Ligon 1988, Ligon et al. 1991) that determines territory size rather than cooperative defence of the territory (e.g. Woolfenden & Fitzpatrick 1990, Hughes et al. 1996, Jansen 1999). That is, a territory must contain a minimum level of resources (e.g. foraging substrates or nest sites) to sustain a breeding unit but this may not be reflected in territory area.

Conclusions

The social organization of the White-browed Treecreeper is typical of many cooperatively breeding birds. They are opportunistic or facultative cooperative breeders in which usually only one, but up to three, male helpers are present in a moderate fraction (35%) of breeding units. They are sedentary, occupying relatively large, all-purpose territories throughout the year. However, unlike many group territorial birds, territory size was not related to the number of occupants. Annual adult survival is high: qualitative comparisons suggest that breeders in cooperative groups may have a slightly better chance of survival than unassisted pairs.

Cooperative groups are formed through male philopatry, in which male offspring delay dispersal and remain in their natal territory for one or more years. Consequently, natal dispersal is female-biased, although there was no skew evident in the sex ratio of the fledglings or the general adult population. Males may attain
breeding positions through inheritance of their natal territory or by filling vacancies created by the death of breeding males in nearby territories. Females also appear to employ several strategies to gain a breeding position. These include “floating” as a non-breeding and non-helping resident in one or more territories awaiting breeding vacancies nearby, and “roaming” in which individuals move over a larger area in search of breeding vacancies. Floating females have the advantage of being able to establish social bonds with the resident males in their neighbourhood before vacancies arise, but nomads are possibly exposed to more breeding vacancies. It was not clear whether novice breeders are able to establish new territories in marginal or previously unoccupied habitat. However, Woolfenden & Fitzpatrick (1991) suggest that the energy and risk involved in such a task is prohibitive for the Florida Scrub Jay, a species that, like the White-browed Treecreeper, has limited opportunities for colonization of new areas.
Chapter 7

Selection of nest sites by the White-browed Treecreeper in north-west Victoria
7.1 Introduction

Obtaining a suitable nest site is a prerequisite for breeding success in nidicolous birds. Therefore, a critical component for conservation management is an understanding of nesting requirements and preferences. This is particularly true for species that nest only in tree hollows but cannot excavate their own holes (obligate secondary hollow-nesters) and therefore, may be limited in their choice of suitable nest sites. The suitability of a hollow as a nest site is fundamentally defined by the relative size of the bird to the hollow opening. All other factors being equal, the safest sites are provided by the smallest opening through which an individual can enter the cavity beyond, as this restricts access to larger predators and competitors (Newton 1994).

Availability of suitable nest sites for obligate hollow-nesting species depends on the abundance and spatial distribution of hollows, the extent of territorial or agonistic behaviour within the population, and the level of conspecific and interspecific competition for hollows (Saunders 1979, Saunders et al. 1982, Nilsson 1984). In response to competition or environmental factors, adaptive specialization in the type or size of hollows used may have evolved, which should be reflected in contemporary nest site selection (Pribil 1998). Accordingly, species may prefer hollows with certain entrance dimensions (Saunders et al. 1982, Newton 1994), depth (Gibbons 1999), orientation (Reller 1972, McComb & Noble 1981a), height above the ground (Nilsson 1984, Sedgwick & Knopf 1990) or position in the tree (Conner 1975, Saunders et al. 1982, Sedgwick & Knopf 1990, Luck 2000).

Habitat management greatly influences the number and type of hollows available to fauna (Inions et al. 1989, Lindenmayer et al. 1991a, Gibbons 1999). In regions that have sustained anthropogenic disturbances, the availability of suitable nesting hollows may have been reduced through loss of mature trees, or lack of recruitment of trees into size-classes capable of developing hollows, which may limit population growth of some bird species (Traill 1993, Bennett et al. 1994, Newton 1994, Garnett & Crowley 2000). However, for some hollow-nesting species, the availability of nest sites is not considered limiting [e.g. Gouldian Finch Erythrura gouldiae (Tidemann et al. 1992), Forest Red-tailed Black Cockatoo Calyptorhynchus banksii naso (Abbott 1998)] or is not currently limiting but is expected to become so as hollow-bearing trees fall without replacement [e.g. Carnaby’s Cockatoo Calyptorhynchus
The nesting requirements of the White-browed Treecreeper have not previously been intensively studied and are poorly documented. Like other Climacteridae, the White-browed Treecreeper is an obligate hollow-nesting species, using holes, spouts and splits in the trunks and branches of live or dead trees (Schodde & Tidemann 1986, Emison et al. 1987, Nest Record Scheme 2000). However, the specific characteristics of hollows used by the White-browed Treecreeper are not known. It is often cited that its nests are placed close to the ground (e.g. Pizzey 1999, Morcombe 2000) but there is little quantitative evidence for this claim.

This chapter presents the first quantitative description of White-browed Treecreeper nest sites. This provides a basis for defining suitable nesting hollows. To determine whether White-browed Treecreepers are using hollows at random or selecting nest sites based on particular features, selected characteristics of nest sites are compared with unused hollows. Finally, the potential for nest sites to limit population growth in White-browed Treecreepers is assessed, in light of their preferences for particular hollow characteristics.

### 7.2 Methods

**Description of nest sites**

Nests were located during intensive nest searches, either by following adult birds carrying nest material or food, visual inspection of hollows or by flushing birds from hollows. Search effort was concentrated in the principal study plot at Yarrara FFR (Fig. 6.1; description in 6.2) but details of nests detected at other locations were also recorded. These were mostly in the Yarrara region (see Fig. 3.1), located in small remnants on private land as well as larger public reserves. Only one nest was found at Wyperfeld National Park. When nests from outside the Yarrara FFR study plot were included in summaries, analyses or comparisons, it is explicitly indicated by the term “from all locations”. Characteristics of the nest tree, nest hollow and a
A qualitative description of the vegetation within a radius of 20 m were recorded for all nests located (Table 7.1).

Table 7.1. Characteristics of hollow-bearing trees and hollows recorded at nest sites and unused hollows\(^1\) at Yarrara FFR.

<table>
<thead>
<tr>
<th>Character</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Qualitative characters</strong></td>
<td></td>
</tr>
<tr>
<td>Tree density</td>
<td>Tree density within 20m radius of hollow-bearing tree was ranked (high, medium, low) relative to tree density in surrounding woodland.</td>
</tr>
<tr>
<td>Shrub density</td>
<td>As per tree density, for shrubs &gt;1.5m high and shrubs &lt;1.5m high.</td>
</tr>
<tr>
<td>Tree species*</td>
<td>Species of tree in which the hollow was located.</td>
</tr>
<tr>
<td>Tree health</td>
<td>Proportion of dead wood visible in the tree, estimated in 10% intervals. Completely dead standing trees were noted.</td>
</tr>
<tr>
<td>Hollow type*</td>
<td>Origin of hollow formation: branch fall scar (hole); fork (hollow formed at base of diverging boughs); spout (broken or split trunk/branch open at the top).</td>
</tr>
<tr>
<td>Hollow position</td>
<td>Location of the hollow in the tree: trunk; primary limb (first division from trunk); secondary branch (second division from trunk).</td>
</tr>
<tr>
<td>Orientation of entrance*</td>
<td>Direction of hollow opening: north (315° - 45°); east (45° - 135°); south (135° - 225°); west (225° - 315°); vertical (open top, no roof).</td>
</tr>
<tr>
<td><strong>Quantitative characters</strong></td>
<td></td>
</tr>
<tr>
<td>Tree diameter* (cm)</td>
<td>Diameter at breast height over bark of the main trunk of the hollow-bearing tree, measured with calibrated diameter tape.</td>
</tr>
<tr>
<td>Limb diameter at hollow (cm)</td>
<td>Diameter of the limb at the hollow, measured with calibrated diameter tape.</td>
</tr>
<tr>
<td>Tree height* (m)</td>
<td>Highest point of the foliage (or dead wood) of the hollow-bearing tree, measured with a clinometer.</td>
</tr>
<tr>
<td>Height of entrance above ground* (m)</td>
<td>Height of the lower lip of the hollow opening from the ground, measured directly with a tape or by using a clinometer for higher hollows.</td>
</tr>
<tr>
<td>Relative entrance height * (%)</td>
<td>Height of entrance above ground, divided by tree height (X 100).</td>
</tr>
<tr>
<td>Entrance dimensions* (cm)</td>
<td>Width and height of the longest axes of the hollow opening, measured with a ruler (if accessible) or estimated (if unaccessible).</td>
</tr>
<tr>
<td>Entrance shape*</td>
<td>Entrance width divided by entrance height.</td>
</tr>
<tr>
<td>Hollow depth (cm)</td>
<td>Distance from the lower lip of opening to the floor of the hollow, measured by inserting a ruler or stick into the hollow (after nesting was finished) or estimating the position of the hollow floor on the outside of the limb.</td>
</tr>
</tbody>
</table>

\(^1\) Only those characteristics marked with an asterisk were recorded at unused hollows.
Selection of nest sites

Assessment of selectivity of nest sites was based on comparisons of characteristics of chosen sites with a subsample of available sites. This approach is more sensitive for detecting selection of nest sites than correlating nest site features with measures of reproductive success, when preferred sites are abundant (Pribil 1998), as may occur for hollow-nesting birds in mature or unmanaged forests (Waters et al. 1990, Newton 1994).

The size (diameter at breast height) of nest trees located in the Yarrara study plot was compared to a random sample of 100 trees from the study plot using t-tests. This was performed separately for each type of tree used for nesting (i.e. live Belah and all dead trees). Selected characteristics of trees and hollows (Table 7.1) were compared between nest sites and 50 hollow-bearing trees and hollows in the Yarrara study plot that were not used for nesting by White-browed Treecreepers during 1998 – 1999. The two closest unused hollow-bearing trees within the same territory for each of the 24 nests were chosen for comparison. Unused hollows of any type or size were included. The distance from the unused hollow-bearing tree to the nest tree was paced out. In one territory (T33), only one other hollow could be located. Thus, three additional hollow-bearing trees were selected at random to achieve a sample of 50 trees. Characteristics were compared between nest trees and unused trees using $\chi^2$ or t-tests for qualitative and quantitative characteristics respectively. A matched pair comparison of each nest with its closest unused hollow was also conducted.

A logistic regression model of hollow use by nesting White-browed Treecreepers at Yarrara FFR was developed, based on the data from the 24 nest sites and 50 unused hollows. Descriptor variables were transformed where necessary to meet the assumption of bivariate normal distribution (Table 7.4) and multicollinearity was addressed in the first instance by excluding one of a pair of variables that had a Pearson correlation coefficient of $|r| > 0.6$. Model building proceeded by stepwise variable selection. Regression diagnostics (standardized residuals, leverage and Cook’s D statistic) and the Hosmer-Lemeshow goodness-of-fit statistic were checked to assess conformity of the data to the assumptions of logistic regression and the model fit (Nicholls 1989). The significance of predictor variables was evaluated from the change in the log likelihood ratio (Hosmer & Lemeshow 1989). The Nagelkerke $R^2$ statistic and the error rate of the fitted model were examined as secondary...
indicators of model adequacy. After screening to remove variables that were poor predictors of hollow use, hierarchical partitioning (see Chapter 2 for rationale and description) was used to corroborate the regression model.

**Are suitable hollows limiting?**

The comparisons of nest sites with unused hollows and the development of models of hollow use aim to identify characteristics of hollows that were used by White-browed Treecreepers to select nest sites. It is also useful to determine the availability of nesting hollows and whether there was a shortage of suitable hollows. That is, were preferred nesting hollows limited? To do this, I classified nest sites as either “high” or “low” quality, based on hollow characteristics identified as important in the modeling results. I used the mean of the distance from each nest to the two closest unused hollows as an indicator of hollow abundance within each territory. I hypothesized that if preferred hollows were limited, then the mean distance would be greater for low quality nests; that is, the abundance of hollows should be lower in territories in which low quality hollows were used. In addition, for hollows to be considered limiting, the alternative hollows to low quality nest sites should be of equal or lower quality than the nesting hollows.

Finally, to be truly limiting, the nest site characteristic in question should impinge on fitness; that is, successful nests should differ from unsuccessful nests with respect to the potentially limiting variable. This decision process to assess the potential for each characteristic to be limiting is summarized in Figure 7.1.
Is the variable limiting?

Determine “high” and “low” quality nest sites.
Use median or inter-quartile range

Are low quality nest sites in areas with low hollow density?
Use t-tests

YES
Suggests variable is limiting

NO
Suggests variable is not limiting

Are alternative hollows to low quality nests usable?
Within range of hollows used as nest sites

YES
Weakens argument for limiting variable

NO
Supports variable is limiting

Are alternative hollows to low quality nests of better quality?
Use paired t-tests, χ² tests

YES
Confirms variable is limiting

NO
Does variable influence fitness? Relate to reproductive success

Figure 7.1 Flow diagram of the decision process used to assess whether hollow characteristics were limiting in the Yarrara study plot, 1998-1999.
7.3 Results

Nest site characteristics

Qualitative characteristics

A total of 32 nests was discovered during the study at various sites, of which 24 were located in the intensive study plot at Yarrara (Table 7.2). At Yarrara, nests were most commonly built in living Belah trees (Fig. 7.2a) but hollows in dead trees and stumps (Fig. 7.2b) were also used. Elsewhere, nests were found in hollows in Buloke and mallee trees. Slender Cypress-pines were only used for nesting once they were dead. Otherwise, generally healthy trees were used, although, by necessity, part of the heartwood must be decaying for hollow formation (Gibbons 1999). Nest trees were usually located in an area of medium to high tree density. Shrub density in the immediate vicinity of nest trees varied. There was no indication of site selection based on the surrounding habitat.

A significant majority (59%) of nests from all locations were in holes caused by branch fall scars in the main trunk or primary limb ($\chi^2 = 11.7, d.f. = 2, P = 0.003, n = 31$ excluding the cut stump; Table 7.2). This proportion was even higher at Yarrara (71%; $\chi^2 = 17.0, d.f. = 2, P < 0.001, n = 23$) where fewer nests were located in spouts, which tend to occur in mallee trees. However, other types of hollows were used for nesting. At Yarrara, three nests were in hollows formed at the fork of diverging boughs, two nests were in deep splits at the top of trunks of dead trees, one was in an open spout of the broken top of a dead tree and one was in the hollow core of a cut stump.

However, White-browed Treecreepers at Yarrara were not actively selecting particular types of hollows for nest sites as there was no significant difference in the frequency of hollow types between the 23 nest sites (excluding the cut stump) and 50 unused hollows ($\chi^2 = 2.5, d.f. = 2, P = 0.29$; Fig. 7.3). Nor were they selecting particular types of trees, with the frequency of nests in live Belah, dead trees and mallee in proportion to their occurrence in the woodland ($\chi^2 = 0.64, d.f. = 2, P = 0.73$; Fig. 7.3).

The orientation of available hollows (i.e. nest sites and unused hollows) did not show a significant departure from random, either when vertical hollows were included ($\chi^2$
Nest site selection

= 2.49, d.f. = 4, P = 0.65) or excluded (χ^2 = 2.16, d.f. = 3, P = 0.54). However, hollows used for nesting were significantly more likely to be opening south and less likely to be opening north, west or vertically than expected from comparison with the 50 unused hollows (χ^2 = 21.2, d.f. = 4, P <0.001; Fig. 7.3). This held when vertical hollows were excluded from the analysis (χ^2 = 12.0, d.f. = 3, P = 0.007). Thus, White-browed Treecreepers appear to be selecting hollows with a southerly orientation from those available in the woodland.
Table 7.2. Qualitative characteristics of nest trees and nest hollows used by White-browed Treecreepers, 1998-99.

<table>
<thead>
<tr>
<th>Character</th>
<th>No. nests – all sites</th>
<th>No. nests – Yarrara FFR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yarrara FFR (intensive study plot)</td>
<td>24</td>
<td>24</td>
</tr>
<tr>
<td>Yarrara region</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Mallanbool FFR</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Wyperfeld NP</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Density of trees in 20m radius</td>
<td></td>
<td></td>
</tr>
<tr>
<td>High</td>
<td>15</td>
<td>9</td>
</tr>
<tr>
<td>Medium</td>
<td>13</td>
<td>11</td>
</tr>
<tr>
<td>Low</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Density of tall shrubs (&gt;1.5m) in 20m radius</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>High</td>
<td>10</td>
<td>8</td>
</tr>
<tr>
<td>Low</td>
<td>15</td>
<td>9</td>
</tr>
<tr>
<td>Density of small shrubs (&lt;1.5m) in 20m radius</td>
<td>14</td>
<td>12</td>
</tr>
<tr>
<td>High</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>Low</td>
<td>8</td>
<td>2</td>
</tr>
<tr>
<td>Tree species</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Casuarina pauper</em></td>
<td>22</td>
<td>19</td>
</tr>
<tr>
<td><em>Callitris gracilis</em></td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td><em>Allocasuarina leuhmannii</em></td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Mallee <em>Eucalyptus spp.</em></td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Tree health</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Good (0-30% dead wood)</td>
<td>23</td>
<td>16</td>
</tr>
<tr>
<td>Fair (31-70% dead wood)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Poor (71-99% dead wood)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Dead</td>
<td>7</td>
<td>6</td>
</tr>
<tr>
<td>Type of hollow</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Branch scar</td>
<td>19</td>
<td>17</td>
</tr>
<tr>
<td>Fork</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Spout</td>
<td>8</td>
<td>3</td>
</tr>
<tr>
<td>Cut stump</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Hollow position</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trunk</td>
<td>21</td>
<td>17</td>
</tr>
<tr>
<td>Primary limb</td>
<td>10</td>
<td>7</td>
</tr>
<tr>
<td>Secondary branch</td>
<td>1</td>
<td>0</td>
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<tr>
<td>Orientation of hollow entrance</td>
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<td></td>
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<tr>
<td>North</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>East</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>South</td>
<td>12</td>
<td>8</td>
</tr>
<tr>
<td>West</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Vertical</td>
<td>7</td>
<td>4</td>
</tr>
</tbody>
</table>
Figure 7.2. (a) Typical nest tree at Yarrara FFR. Hollow entrance is indicated by the red arrow. (b) Dead tree used for nesting. Hollow entrance is indicated by the red arrow. (c) Typical nest hollow entrance in live Belah tree.
Figure 7.3. Proportion of nests (n = 24) and unused hollows (n = 50) at Yarrara FFR partitioned by (a) tree type, (b) hollow type and (c) hollow entrance orientation.
Quantitative characteristics

For all nests located (Table 7.3a), nest trees had a mean diameter at breast height (DBH) of 32.2 cm, although the average diameter of the trunk or limb at the nest hollow was only 25 cm. Nest trees were nearly 10 m high on average. The smallest live tree used for nesting had a DBH of 20 cm. The smallest dead tree in which a nest was built was 14 cm in diameter at breast height (all bark was shed), although no eggs were laid in this nest. Nest entrances were a mean of 2.9 m above the ground and located just over a third of the way up the nest tree (Fig. 7.2a). Hollow entrances were typically narrow (mean width: 4.7 cm) and elongated (mean height: 12.5 cm) such that they were oval or teardrop shaped (Fig. 7.2c). Hollow depth varied greatly, from 3 cm (this nest was prepared but not used) to 80 cm, with a mean of around 25 cm.

The subset of nest sites within the Yarrara study plot was representative of all nest sites, as indicated by the similarity in the means and extent of variation in the respective data sets (Table 7.3a cf. Table 7.3b). At Yarrara, there were two main types of nest trees – live Belah and dead trees (usually Cypress). Differences between these nest tree types account for much of the variation in nest site characteristics when all nests at Yarrara are pooled (Table 7.3b). For example, the coefficients of variation for nest tree height, height of the entrance relative to the tree and entrance height were at least halved for nests in live Belah trees, compared to all nests at Yarrara (Table 7.3b cf. Table 7.3c). Therefore, a more precise profile of nest characteristics is gained for live Belah (Table 7.3c) and dead trees (Table 7.3d) by considering the tree types independently. Nest hollow characteristics were more variable in dead trees, especially tree height and entrance dimensions. However, the mean height of the entrance above the ground (2.3 ± 0.4 m) remained similar to that in live Belah (3.0 ± 0.2) (Mann-Whitney z = -1.06, P = 0.29), despite obvious differences in tree size, and therefore relative entrance height (Mann-Whitney z = 2.6, P = 0.009).

Nests in live Belah (n = 18) and dead trees (n = 6) were located in significantly larger trees than 100 randomly chosen trees (live Belah DBH: t = 5.92, d.f. = 116, P <0.001; dead trees Log$_{10}$(DBH): t = 4.77, d.f. = 104, P <0.001; Fig. 7.4). However, when compared to 50 unused hollows, nest hollows differed only in that their entrances were further from the ground (Table 7.4). This was also the only
characteristic that differed in matched pair comparisons between each nest and its closest unused hollow ($t_{\text{paired}} = 2.07, P = 0.050$).

### Table 7.3. Quantitative characteristics of nest sites used by White-browed Treecreepers, 1998-99 (c.v. = coefficient of variation).

#### a) All nests

<table>
<thead>
<tr>
<th>Character</th>
<th>$n$</th>
<th>Mean ± s.e.</th>
<th>Range</th>
<th>c.v.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree DBH (cm)</td>
<td>32</td>
<td>32.2 ± 1.8</td>
<td>14 – 58</td>
<td>31.3</td>
</tr>
<tr>
<td>Limb diameter at nest hollow (cm)</td>
<td>27</td>
<td>24.9 ± 1.5</td>
<td>13 – 43</td>
<td>32.1</td>
</tr>
<tr>
<td>Tree height (m)</td>
<td>32</td>
<td>9.49 ± 0.6</td>
<td>0.85 – 16</td>
<td>37.8</td>
</tr>
<tr>
<td>Height of entrance above ground (m)</td>
<td>32</td>
<td>2.88 ± 0.2</td>
<td>0.85 – 5.2</td>
<td>31.4</td>
</tr>
<tr>
<td>Height of entrance relative to tree (%)</td>
<td>32</td>
<td>36.0 ± 3.4</td>
<td>18 – 100</td>
<td>53.4</td>
</tr>
<tr>
<td>Entrance width (cm)</td>
<td>32</td>
<td>4.70 ± 0.5</td>
<td>2.5 – 12</td>
<td>56.6</td>
</tr>
<tr>
<td>Entrance height (cm)</td>
<td>32</td>
<td>12.5 ± 2.3</td>
<td>4 – 65</td>
<td>104.7</td>
</tr>
<tr>
<td>Entrance shape (width/height)</td>
<td>32</td>
<td>0.58 ± 0.08</td>
<td>0.05 – 1.8</td>
<td>74.6</td>
</tr>
<tr>
<td>Hollow depth (cm)</td>
<td>29</td>
<td>25.2 ± 3.2</td>
<td>3 – 80</td>
<td>68.9</td>
</tr>
</tbody>
</table>

#### b) All nests in Yarrara study plot

<table>
<thead>
<tr>
<th>Character</th>
<th>$n$</th>
<th>Mean ± s.e.</th>
<th>Range</th>
<th>c.v.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree DBH (cm)</td>
<td>24</td>
<td>32.9 ± 2.1</td>
<td>14 – 58</td>
<td>31.2</td>
</tr>
<tr>
<td>Limb diameter at nest hollow (cm)</td>
<td>22</td>
<td>25.4 ± 1.5</td>
<td>13 – 40</td>
<td>27.9</td>
</tr>
<tr>
<td>Tree height (m)</td>
<td>24</td>
<td>9.51 ± 0.7</td>
<td>0.85 – 16</td>
<td>37.0</td>
</tr>
<tr>
<td>Height of entrance above ground (m)</td>
<td>24</td>
<td>2.84 ± 0.2</td>
<td>0.85 – 5.2</td>
<td>33.6</td>
</tr>
<tr>
<td>Height of entrance relative to tree (%)</td>
<td>24</td>
<td>35.1 ± 3.9</td>
<td>18 – 100</td>
<td>54.2</td>
</tr>
<tr>
<td>Entrance width (cm)</td>
<td>24</td>
<td>4.56 ± 0.6</td>
<td>2.5 – 12</td>
<td>60.1</td>
</tr>
<tr>
<td>Entrance height (cm)</td>
<td>24</td>
<td>13.5 ± 2.9</td>
<td>5 – 65</td>
<td>106.1</td>
</tr>
<tr>
<td>Entrance shape (width/height)</td>
<td>24</td>
<td>0.52 ± 0.08</td>
<td>0.05 – 1.67</td>
<td>76.3</td>
</tr>
<tr>
<td>Hollow depth (cm)</td>
<td>22</td>
<td>25.4 ± 4.0</td>
<td>3 – 80</td>
<td>73.9</td>
</tr>
</tbody>
</table>
Table 7.3 (continued). Quantitative characteristics of nest sites.

c) Nests in live trees (Yarrara study plot only)

<table>
<thead>
<tr>
<th>Character</th>
<th>n</th>
<th>Mean ± s.e.</th>
<th>Range</th>
<th>c.v.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree DBH (cm)</td>
<td>18</td>
<td>36.4 ± 2.1</td>
<td>20 – 58</td>
<td>25.0</td>
</tr>
<tr>
<td>Limb diameter at nest hollow (cm)</td>
<td>16</td>
<td>27.2 ± 1.8</td>
<td>15 – 40</td>
<td>25.8</td>
</tr>
<tr>
<td>Tree height (m)</td>
<td>18</td>
<td>11.1 ± 0.5</td>
<td>8 – 16</td>
<td>18.4</td>
</tr>
<tr>
<td>Height of entrance above ground (m)</td>
<td>18</td>
<td>3.0 ± 0.2</td>
<td>1.8 – 5.2</td>
<td>30.5</td>
</tr>
<tr>
<td>Height of entrance relative to tree (%)</td>
<td>18</td>
<td>27.3 ± 1.8</td>
<td>18 – 44</td>
<td>27.7</td>
</tr>
<tr>
<td>Entrance width (cm)</td>
<td>18</td>
<td>4.0 ± 0.5</td>
<td>2.5 – 10</td>
<td>56.1</td>
</tr>
<tr>
<td>Entrance height (cm)</td>
<td>18</td>
<td>8.8 ± 0.7</td>
<td>5 – 15</td>
<td>33.3</td>
</tr>
<tr>
<td>Entrance shape (width/height)</td>
<td>18</td>
<td>0.53 ± 0.09</td>
<td>0.2 – 1.67</td>
<td>74.6</td>
</tr>
<tr>
<td>Hollow depth (cm)</td>
<td>16</td>
<td>23.3 ± 4.5</td>
<td>8 – 80</td>
<td>76.5</td>
</tr>
</tbody>
</table>

d) Nests in dead trees and stumps (Yarrara study plot only)

<table>
<thead>
<tr>
<th>Character</th>
<th>n</th>
<th>Mean ± s.e.</th>
<th>Range</th>
<th>c.v.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree DBH (cm)</td>
<td>6</td>
<td>22.5 ± 2.3</td>
<td>14 – 29</td>
<td>24.9</td>
</tr>
<tr>
<td>Limb diameter at nest hollow (cm)</td>
<td>6</td>
<td>20.6 ± 2.1</td>
<td>13 – 26</td>
<td>24.5</td>
</tr>
<tr>
<td>Tree height (m)</td>
<td>6</td>
<td>4.6 ± 0.9</td>
<td>0.85 – 7.4</td>
<td>47.4</td>
</tr>
<tr>
<td>Height of entrance above ground (m)</td>
<td>6</td>
<td>2.3 ± 0.4</td>
<td>0.85 – 3.5</td>
<td>41.0</td>
</tr>
<tr>
<td>Height of entrance relative to tree (%)</td>
<td>6</td>
<td>58.7 ± 9.9</td>
<td>27 – 100</td>
<td>41.1</td>
</tr>
<tr>
<td>Entrance width (cm)</td>
<td>6</td>
<td>6.3 ± 1.5</td>
<td>3 – 12</td>
<td>57.6</td>
</tr>
<tr>
<td>Entrance height (cm)</td>
<td>6</td>
<td>27.5 ± 9.9</td>
<td>5 – 65</td>
<td>88.5</td>
</tr>
<tr>
<td>Entrance shape (width/height)</td>
<td>6</td>
<td>0.49 ± 0.18</td>
<td>0.05 – 1.0</td>
<td>89.2</td>
</tr>
<tr>
<td>Hollow depth (cm)</td>
<td>6</td>
<td>30.8 ± 8.9</td>
<td>3 – 65</td>
<td>70.6</td>
</tr>
</tbody>
</table>
Figure 7.4. Frequency distribution of the diameter at breast height of nest trees in (a) live Belah \( (n = 18) \) and (b) dead trees \( (n = 6) \) in comparison with 100 random trees in the study plot at Yarrara FFR.
Table 7.4. Comparison of the characteristics of nest sites and unused hollows in the study plot at Yarrara FFR (mean ± s.e.).

<table>
<thead>
<tr>
<th>Character</th>
<th>Nest (n = 24)</th>
<th>Unused (n = 50)</th>
<th>t_{22}</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree DBH (cm)</td>
<td>32.9 ± 2.1</td>
<td>32.2 ± 1.7</td>
<td>0.265</td>
<td>0.792</td>
</tr>
<tr>
<td>Tree height (m)¹</td>
<td>9.51 ± 0.72</td>
<td>8.84 ± 0.54</td>
<td>0.728</td>
<td>0.469</td>
</tr>
<tr>
<td>Height of entrance above ground (m)</td>
<td>2.84 ± 0.19</td>
<td>2.35 ± 0.14</td>
<td>2.040</td>
<td>0.045</td>
</tr>
<tr>
<td>Height of entrance relative to tree (%)²</td>
<td>35.1 ± 3.9</td>
<td>32.0 ± 2.7</td>
<td>0.860</td>
<td>0.390</td>
</tr>
<tr>
<td>Entrance width (cm)³</td>
<td>4.56 ± 0.56</td>
<td>5.3 ± 0.45</td>
<td>-1.193</td>
<td>0.237</td>
</tr>
<tr>
<td>Entrance height (cm)³</td>
<td>13.5 ± 2.9</td>
<td>13.4 ± 2.1</td>
<td>0.214</td>
<td>0.831</td>
</tr>
<tr>
<td>Entrance shape (width/height)³</td>
<td>0.52 ± 0.08</td>
<td>0.59 ± 0.06</td>
<td>-1.012</td>
<td>0.315</td>
</tr>
</tbody>
</table>

¹ Transformed: √Tree height
² Transformed: Arcsine √(Height of entrance relative to tree / 100)
³ Transformed: Log_{10} (x+1)

Nest structure

Nests were constructed well below the entrance lip of the hollow, where the hollow was sufficiently deep. The floor of the hollow was covered with a loosely formed, shallow saucer-shaped nest made from grass, twigs and Belah branchlets. The nest was extensively lined with feathers, fur (rabbit and kangaroo), seed pods of grasses and daisies, husky bark and wool. The lining was often 3 - 5 cm thick, providing ample insulation and protection for the eggs and nestlings. The presence of wool in several nests was surprising because neither live nor dead sheep were ever seen in the interior of the reserve. Thus, the wool may have been procured from perimeter fences, up to 1 km from the nest sites, indicating that individuals may travel beyond their usual home range in search of nesting material.

Re-use of nesting hollows

Hollows were regularly re-used both between breeding seasons and for second broods in the same season (Table 7.5). Following successful nesting attempts, 60% of breeding units that re-nested in the same season used the same hollow. However, replacement clutches after failed nests were invariably laid in a different hollow (Table 7.5), relatively close to the first nest site (Fig. 6.5). Seven breeding units (64%) used the same hollow for their first nest of the season in 1998 and 1999 (Table
Nest site selection

7.5). Nests were often located at the periphery of the breeding unit’s territory (e.g. T1, T3, T4, T6, T7, T8, T11, T17, T24, T30; Fig. 6.5).

Table 7.5. Sequence of nest occupancy by breeding units of the White-browed Treecreeper in the Yarrara study plot, 1998-99. Nest numbers correspond to those in Figure 6.5. Successful nests (s) fledged at least one offspring, failed nests (f) did not fledge any young. dnb = did not breed, although in T33 a nest was prepared in 1999.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>T1</td>
<td>N1 (s)</td>
<td>N19 (s)</td>
<td>N19 (f)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>T2</td>
<td>N2 (s)</td>
<td>N2 (s)</td>
<td>N2 (s)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>T3</td>
<td>N3 (f)</td>
<td>N18 (s)</td>
<td>N3 (s)</td>
<td>N18 (s)</td>
<td></td>
</tr>
<tr>
<td>T4</td>
<td>N4 (s)</td>
<td>N4 (f)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T6</td>
<td>N6 (s)</td>
<td>N6 (s)</td>
<td>N6 (f)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>T7</td>
<td>N7 (f)</td>
<td>N16 (s)</td>
<td>N20 (s)</td>
<td>N16 (f)</td>
<td></td>
</tr>
<tr>
<td>T8</td>
<td>N8 (f)</td>
<td>N14 (s)</td>
<td>N8 (f)</td>
<td>N14 (s)</td>
<td></td>
</tr>
<tr>
<td>T11</td>
<td>N11 (s)</td>
<td>N11 (s)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T12</td>
<td>N12 (s)</td>
<td>N21 (s)</td>
<td>N21 (s)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>T13</td>
<td>N13 (f)</td>
<td>N22 (s)</td>
<td>N13 (f)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>T17</td>
<td>N17 (f)</td>
<td>N17 (s)</td>
<td>N17 (f)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>T24</td>
<td>dnb</td>
<td></td>
<td>N24 (s)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>T25</td>
<td>dnb</td>
<td></td>
<td>N25 (s)</td>
<td>N25 (f)</td>
<td></td>
</tr>
<tr>
<td>T27</td>
<td>dnb</td>
<td></td>
<td>N27 (s)</td>
<td>N8 (f)</td>
<td></td>
</tr>
<tr>
<td>T30</td>
<td>dnb</td>
<td></td>
<td>N23 (f)</td>
<td>N30 (f)</td>
<td></td>
</tr>
<tr>
<td>T33</td>
<td>dnb</td>
<td></td>
<td>N33 (dnb)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Model of nest site selection

After preliminary data screening, five continuous variables (Tree diameter, Height of entrance above ground, Relative entrance height, Entrance width and Entrance height) and three categorical variables (Tree type – live Belah / live Mallee / dead tree –, Hollow type and Orientation of entrance) were included in the logistic regression analysis. Only two variables were selected in the preferred model of hollow use: Height of entrance above ground and Orientation of entrance (Table 7.6).
Nest site selection

The change in the log likelihood ratio associated with this model ($\chi^2 = 10.59, P = 0.06$) was marginally above the critical $\alpha$ level of 0.05, and thus, was strictly not significantly different from the null model. This was largely due to $\chi^2$-distribution having 5 degrees of freedom, due to the inclusion of a categorical factor with 5 levels. (Note that if the orientation categories are truncated to South and All other directions, the $\chi^2$ value is virtually unchanged at 10.22 but this change in log likelihood is highly significant ($P = 0.006$) because there are only 2 degrees of freedom.) The explanatory power of the preferred model was poor (Nagelkerke $R^2 = 0.186$) with an overall classification error rate of 25.7%. The specificity was 92% (ability to correctly predict a hollow was not used for nesting) but the sensitivity was only 37.5% (ability to correctly predict the presence of a nest). Nonetheless, it was preferred to the statistically significant model selected by forward stepwise selection that included only Height of entrance above ground ($\chi^2 = 4.14, d.f. = 1, P = 0.04$), but explained only 7.6% of the variance, had an error rate of 32.4%, specificity of 94% and sensitivity of 12.5%. Therefore, the preferred model provided a more parsimonious model with only minor reductions in model performance.

Table 7.6. Logistic regression model of hollow use by the White-browed Treecreeper.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Co-efficient</th>
<th>s.e.</th>
<th>Wald statistic</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-2.718</td>
<td>1.150</td>
<td>5.588</td>
<td>0.018</td>
</tr>
<tr>
<td>Height of entrance above ground</td>
<td>0.509</td>
<td>0.294</td>
<td>2.995</td>
<td>0.084</td>
</tr>
<tr>
<td>Orientation</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>North a</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>East</td>
<td>0.487</td>
<td>0.925</td>
<td>0.278</td>
<td>0.598</td>
</tr>
<tr>
<td>South</td>
<td>1.989</td>
<td>0.926</td>
<td>4.612</td>
<td>0.032</td>
</tr>
<tr>
<td>West</td>
<td>0.454</td>
<td>0.882</td>
<td>0.264</td>
<td>0.607</td>
</tr>
<tr>
<td>Vertical</td>
<td>0.406</td>
<td>0.928</td>
<td>0.191</td>
<td>0.662</td>
</tr>
</tbody>
</table>

a Orientation of entrance categories were contrasted against north facing hollows. Thus, co-efficients refer to the probability of hollow use relative to north facing hollows.

The probability that White-browed Treecreepers would nest in a hollow is predicted to increase with height (>70% of nests were further than 2.25m from the ground) and in south facing hollows (33% more likely to nest in south facing hollow at the mean nest height of 2.8 m) (Fig. 7.5).
Figure 7.5. Predicted probability of hollow use (± s.e.) according to the preferred logistic regression model (Table 7.6). Effect of (a) height of hollow entrance above the ground and (b) orientation of hollow entrance. In (a), orientation is set to south facing and in (b) height above ground is set to the mean nest height of 2.8 m.
Tree diameter, tree type and hollow type were not included in hierarchical partitioning because they were least important in the logistic regression. The hierarchical partitioning results support the inclusion of Orientation of entrance in the preferred model of hollow use (Fig. 7.6). Of the variation in nest site characteristics attributable to the independent effects of the five parameters included in the hierarchical partition, twice as much was associated with Orientation of entrance (54%) than any other parameter, including Height of entrance above the ground (26%). The Relative entrance height (9%), Entrance width (8%) and Entrance height (3%) were poor explanatory variables of hollow use.

![Figure 7.6. Variation in hollow use by the White-browed Treecreeper explained by selected hollow characteristics. The solid bars indicate the amount of variation attributable to the independent effect of a given variable; the striped bars indicate variation attributable to the joint effects of two or more variables.](image-url)
Are suitable hollows limiting?

I. Logistic regression results as an index of nest site quality

If White-browed Treecreepers were selecting nest sites on the basis of hollow orientation and height of the entrance above the ground, the predicted probability of hollow use (Pr (x)) from the logistic regression provides an index of “nest site quality”. Thus, if suitable hollows were limiting, low quality nests should only be used in territories with a low density of hollows. There was not a significant correlation between Pr (x) of nest sites and the mean distance to the two nearest unused hollows ($r = -0.26, n = 24, P = 0.22$), which suggests that suitable hollows were not limiting. However, this does not account for the quality of the alternative hollows. By plotting the predicted probability of use of nest sites against that of the closest unused hollows, the quality of alternative hollows can be examined. It is predicted that White-browed Treecreepers should only use hollows of inferior quality (i.e. Pr (nest site) < Pr (unused hollow), as indicated by sites above the diagonal line in Fig. 7.7) when alternative hollows are rare or unsuitable. Indeed, the Pr (x) of most nest sites was greater than that of unused hollows (Fig. 7.7). The distance from nest sites to unused hollows of superior quality (sites above the diagonal line) showed a trend to be greater than the distance from nest sites to unused hollows of lower quality (sites below the diagonal line) ($t = 1.259, d.f. = 45, P_{1-tail} = 0.08$, after Log$_{10}$ transformation of distances).

In those cases in which White-browed Treecreepers used hollows of apparently inferior quality, the viability of the closest alternative hollows was often compromised by factors not considered in the index of nest site quality. For example, the entrances to the unused hollows associated with nests 24 and 16 were narrower than any hollow used for nesting. The entrance height of the closest alternative hollow to nest 4 was greater than the 3rd inter-quartile value for the entrance height of all nest sites, and the closest unused hollow to nest 2 was a fork hollow with a large vertical entrance. These unsuitable unused hollows account for the three shortest distances (13m, 14m and 24m) above the diagonal line in Figure 7.7, endorsing the trend indicated above, and suggesting lower quality nest sites were only used when the abundance of hollows was low.
**Figure 7.7.** The predicted probability of hollow use (Pr (x)) of nest sites relative to the predicted probability of hollow use of the closest (n = 24) and second closest (n = 23) unused hollow. For nest sites above the diagonal line, in which the Pr (x) was lower than that of an unused hollow, the distance (m) to the unused hollow is indicated in brackets.

### II. Interrogation of single variables via the decision process

Tree diameter, Height of entrance above the ground, Entrance orientation, Entrance width and Entrance height were all initially considered characteristics that could potentially limit the availability of suitable nest sites for the White-browed Treecreeper, based on other studies of the limiting factors for hollow-nesting birds (Saunders *et al.* 1982, Nilsson 1984, Sedgwick & Knopf 1990, Newton 1994, Mawson & Long 1994). Thus, each was examined as per the decision process outlined in Figure 7.1. The results are summarized in Table 7.7.

Nest sites located in smaller trees were not further from unused hollows than nests in larger trees. Moreover, alternative hollows to the ‘low quality’ smaller trees tended to be in larger trees than the nest sites. This suggests that the abundance of large hollow-bearing trees was not limiting the availability of suitable nest sites.
Nests that were closer to the ground (low quality) were not further from unused hollows than nests located higher above the ground (high quality). However, alternative hollows to low nest sites were not significantly higher, suggesting a better nest site may not have been available. There was a significant negative correlation between the height difference and the distance between low quality nest sites and the closest alternative hollow ($r = -0.76$, $n = 12$, $P = 0.004$). This suggests that when lower hollows were occupied, higher hollows in the territory were rare. The alternative higher hollows were usable, although the two closest of these (at nest 2 and nest 13) had large, circular vertical entrances that tend to be avoided. The longest distances from a low quality nest to a viable, higher, unused hollow were associated with nests 27 and 33 (see Fig. 7.7).

Nest sites opening to the north or vertically (low quality) were further from unused hollows than south-facing (high quality) nest sites. The entrance orientation of the unused hollows closest to low quality nest sites was randomly distributed. Only three of these alternative hollows opened to the south (135° - 225°). In two of these, the entrance was too small for treecreepers to use, and the third, which was viable, was associated with nest 33. Six other alternative hollows opened in a generally southerly direction (90° - 135° or 225° - 270°). Of these, one was too small, two had openings above the 3rd inter-quartile for entrance height (i.e. long splits) and the other three appeared viable alternatives (two of which were associated with nest 27). Thus, in most cases, unused south-facing hollows located in territories with north-facing nest sites were unsuitable for occupation due to other factors. It appears that hollows opening to the north or vertically were only used for nesting when south-facing hollows were rare or were not suitable for other reasons.

The ideal entrance dimensions of a potential nesting hollow were assumed to be the minimum size that a White-browed Treecreeper could enter; that is, hollows with smaller openings were considered to be higher quality. However, based on the minima for entrance width and height in occupied hollows, a minimum size is reached below which hollows become either too narrow (<2.5 cm) or too short (<5 cm) to be used.

Unused hollows were more abundant in the vicinity of nesting hollows with narrow entrances (high quality) than nests with wider entrances (low quality) and alternative hollows to low quality nests did not have significantly narrower entrances, which
suggests entrance width may be a limiting factor on nest site availability. However, there was not a significant correlation between the difference in entrance width and distance between low quality nest sites and the closest unused hollow \( (r = 0.46, n = 10, P = 0.18) \). Eight viable unused hollows with narrower entrances than occupied low quality nest sites were identified. Of these, one was north-facing in a territory with a south-facing nest and another was a long narrow slit, both of which were usable but probably less suitable than the occupied nest sites. Therefore, six viable alternatives in four territories remain. Two of these were associated with nest 23, which ultimately lost its eggs to a predator, suggesting the smaller unused hollows may have provided a safer nest site. A further two viable alternatives were associated with nest 27 and one each with nest 12 and nest 22. Thus, only a minority of low quality nest sites had viable alternative hollows with respect to entrance width, and all of those were considerable distances from the occupied nest site (>55 m), indicating a scarcity of hollows in these territories.

There was not a significant difference in the distance to unused hollows from high and low quality nest sites, when quality was differentiated on the basis of entrance height. Unused hollows in territories with low quality nest sites did not have significantly shorter openings than their associated occupied nest site, suggesting better quality hollows may not have been available. However, there was not a significant correlation between the difference in entrance height and distance between low quality nest sites and the closest unused hollow \( (r = 0.47, n = 11, P = 0.14) \). Ten viable unused hollows with shorter entrances than the occupied hollows were identified from the 11 territories with low quality nest sites. Of these, three were vertical opening fork or spout hollows that were usable but probably less suitable than the occupied nest sites. Therefore, seven viable alternatives in five territories remain, four of which were less than 40 m from the occupied hollow. Thus, alternative hollows of higher quality (in terms of entrance height) were in close proximity to several of the low quality nests, indicating that entrance height was probably not limiting nest site selection.
Table 7.7. Assessment of selected characteristics of hollows as factors limiting the availability of suitable nest sites (following the decision process outlined in Fig. 7.1).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Definition of Quality</th>
<th>Are low quality nests further from unused hollows? ¹</th>
<th>Are alternative hollows to low quality nests of superior quality? ², ³</th>
<th>Is the variable limiting?</th>
</tr>
</thead>
</table>
| Tree diameter      | High > median (30.75 cm) Low < median (30.75 cm) | NO  
  \( t_{22} = -0.20, P_{1-tail} = 0.42 \) | YES  
  Closest: \( t_{11} = -1.727, P_{1-tail} = 0.056 \)  
  2nd Closest: \( t_{10} = -2.49, P_{1-tail} = 0.016 \) | NO          |
| Height above ground| High > median (2.85m) Low < median (2.85m) | NO  
  \( t_{22} = 0.28, P_{1-tail} = 0.39 \) | NO  
  Closest: \( t_{11} = -0.23, P_{1-tail} = 0.41 \)  
  2nd Closest: \( t_{10} = -0.05, P_{1-tail} = 0.48 \) | POSSIBLY    |
| Entrance orientation| High: 90° - 270°  
  Low: 271° - 89° & vertical | YES  
  \( t_{22} = -2.0, P_{1-tail} = 0.029 \) | NO  
  5 categories: \( \chi^2 = 2, d.f. = 4, P = 0.74 \)  
  3 categories: \( \chi^2 = 0.62, d.f. = 2, P = 0.74 \) | PROBABLY    |
| Entrance width     | High ≤ median (3.0 cm) Low > median (3.0 cm) | YES  
  \( t_{22} = -2.17, P_{1-tail} = 0.021 \) | NO  
  Closest: \( t_{9} = 1.36, P_{1-tail} = 0.10 \)  
  2nd Closest: \( t_{8} = 0.97, P_{1-tail} = 0.18 \) | PROBABLY    |
| Entrance height    | High ≤ median (9.0 cm) Low > median (9.0 cm) | NO  
  \( t_{22} = 0.20, P_{1-tail} = 0.58 \) | NO  
  Closest: \( t_{10} = 0.96, P_{1-tail} = 0.18 \)  
  2nd Closest: \( t_{8} = 0.23, P_{1-tail} = 0.41 \) | NO          |

¹ The mean distance \([\log_{10}(x+1)] \) where necessary) to the two closest unused hollows per nest was compared between high and low quality nests (t-test).

² Paired t-tests were used to compare characteristics of nest sites with the closest and 2nd closest unused hollow, respectively. There were different sample sizes for the closest and 2nd closest comparisons (only one unused hollow associated with nest 33, which was a low quality nest for all variables).

³ The entrance orientation of all unused hollows associated with low quality nest sites was placed in one of five categories (N, E, S, W, vertical). Frequencies within each category were then compared to the \( \chi^2 \) distribution to determine whether unused hollows were equally distributed across the five categories. The comparison was then repeated with only three categories (N, S and vertical).
III. Influence of nest site characteristics on reproductive success

The effect of nest site quality on reproductive success was examined for those hollow characteristics that were determined to be potentially limiting the availability of suitable nest sites (i.e. Height of entrance above ground, Entrance orientation and Entrance width; see Table 7.7). Nest sites were categorized as ‘successful’ hollows (at least one fledgling) and ‘unsuccessful’ hollows (complete failure) (Table 7.5). Each nest was only counted once, irrespective of the number of times it was used. Seven nests had both successful and unsuccessful attempts: nest 19 was classified as successful because the failed attempt was due to abandonment rather than predation, nests 3, 4, 6, 16 and 25 were classified as successful because 50% or more of attempts fledged young. Nest 17 was classified as unsuccessful because two of three attempts failed. Nest 33 was categorized as unsuccessful.

Successful nests were not significantly more likely to be facing south (or in any other orientation) than unsuccessful nests ($\chi^2 = 5.48, d.f. = 4, P = 0.24$; Table 7.8). However, the success rate of south-facing nests was very high (88%), indicating that occupation of south-facing hollows results in high reproductive success. Successful hollows did not have significantly narrower entrances ($t = -0.47, d.f. = 22, P_{1\text{-tail}} = 0.32$) and were not significantly higher above the ground ($t = 0.66, d.f. = 22, P_{1\text{-tail}} = 0.26$) than unsuccessful hollows (Table 7.8). However, the mean values were indicative of the trends expected if higher reproductive success was attributable to higher hollows with narrower openings. Excluding nests with ambiguous success rates (success in 50% of attempts) did not alter the significance of any comparisons.

Table 7.8. Potentially limiting nest site characteristics of successful and unsuccessful nests.

<table>
<thead>
<tr>
<th>Character</th>
<th>Successful (n = 17)</th>
<th>Unsuccessful (n = 7)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Entrance orientation (count)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>North</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>East</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>South</td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td>West</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Vertical</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Entrance width (cm) (mean ± s.d.)</td>
<td>4.3 ± 2.3</td>
<td>5.2 ± 3.8</td>
</tr>
<tr>
<td>Height above ground (m) (mean ± s.d.)</td>
<td>2.9 ± 1.0</td>
<td>2.6 ± 0.8</td>
</tr>
</tbody>
</table>
7.4 Discussion

Characteristics and selection of nest sites

Birds that nest in hollows are generally acknowledged to achieve greater reproductive success than open-nesting species under the same breeding conditions, due to increased protection from predators afforded by the hollow (Nice 1957, Woinarski 1989). However, Nilsson (1986) suggests that reproductive success in hollow-nesting species may be tempered by increased interference competition and nestling losses from hyperthermia and nest parasites. Thus, the counter-balancing selection pressures of predation risk, competition and environmental conditions shape the nest site preferences of hollow-nesting species (Nilsson 1986, Newton 1994). Nest site selection by the White-browed Treecreeper can be interpreted in the context of these selective agents.

White-browed Treecreeper nests were located in trees larger than the average size in the woodland. However, this reflects the positive relationship between tree size and the presence and abundance of hollows (Lindenmayer et al. 1993, Bennett et al. 1994, Gibbons 1999), rather than that individuals were selecting the larger hollow-bearing trees for nest sites. White-browed Treecreepers selected hollows that were, on average, higher above the ground and more likely to be facing south than unused hollows. Further, the hierarchical partitioning suggests the independent effect of hollow orientation in explaining nest site selection was twice that of height above the ground. This is an unusual result in that studies of obligate hollow-nesting fauna in Australia have generally not found evidence of hollow selection based to any extent on hollow orientation (Saunders 1979, Saunders et al. 1982, Inions et al. 1989, Nelson & Morris 1994, Garnett et al. 1999, Luck 2000, but see Lumsden et al. in press).

The preference for hollows that open in a southerly direction may be an important thermoregulatory strategy (McComb & Noble 1981b). Temperatures in this region of Victoria exceed 35° C on an average of 2.8 days in November and 6.3 days in December [data refers to Mildura (34’ 23’ S, 142° 08’ E) between 1946 - 1996 (Commonwealth Bureau of Meteorology 2000)]. This is probably sufficient to cause heat stress in those broods that are still in the nest at this time. Selection of hollows with an entrance facing in a generally southerly direction reduces exposure to solar
radiation and hot northerly winds, yet allows ventilation by the cooler southerly breezes. Thus, nestling losses from hyperthermia or sub-lethal effects of heat stress (e.g. reduced growth) may be prevented or reduced by nesting in hollows with a southerly orientation. Furthermore, most summer storms in north-west Victoria approach from the north-west. Therefore, hollows with entrances facing south may be less prone to inundation during severe rain. In contrast, in North America, Reller (1972) suggested that two species of woodpecker excavate cavities in a south-westerly direction to increase ventilation and warming during cool weather. Similarly, Lumsden et al. (*in press*) suggested bats in northern Victoria select diurnal roosts facing north to maximize exposure to solar radiation, which may provide energetic savings.

The preference shown by the White-browed Treecreeper in this study for nesting in hollows higher above the ground is contrary to the popular belief that this species nests close to the ground (e.g. Pizzey 1999, Morcombe 2000). In the absence of quantitative comparative data on hollow selection, this view has probably arisen due to the physiognomy of their usual habitat (i.e. low-stature woodland or Mulga scrub) rather than a real preference for low hollows. The availability of higher hollows may have been greater in this study than elsewhere in their range, as indicated by significantly higher nest sites than those reported to the Nest Record Scheme (mean of 2.3 m, \(n = 20; t_{50} = 2.05, P = 0.046\)).

The selection of higher hollows probably reduces predation risk from terrestrial predators, as has been postulated for the Brown Treecreeper (Noske 1991) and demonstrated for hole-nesting species in the northern hemisphere (Nilsson 1984). The predominant predators of White-browed Treecreeper nests are likely to be semi-arboreal reptiles, such as goannas, bearded dragons and snakes (A. Bennett *pers. comm.*, A. Hawtin *pers. comm.; pers. obs.*). This may reduce the advantage gained from nesting higher above the ground, although nest detection and access may still be more difficult for higher hollows. Alternatively, it may be that higher hollows have smaller entrances, which prevents entry by larger predators. Gibbons (1999) found that the entry size of hollows in six species of *Eucalyptus* was indicative of the diameter of the branches shed during hollow formation. Thus, as branch diameter generally decreases with height, entrance dimensions should co-vary accordingly. Although there was no correlation between height above the ground and hollow
entrance dimensions in the sample of hollows measured in this study, use of higher
hollows may reflect historic conditions and past selection pressures.

Seventy per cent of White-browed Treecreeper nests at Yarrara were located in
hollows formed through branch fall scars. A similar percentage of all nest sites were
located in the main trunk, and two-thirds of all nests were in healthy trees (0% - 30%
dead wood). Whilst this portrays a typical profile for nest hollows, there was not a
significant departure from a random selection of available hollows, with respect to
the species, size and condition of the nest tree, the type of hollow or its position in
the tree, and the dimensions of the hollow entrance. Entrance width has regularly
been shown to influence hollow suitability or to differentiate hollow use between
species (e.g. Pinkowski 1976, McComb & Noble 1981a, Saunders et al. 1982, Pell
& Tidemann 1987, Gibbons 1999, Luck 2000). Thus, it was surprising that hollow
entrance dimensions did not appear to influence nest site selection, although
openings were generally narrow and elongated. This could be interpreted in three
ways: (a) there was a super-abundance of hollows with the preferred entrance
dimensions resulting in little variation in the parameters measured, (b) there was a
paucity of hollows with the preferred entrance dimensions forcing birds to use sub-
optimal hollows, or (c) birds were not selecting hollows on the basis of entrance
dimensions. Given the extent of variation solely within used nest sites (Table 3), the
first option can be discounted. The veracity of the second and third options is
discussed later, in the context of limiting factors.

Depth of the hollow cavity was not assessed for unused hollows, as it was not
possible to measure the internal dimensions of many hollows. Therefore, hollow
depth was not included in the assessment of nest site selectivity. However, depth may
be a critical determinant of hollow use, as has been established for several species of
arboreal mammal (Inions et al. 1989, Gibbons 1999) and cockatoo (Saunders et al.
1982). Nests in shallow hollows would be easy prey for reptiles or Butcherbirds
Cracticus spp., and the risk of nestlings accidentally falling out of the hollow
presumably decreases with hollow depth. Thus, it is probable that White-browed
Treecreepers avoid extremely shallow hollows, as indicated by the mean depth of 25
cm for those nests (n = 29) that were measured. It is salient that no eggs were laid in
nest 33, which was only 3 cm deep, possibly because the risk of failure was greater
than the costs of breeding. Once a certain depth is reached, suitability is probably not
greatly influenced by depth, although very deep hollows may also be rejected due to
the energy requirements of repeatedly climbing in and out of the hollow to tend to
the brood. Rufous Treecreepers sometimes add bark and twigs to the floor of hollows
thereby elevating the nest site and effectively decreasing the depth of the hollow
(Luck 2000). Although I found no evidence of this behaviour, White-browed
Treecreepers may similarly manipulate the internal dimensions of hollows to better
suit their needs.

The high error rate and the considerable amount of variation that remained
unexplained by the logistic regression model suggests that White-browed
Treecreepers were flexible in their choice of nest site and were influenced by the
interaction of a number of measured and unmeasured (e.g. internal dimensions)
factors. The short duration of the study and the possibility that shallow depressions
or ‘false hollows’ were sometimes counted as unused hollows may have introduced
further observer error to the model. However, the use of splits, spouts, forks, dead
trees with broken trunks and even cut stumps, as has been reported for the Brown
Tree creeper (Traill 1993), indicates the willingness of White-browed Treecreepers to
use a variety of hollow types. The dimensions of these atypical nest sites, which were
frequently in dead trees, differed markedly from the usual hollows in trunks and were
the source of much of the variability in nest site characteristics, and hence the
relatively poor performance of the nest site model. However, the variety of hollows
used emphasizes the importance of dead trees in providing supplementary or
alternative nest sites in territories where typical nesting hollows may not be readily
available.

**Inter-specific competition for hollows**

There was potential for overlap in hollow use with other hollow-dependent avifauna,
with the consequence that competition for nest sites may have constrained some
White-browed Treecreepers to sub-optimal hollows. Several sympatric species of
parrot (e.g. Budgerigar *Melopsittacus undulatus* and Blue Bonnet *Psephotus
haematogaster*) frequently nest in *Casuarina, Allocasuarina* or *Callitris* woodland
and use hollows with entrance diameters between 3 cm and 10 cm (Higgins 1999).
Such competitors are likely to dominate the smaller White-browed Treecreeper.
Budgerigars are known to use Brown Treecreeper hollows and will usurp hollows
occupied by Tree Martins *Hirundo nigricans* or Striated Pardalotes *Pardalotus striatus* (Higgins 1999), suggesting they would be capable of displacing White-browed Treecreepers from their hollows. Furthermore, a Red-rumped Parrot *Psophthus haematonotus* was detected nesting in a hollow subsequently used by White-browed Treecreepers, providing direct evidence for the potential for interference competition. Similarly, an Australian Owlet-nightjar *Aegotheles cristatus* roosted in a hollow previously used by White-browed Treecreepers.

In northeastern NSW, Brown Treecreepers used a hollow occupied in the previous season by White-throated Treecreepers (Noske 1991), which are similar in size to White-browed Treecreepers. This suggests Brown Treecreepers and White-browed Treecreepers would be direct competitors for hollows where they co-occur, which tends to be at the margins of the larger woodland blocks and in smaller remnants; Brown Treecreepers were not detected nesting in the study plot in the interior of Yarrara FFR. The larger and more social Brown Treecreeper probably dominates the White-browed Treecreeper in aggressive interactions (e.g. Noske 1979) and would be the likely victor in disputes over hollow ownership.

The exotic Common Starling *Sturnus vulgaris* is now present throughout much of north-west Victoria, particularly near towns and in open farmland (*personal observation*). This aggressive and dominant competitor uses hollows with entrance diameters as small as 3.5 cm (van Balen *et al.* 1982 in Newton 1994), and has the potential to reduce breeding success of native species by excluding them from nesting hollows (Pell & Tidemann 1997). Chestnut-rumped Thornbill *Acanthiza uropygialis* and Southern Whiteface *Aphelocephala leucopsis* may compete with the White-browed Treecreeper for smaller hollows, although the treecreeper would be expected to dominate interactions.

**Development, occurrence and abundance of hollows**

A common theme among studies investigating the distribution and availability of hollows is the patchy distribution of hollow-bearing trees at both the landscape and site scale. For a particular tree species, landscape factors such as management history, stand age, slope, topographic position, edaphic and climatic conditions influence the abundance of hollows (Saunders *et al.* 1982, Lindenmayer *et al.* 1991a, 1991b, 2000; Newton 1994; van Balen *et al.* 1982).
Within a stand, hollows are more likely to occur in older, and hence, larger trees (Lindenmayer et al. 1991a, 1993, Bennett et al. 1994, Gibbons 1999, Soderquist & Lee 1994, Soderquist 1999). This is because older trees have had longer exposure to the agents of hollow development, such as fungal infection and insect attack, that cause decay in the heartwood (Saunders 1979, Mackowski 1984, Gibbons 1999). Older trees are also more prone to shed branches, either as part of the process of senescence or from repeated exposure to fire, lightening or strong winds, which provides access to internal cavities (Inions et al. 1989, Lindenmayer et al. 1993, Gibbons 1999). The importance of dead trees in the provision of hollows is also widely recognized (Lindenmayer et al. 1991a, Bennett et al. 1994).

Studies of hollow ontogeny and occurrence in Australia have focused on eucalypts, particularly in montane forests (e.g. Mackowski 1984, Lindenmayer et al. 1993, Soderquist & Lee 1994, Gibbons 1999). However, the processes and rate of hollow formation may differ greatly between species due to variation in susceptibility to fungal and insect invasion, growth form, growth rate, ability to occlude wounds or preference for topographical position with coincident variation in fire intensity or wind sheer (Lindenmayer et al. 1993, Bennett et al. 1994, Gibbons 1999). Species of Allocasuarina, Casuarina and Callitris are slow growing with very hard timber that is resistant to decay and insect invasion. Therefore, the abundance of hollow-bearing trees in Belah, Buloke and Slender Cypress-pine woodland is likely to be relatively low.

Growth rate may influence the abundance of hollows in trees of a given diameter (Lindenmayer et al. 1993). Belah stems grow at approximately 10 cm DBH every 50 to 80 years, depending on environmental conditions (Westbrooke 1998). This is much slower than montane Eucalyptus species (Ashton 1976, Gibbons 1999) and slower than most growth rate estimates for eucalypts in drier and lower areas as well (Inions et al. 1989, Mawson & Long 1994, Stoneman et al. 1997). Thus, the average size of Belah stems of hollow-bearing age will generally be smaller than for eucalypts. This implies that, compared to eucalypt woodlands, Belah woodlands may contain a relatively large proportion of small hollows (although absolute abundance may be lower) as the ratio of large to small hollows is related to stem age and size (Bennett et al. 1994).
The availability of hollows for occupation by fauna will be influenced by the rate at which hollows develop and the age at which trees first form hollows. Based on the age estimates of Westbrooke (1998), the mean age of all live hollow-bearing Belah stems measured at Yarrara ($n = 56$, mean DBH = 37 cm) was a minimum of 150-200 years. The smallest live Belah stem that contained a White-browed Treecreeper nest at Yarrara (20 cm DBH) was probably more than 100 years old, although an unused hollow was found in a Belah of only 13 cm DBH, estimated to be 75-80 years old (estimates after Westbrooke 1998). Importantly, hollows only appear to develop in *Callitris* stems once they are dead (Bennett *et al.* 1994; personal observation). Thus, the interval between seedling regeneration and the development of usable hollows (for White-browed Treecreepers) in Belah and Slender Cypress-pine woodlands is at least 100 years.

When Yarrara FFR was managed as a forestry reserve, Slender Cypress-pine was selectively logged because it was preferred for building and fencing. Following drought in the 1940s, it is purported that all remaining Cypress died and many were subsequently removed as dead trees (H. Schilling, *personal communication*). Limited regeneration of Cypress is now occurring in Yarrara FFR. The specific environmental and climatic conditions required for Belah seedling regeneration are not clear but it appears that successive years of very high rainfall are required (Westbrooke 1998; K. Callister, *personal communication*). Consequently, Belah regeneration in Victoria has been largely confined to two events in the last 130 years (K. Callister, *personal communication*). New Belah stems will form from suckering but this is insufficient to perpetuate extensive areas of Belah woodland (Chesterfield & Parsons 1985). Consequently, Yarrara FFR is now dominated by mature Belah, although younger Belah cohorts and pockets of small stems arising from suckering are also present. Slender Cypress-pine now occurs only as saplings along the abandoned irrigation channels and as stumps and standing dead trees scattered throughout the reserve.

Thus, hollows are widely recognized as a critical resource in many habitat types. However, the potential for hollows to be limiting may be particularly acute in Belah and Pine-Buloke woodlands due to their resistance to decay, slow growth rates, age of initial hollow development, limited recruitment of new trees and management history.
The potential for hollows to be limiting

The prevalence of hollow-dependent species amongst Australian birds (Saunders et al. 1982) and mammals (Smith & Hume 1984, Tidemann & Flavel 1987, Gibbons 1999) has stimulated much research on the potential of hollows to limit the growth of faunal populations in Australia. These studies have found that the retention and perpetuation of hollow-bearing trees is crucial for wildlife conservation in forests managed intensively for wood products (e.g. Smith & Lindenmayer 1988, Lindenmayer et al. 1990a, 1990b, 1991b, Nelson & Morris 1994, Kavanagh et al. 1995, Lindenmayer 1995, Traill & Lill 1997, Loyn et al. 2001) and in agricultural landscapes (e.g. Abensperg-Traun & Smith 1993, Bennett et al. 1994, Saunders & Ingram 1998, van der Ree 2000). Thus, the availability of hollows is a primary factor that determines the viability and expansion of populations of hollow-dependent wildlife.

In his review of hollows as a limiting factor on populations of hole-nesting birds, Newton (1994) distinguishes between circumstantial and experimental evidence. Circumstantial evidence refers to studies in which the spatial or temporal variation in the density of hollow-nesting birds parallels variation in the availability of nest hollows, whereas experimental evidence requires manipulation of nest site availability to regulate population density. In this study, I used a quasi-circumstantial approach by relating putative nest site quality to spatial variation in the density of tree hollows at the territory scale, to evaluate the potential of hollow availability to limit population growth of White-browed Treecreepers. That is, were breeders confined to lower quality nest sites or constrained from breeding due to a shortage of hollows, and if so, did this impinge on reproductive success?

Most of the hollows at Yarrara were located in either live Belah or dead standing Cypress trees. Although the percentage of hollows used by White-browed Treecreepers was not determined, clearly less than 50% of all hollows were used during the period of investigation, hinting that hollows may not be limiting. However, actual availability of hollows may be substantially less than apparent availability due to factors such as selectivity of certain hollow characteristics, spacing of hollows, antagonistic and competitive behaviour of conspecifics and heterospecifics, parasitic infestation, dampness or decay of hollows (Saunders et al. 1982, Lindenmayer et al. 1990c, Bennett et al. 1994, Newton 1994). Therefore, the
potential for hollows to be limiting may be far greater than initially apparent from the absolute density and proportional use of all hollows.

Three lines of evidence suggest that hollows were a potentially limiting resource for White-browed Treecreepers in some territories at Yarrara FFR. First, the sensitivity of the logistic regression model of hollow use was very low; that is, it regularly predicted hollows would not be used when, in fact, they were occupied. This suggests that in addition to ‘good quality’ hollows (based on entrance orientation and height of the hollow above the ground), many hollows of lower quality were also used. The use of ‘sub-optimal’ nest sites may indicate that suitable hollows were unavailable in some territories.

Second, the interaction between nest site quality, quality of alternative hollows and the relative abundance of hollows (Fig. 7.1) showed that breeding pairs that used low quality nest sites were generally in territories with a scarcity of viable alternative hollows (Table 7.7). This broader perspective of nest site quality considered five characteristics and indicated nest site selection was influenced by three pivotal characteristics of hollows. It follows that if the available hollows lack these key characteristics, the breeding potential of individuals may be limited.

The ultimate limiting feature of nest site selection was the occurrence of hollows with openings wider than 2.5 cm and appropriate internal dimensions. In decreasing order of importance (from Table 7.7), White-browed Treecreepers chose hollows with a southerly aspect, with the narrowest entrance and preferred higher hollows to those closer to the ground. These general rules were only violated when hollows were scarce in a territory, suggesting that high quality nest sites were limited. Nests 27 and 33, both of which rated poorly in many nest site features, provide the strongest evidence for this conclusion. Only one other hollow could be located within the territory of nest 33 and the closest unused hollow to nest 27 was over 100 m away, suggesting hollows were rare in both these territories. The validity of the features used to rank nest site quality was supported by the fact that the female, despite being sexually mature, did not lay in nest 33, and that the pair from nest 27 re-nested (unsuccessfully) in an abandoned nest within a neighbouring territory, which appeared to be an extraordinary risk if hollows were not in short supply.
The third piece of evidence that nest sites were limiting were the patterns of hollow re-use. Sixty per cent of breeding units used the same hollow in successive seasons, although this may reflect selectivity more than limitation. Moreover, the same hollow was used in the same season by different pairs of White-browed Treecreepers on one occasion (nest 8) and by White-browed Treecreepers and different species in two other instances (nests 4 and 18). Successive use of hollows is often interpreted as an argument for nest site limitation (Newton 1994). Additionally, a Galah Cacatua rosiecapilla nest was located in the same tree as one White-browed Treecreeper nest. Galahs aggressively defend the area immediately around their nest hollow from all species, particularly during the early stages of nesting (Saunders et al. 1982). This may have denied the White-browed Treecreepers access to the tree even though they were not direct competitors for the same hollow. Consequently, the White-browed Treecreepers may have been relegated to an inferior nest site (i.e. nest 8, in which both attempts failed) until the agonistic behaviour of the Galahs ceased.

Conversely, re-use patterns could be used to argue against nest site limitation in some territories (e.g. Tidemann et al. 1999). In several territories, more than one hollow was used within the same season, typically but not universally, after a failed nest attempt. The alacrity with which new nest sites were located suggests hollows were not depleted in these territories. Similarly, that breeding units should seek out new hollows between seasons, despite success in the original hollow (e.g. T1, T12) implies that hollows were not severely limited in these territories.

The evidence presented above indicates there was variability in nest site quality and that some White-browed Treecreepers occupied apparently inferior hollows because they were constrained in their choice of nest site by a shortage of preferred hollows. Whether this translates to a limiting resource depends firstly on whether there would have been more breeding units had there been a greater abundance of high quality nest hollows. There was potential for an increase in the breeding population via recruitment of surplus individuals in the resident population (e.g. floating non-breeding females and helper males) or fledglings that currently disperse that was not taken up. In the absence of experimental manipulations, it is not possible to confirm whether the current population density was maintained by nest site availability or other limits to population growth, such as food availability or social constraints (Newton 1994). However, there was an asymmetric distribution of nest sites, in that
most territories contained several high quality nest sites (both used and unused) whereas hollows of any type, and especially of preferred specifications, were scarce in other territories. As Newton (1994) points out, it may not be a shortage of sites per se that limits density, but a shortage of sites outside the territories of existing breeding units.

Secondly, was reproductive success compromised in those breeding units confined to low quality nest sites? There was no difference in hollow orientation, height of the hollow above ground or entrance width between successful and unsuccessful nests, and so reproductive success did not appear to be limited by the availability of high quality nest sites. However, the demarcation of high and low quality nest sites in this comparison was based on median characteristics and may not realistically represent the relative risks of nest failure. If the majority of nests were actually in high quality nest sites, *individual* reproductive success may not be correlated with nest site features, even though those same features may limit the overall reproductive capacity of the *population* (Pribil 1998, Bisson & Stutchbury 2000). Although individual reproductive success was not reduced in those breeding units that used low quality nest sites, there may have been undetected energetic costs involved in defending exposed or easily accessible nests. Furthermore, climatic conditions during this study may not have exacerbated differences in reproductive success between high and low quality nest sites, mitigating the limiting effects of nest site availability on population growth.

**Conclusions**

I propose that the density of the White-browed Treecreeper population in the mature Belah woodland at Yarrara FFR is potentially limited by the availability of suitable hollows for nesting. There appeared to be a shortage of south-facing hollows with entrances marginally wider than 2.5 cm and more than 2.5 m above the ground, across a significant minority of the study area. The scarcity of hollows in several territories, and the use of low quality nest sites, suggests additional breeding units may have been accommodated had high quality nest sites been more abundant. However, there was considerable spatial variation in hollow abundance that, in concert with the territoriality of White-browed Treecreepers, restricted the actual availability of hollows to less than the absolute abundance of hollows. Interspecific
agonistic behaviour accentuated this shortfall. However, the magnitude of this constraint on population growth is predicted to be small, with other factors, such as foraging resources, predation, social cohesion, breeding productivity and life-history attributes, also limiting the rate of population growth. There were several suitable hollows in most territories. Clearly, in these territories, factors other than nest site availability are limiting population density.

Management of Belah / Slender Cypress-pine / Buloke woodlands for White-browed Treecreeper conservation must encourage a mixed-age structure that provides a range of hollow types and sizes. This is a challenging prospect in light of the limited regeneration and slow growth rate of these species and the time lag between germination and hollow formation. There is considerable potential for overlap in hollow use with other species, which, in the absence of smaller hollows, may exclude White-browed Treecreepers from some areas. Competition with species of a similar size may be eased by presence of a variety of hollow types. For example, bats use similar-sized hollows to White-browed Treecreepers but some bats prefer spouts where available (Lumsden et al. in press), decreasing demand for branch fall hollows. White-browed Treecreepers may be able to use hollows in other tree species in habitat contiguous with Belah, in which hollows are more abundant (e.g. mallee, Black Box). However, White-browed Treecreepers are unlikely to occupy patches of pure mallee or Black Box (Chapter 2), and these habitats must be viewed more as supplementary than alternative sources of nest sites. Failure to ensure the recruitment of hollow-bearing trees into the mature woodland will result in a decline in hollow abundance as live trees die and standing dead trees collapse. This would see a dramatic rise in the potential for nest site availability to limit the population growth and density of White-browed Treecreepers. This prospect is particularly relevant in smaller remnants and those woodlands that are still grazed.
Chapter 8

8.1 Introduction

Many aspects of avian breeding biology are evolutionarily conservative (Ligon 1993, Cockburn 1996), so it is not surprising that several fundamental elements of breeding are similar amongst the four species of Australian treecreeper that have been closely studied. The Brown Treecreeper, Red-browed Treecreeper, White-throated Treecreeper and Rufous Treecreeper are all socially monogamous, have small clutches, long incubation and nestling periods, and bi-parental care, although incubation is the sole responsibility of the female (Noske 1982b, 1991, Luck 2000; V. Doerr and E. Doerr, personal communication). Furthermore, the Brown Treecreeper, Rufous Treecreeper and, to a lesser degree, the Red-browed Treecreeper have many behavioural traits in common, related to their cooperative breeding strategy (e.g. prolonged periods of juvenile dependency, helping behaviour and cross-territorial feeding).

However, the Black-tailed Treecreeper and, until now, the White-browed Treecreeper have not been subject to intensive observation. Consequently, there is a gaping hole in the scientific and popular ornithological literature where information on the White-browed Treecreeper’s breeding biology should exist. Recent reviews comparing life-history traits of cooperatively and non-cooperatively breeding species excluded the White-browed Treecreeper from their analyses due to the ambiguity surrounding their breeding strategy and lack of data for basic breeding parameters (Poiani & Elgar 1994, Poiani & Jermiin 1994, Cockburn 1996, Arnold & Owens 1998, Russell 2000). Popular field guides generally overlook the breeding biology of White-browed Treecreepers altogether (e.g. Simpson et al. 1993, Pizzey 1999) rather than include erroneous information.

I have already confirmed that White-browed Treecreepers are facultative cooperative breeders (Chapter 6); the overarching objective of this chapter is to present the first comprehensive study of White-browed Treecreeper breeding behaviour. To this end, specific study questions raised in this chapter include:

- When does the breeding season commence and for how long does it continue?
- How many eggs are laid in an average clutch?
- What is the duration of the incubation and nestling periods?
• What is the role of the female, the breeding male and any helpers during the incubation and nestling stages?

• What factors influence the level of brood care provided by members of a breeding unit?

• What happens after the fledglings leave the nest?

A major theme of this chapter is to compare the breeding behaviour of individuals in cooperative groups and pairs in order to explore mechanisms by which helpers may increase both their own fitness, and that of the breeders they assist; that is, what are the benefits of cooperative breeding? These comparisons form the bulk of this chapter. However, unassisted pairs provide an estimate of breeder-only care; that is, reproductive costs likely to be incurred in the absence of helpers. This permits an assessment of parental investment strategies adopted by individuals in cooperatively breeding groups (Clutton-Brock 1991, Hatchwell 1999), evaluated in terms of breeder-only reproductive costs. It is expected that individuals will respond to variation in reproductive costs during the nesting cycle, manifest as a shift in investment strategy, provided that the change in investment strategy does not jeopardise the fitness of the parents or the brood.

8.2 Methods

Duration of nesting stages

General field methods for establishing a colour-banded population at Yarrara FFR and finding nests were described in Chapters 6 and 7, respectively. All data were collected exclusively from the intensive study plot at Yarrara FFR (Fig. 6.1), except for clutch size data, which was supplemented with records from nests located elsewhere. Once located, nests were monitored daily when egg laying, hatching or fledging was imminent, but longer intervals between inspections elapsed during the incubation and nestling stages. Where possible, nest contents were observed directly to determine the stage of nesting. However, some nests could not be viewed directly, in which case their status was inferred from behavioural observations.
Definition of the incubation and nestling stages followed Rowley et al. (1991). The day on which the final egg of a clutch was laid was considered the first day of incubation. Incubation continued until the last egg hatched. Likewise, the day of hatching was considered the first day of the nestling stage. Note that for asynchronously hatching clutches there may be overlap between the incubating and nestling stages. Fledging date was determined from nest inspections on successive days and deemed to be the first day that a nest was empty. When the interval between nest inspections was more than one day, fledging date was estimated as the mid-point between inspections. Older nestlings were sometimes flushed from the nest hollow upon inspection. This was considered the fledging date, although it may slightly under-estimate the normal nestling period.

**Nesting behaviour**

Nesting behaviour was observed from September through to December in both 1998 and 1999. Nests were observed during the construction, incubation and nestling stages. Observation bouts (hereafter called nest watches) were usually 2 hours in duration, but a few were only 90 minutes. Observers sat in the open, 20-50 m from the nest and maintained a constant watch of the hollow entrance using 10 X 50 binoculars and/or a 20-60 X magnification zoom spotting scope. Birds did not appear to be agitated by, or aware of, the observer. Nest watches commenced 5 min after the observer arrived at a nest, in case the activity disturbed nesting behaviour. As birds often visited the nest during the 5-min delay, it was assumed any disturbance was negligible. Nest watches were conducted at any time during daylight hours, but were concentrated from soon after first light to noon and again in the late afternoon. Nest watches were abandoned if there was more than a light shower of rain or in extreme heat. However, some watches that commenced mid-morning concluded in very hot conditions.

As individuals could not be observed whilst in the hollow, behaviour was inferred from direct observations (Table 8.1). Nest construction was assumed when individuals were observed repeatedly carrying nest material into a hollow, without

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1 The majority of nest watches was conducted by JQR, but trained field assistants were responsible for a significant minority.
spending long periods in the hollow. The identity of individuals entering the hollow with such material and the time spent in the hollow were recorded.

When not confirmed from direct inspection, incubation was deemed to have commenced when the female entered the hollow without food or nest material and remained inside for extended periods. Observations during the incubation stage recorded the identity of individuals entering the hollow, whether they were carrying any food or nest material and the time spent in the hollow.

When all adults entered the hollow with food items, particularly the female, it was assumed that nestlings were present. The begging calls of young chicks could usually be heard to confirm nest status. Observations recorded during the nestling stage included the identity of individuals arriving at the hollow, contents of their bill (i.e. empty, nest material or food), time spent in the hollow, distribution of food items and removal of faecal sacs. Food items were identified as accurately as possible or simply classified as small (held in the tip of the bill), medium (about the size of the bill) or large (obviously larger than the bill). Any displays, nest defence, social interactions or unusual behaviours were noted.

During the nestling stage, male birds often gave their food item to the female at the hollow entrance. It was assumed that the female then fed the nestlings but it could not be verified that all food was transferred to the nestlings because the female was observed to occasionally eat it herself. Therefore, the more general term ‘provisioning rate’ is used to indicate food delivery to either the female or the nestlings directly. Provisioning rates were calculated as the number of provisioning visits per hour per nest for each attendant at a nest.

The timing of each nest watch (i.e. days since laying or nestling age) was determined either empirically or retrospectively from confirmed laying, hatching or fledging dates. The incubation stage was split into two phases: days 1 to 9, and days 10 to hatching. The nestling stage was considered in three phases: week 1, week 2 and week 3 to fledging. At each nest, watches were conducted in as many of these phases as possible, to quantify variation in behaviour within the incubation and nestling stages. Similarly, effort was made to observe each nest during each part of the day (early morning, midday, late afternoon) at least once in the incubating and nestling
stages. This reduced potential bias from observations collected during only one part of the day and enabled assessment of daily patterns of behaviour.

Table 8.1. Description of nesting behaviours recorded during nest watches.

<table>
<thead>
<tr>
<th>Stage of nesting</th>
<th>Behaviour</th>
<th>Description</th>
<th>Recorded</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Construction</strong></td>
<td>Nest building</td>
<td>Enter hollow carrying nesting material</td>
<td>Visits/hr</td>
</tr>
<tr>
<td><strong>Incubation</strong></td>
<td>Incubating</td>
<td>Remain in hollow for &gt;1 minute</td>
<td>% time in nest (attentiveness), # bouts/hr, Duration of bout</td>
</tr>
<tr>
<td></td>
<td>Provisioning</td>
<td>Male feeds female at hollow entrance or in hollow</td>
<td>Feeds/hr</td>
</tr>
<tr>
<td><strong>Nestling</strong></td>
<td>Brooding</td>
<td>Remain in hollow for &gt;1 minute</td>
<td>% time in nest, # bouts/hr, Duration of bout</td>
</tr>
<tr>
<td></td>
<td>Provisioning</td>
<td>Arrive at hollow with food and (i) enter hollow, (ii) transfer to female at entrance or (iii) feed nestlings at entrance. Depart without food.</td>
<td>Visits/hr, size of food item, identify food item</td>
</tr>
<tr>
<td><strong>Nest maintenance</strong></td>
<td>Enter hollow carrying nesting material</td>
<td>Visits/hr</td>
<td></td>
</tr>
<tr>
<td><strong>Cleaning nest</strong></td>
<td>Depart from hollow carrying faecal sac</td>
<td>Frequency/hr</td>
<td></td>
</tr>
<tr>
<td><strong>Throughout</strong></td>
<td>Sweeping</td>
<td>Drags material across bark in vicinity of hollow (see text)</td>
<td>Frequency/hr, Duration of bout</td>
</tr>
<tr>
<td></td>
<td>Inspection</td>
<td>Arrive at nest without food or nest material, peer inside, depart</td>
<td>Noted only</td>
</tr>
</tbody>
</table>

Genetic parentage was not confirmed in this study. Therefore, several assumptions about White-browed Treecreeper sociality were made when assigning social status to individuals within a breeding unit. First, monogamy was presupposed. Thus, if only one male or female attended a nest, they were assumed to be the genetic parents. Second, a male age-based dominance hierarchy was presumed (Higgins et al. 2001). Thus, male yearlings were sub-ordinate to older males, who were assumed to breed with the female. Finally, when the age of co-existing males could not be confirmed, the primary (breeding) male was deemed to be the individual that contributed most to the nesting effort, summed over nest construction and maintenance, care of the
incubating female and nestling provisioning. In light of the relative provisioning rates of known father-son pairs (see results), this third assumption may have led to the incorrect classification of the primary male in some instances.

Unbanded adult birds were assumed to be the same individual where repeatedly encountered at the same nest. As White-browed Treecreepers are sexually dichromatic, identification of individuals was assisted by noting their gender if the colour bands were partially obscured or not visible. However, provisioning visits by unidentified banded birds (only 1.67% of all visits) were re-allocated to identified attendants at a nest in proportion to the percentage of feeding visits by identified birds for that nest watch (sensu Clarke 1984). This results in an “adjusted” rate of provisioning for each attendant that is the sum of their known rate and their share of the unidentified visits.

**Data analysis**

All measures of behaviour (Table 8.1) were calculated for each individual during each nest watch. These values were used for determining variation in behaviour with time of day, day of incubation or nestling age. However, as the number of nest watches per breeding unit varied, a single value per breeding unit was required for comparisons between breeding strategies to avoid pseudoreplication. Accordingly, behavioural indices were calculated per individual per clutch (i.e. means of all nest watches per nest attempt) and per breeding unit (i.e. means of all nest watches across multiple nest attempts per breeding season). Analyses based on breeding unit means are more robust because data generated per clutch may not be truly independent. Data were not pooled between breeding seasons because group composition varied in many territories between seasons.

Means are given with their standard error unless otherwise designated, and were compared, after transformation where necessary, using *t*-tests, Analysis of Variance (ANOVA) or Analysis of Covariance (ANCOVA). Breeding strategy, season, brood number (i.e. first or second brood) and brood size (number of nestlings) were all considered fixed effects in ANOVA. Although season does not strictly fulfill all the criteria of a fixed effect (Bennington & Thayne 1994), differences between years were of specific interest and the sample of two years was thought insufficient to be
representative of a larger population of ‘all years’. Comparisons between individuals or breeding units were treated as random effects. Non-parametric methods were used where transformations did not normalize the data or stabilize the variance.

8.3 Results

Courtship

Courtship and pre-mating behaviour began in early August in both years. Courtship displays were usually staged on horizontal limbs or fallen logs. Males approached females with their wings half-open and bent and their necks extended so that their heads were tilted upwards at 45°. The male then danced up to and around the female, who was stationary, with his wings fluttering gently and his whole body twitching as he hopped up and down in rapid succession. On occasions, the female responded by also twitching and quivering but remained relatively stationary. During these displays and at other times leading up to breeding, the male frequently presented the female with food items, which, curiously, were often the bright red or orange berries from saltbush shrubs, although arthropods were also offered. Females spent considerable time inspecting prospective hollows during the pre-mating phase. Two females were detected inspecting their future nest sites 37 days and 16 days before egg laying.

Breeding phenology

First clutches were laid within a 13 week period from late August to mid November over the course of the study, but the timing of breeding differed between seasons (Fig. 8.1). In 1998, first clutches were initiated at regular intervals with the majority (6 of 11) in October (mean: October 14). The average laying date of first clutches was one month earlier in 1999 (September 11), with 13 of 14 first clutches commenced by the end of September. Breeding was highly synchronized in 1999, with 71% of first clutches laid in the first two weeks of September.
The laying date of the first egg of the first clutch of the season was expressed as the number of days from August 25, which was one day before the earliest recorded laying date. This value was log\(_{10}\) transformed for analyses. Variation in laying date amongst breeding units across both seasons combined was not significant (\(F_{13, 24} = 0.635, P = 0.784\)). However, the effect of season on mean laying date was highly significant (\(t_{23} = 4.31, P < 0.001\)). A matched-pair comparison of laying date between years for those breeding units with data in both years emphasizes the earlier breeding in 1999 (Paired sample \(t\)-test: \(t = 5.51, P < 0.001, n = 11\)).

Replacement clutches (i.e. a second clutch laid following the failure of the first clutch) were observed in both years (Fig. 8.1). However, second broods (i.e. a second clutch laid after successfully fledging offspring) were only detected in 1999, but were attempted by 77% of breeding units in that season (Fig. 8.1). Second clutches (replacement or second broods) were laid from early October until late November, with a peak in second brood clutches in mid-November in 1999 (Fig. 8.1). However, later clutches were rarely successful and nesting was invariably finished by mid-January. Fledglings were nutritionally dependent on their parents (and/or helpers) to some degree for at least 5 weeks (see below: Post-fledging). Thus, within the population, the period devoted to breeding, inclusive of courtship and pre-mating ritual to nutritional independence of the fledglings, covered six months from early August until February.
Figure 8.1. Laying date of the first egg in White-browed Treecreeper nests at Yarrara FFR, 1998 - 1999. Date is expressed as weeks since August 25, the day before the earliest detected laying date. Replacement clutch = second clutch laid after failed first nest; Second brood = second clutch laid after successful first nest. $n = 40$ nests.
Nest construction

Both parents carried nesting material into the hollow during nest construction, as well as later in the nesting cycle when the material was presumably used to repair or add to the existing nest. Helpers also provided nesting material in 5 of the 9 breeding unit-years monitored. The duration of the construction period was not ascertained precisely. Eggs were laid between 3 - 9 days (median of 6) after nests were first detected in eight nests that were found prior to incubation. This underestimates the duration of the construction stage because it is likely that construction began before nests were detected. However, nests can be completed quickly under some circumstances. In 1998, one female laid a replacement clutch in a new hollow 2 - 4 days after her first clutch was preyed upon. It is possible that the second hollow had been used in previous seasons but the nest would have required re-building. The same female used the same sequence of nests in 1999, with a re-laying interval of 7 days.

Nest watches during the nest construction stage were infrequent but from limited data it was clear that construction was spasmodic and the roles of the male and female were variable. For example, during one 2-hour nest watch, the female spent 43% of the time in the hollow (presumably working on the nest) but retrieved only one batch of nesting material, whilst the male provided nesting material at a rate of 2.5 visits/hr. He also fed her three times during the nest watch. At another nest, the female returned with nesting material four times in the first half-hour but was not seen again in the next 1.5 hrs. Yet the male made no contribution during the 2 hours at this nest. No visits at all were detected during several nest watches that were assumed to be during construction. This may reflect recesses in intermittent bouts of activity on nest construction or a delay between the completion of the nest and the commencement of laying.

Copulation

Copulation was only observed twice, between the same pair early in the morning on consecutive days. The first occasion was 5 days before eggs were laid. Before copulation, the male led the female along a horizontal branch with his head lowered and his tail raised and fanned, his whole body gently quivering and rotating from side to side with each hop. The female followed in a similar manner. The male then
turned to face the female and they continued to quiver and hop vigorously with their heads down and nearly abutting. The male paused at the side of the female as they ‘danced’ side-by-side before moving behind the female and mounting her. Copulation was brief (1-2 seconds) and the pair departed immediately after the male dismounted.

**Egg laying**

Mean clutch size was $1.93 \pm 0.06$ eggs in 43 nests found at all locations during the study and checked at least twice. This assumes there was no partial predation of clutches before they were discovered, an occurrence that was not observed in nests that were monitored intensely. Clutches ranged from 1 to 3 eggs, with 5 x C1, 36 x C2 and 2 x C3 detected. The interval between laying successive eggs was 24 hours, such that clutches of two or more were laid over at least two days ($n = 6$).

**Incubation**

**Incubation period**

The mean duration of the incubation period for the seven clutches for which it could be accurately determined was 17 – 18 days, although both the median and mode were one day longer (Table 8.2). Extremes in the incubation period ranged from 15 – 16 days to 19 – 20 days, depending on the error in estimating dates. Hatching was usually synchronous with eggs in clutches of more than one hatching within 24 hours. However, asynchronous hatching was recorded with eggs hatching up to 48 hours apart at N17 in 1999.
Table 8.2. Duration of the incubation stage in seven breeding units of the White-browed Treecreeper at Yarrara FFR. All dates are 1999, except where indicated.

<table>
<thead>
<tr>
<th>Breeding unit</th>
<th>Date last egg laid</th>
<th>Hatching date</th>
<th>Incubation period (days)</th>
<th>Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>T11</td>
<td>September 16</td>
<td>October 4</td>
<td>18 – 19</td>
<td>24 hrs</td>
</tr>
<tr>
<td>T4</td>
<td>October 11</td>
<td>October 27</td>
<td>16 – 17</td>
<td></td>
</tr>
<tr>
<td>T30</td>
<td>October 28</td>
<td>November 15</td>
<td>17 – 19</td>
<td>48 hrs</td>
</tr>
<tr>
<td>T12 (2nd brood)</td>
<td>November 12</td>
<td>November 27</td>
<td>15 – 17</td>
<td>48 hrs</td>
</tr>
<tr>
<td>T17 (2nd brood)</td>
<td>November 13</td>
<td>Nov 29 - Dec 1°</td>
<td>18 – 19</td>
<td>12 hrs</td>
</tr>
<tr>
<td>T13 (2nd brood)</td>
<td>November 29</td>
<td>December 15</td>
<td>16 – 17</td>
<td>24 hrs</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>mean</td>
<td>17 – 18</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>median</td>
<td>18 – 19</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>mode</td>
<td>18 – 19</td>
</tr>
</tbody>
</table>

° Asynchronous hatching (see text): later date used for determining incubation period.

**Incubation behaviour**

After excluding two nest watches conducted during excessive heat and two in which it was doubtful incubation had begun, 64 nest watches totaling 130 hours of observation were included for analysis. Incubation behaviour was monitored in 8 breeding units in 1998 (9 nest attempts: $n = 23$ nest watches) and 13 breeding units in 1999 (20 nest attempts: $n = 41$ nest watches).

**Attentiveness**

Only the female incubated the clutch. Overall, mean female attentiveness per nest watch was 60.3 ± 1.4% ($n = 64$ nest watches). This changed little when multiple nest watches for the same female were pooled within each nesting attempt (59.8 ± 1.5%, $n = 29$ nest attempts) or within each breeding season (59.1 ± 1.8 %, $n = 21$ breeding unit-years). In simple correlation, attentiveness (arcsine transformed) decreased significantly in the late afternoon and evening ($r = -0.411$, $P = 0.001$, $n = 64$ nest watches) but was not correlated with the day of incubation ($r = 0.089$, $P = 0.483$, $n = 64$ nest watches). To investigate these relationships further, the incubation period was divided into three equal 6-day phases, and the effect of incubation phase (fixed effect) and time of day (co-variate) on attentiveness examined in an analysis of covariance (ANCOVA). There was no significant variation in attentiveness between
the three incubation phases, but attentiveness decreased significantly in the latter part of the day (Fig. 8.2). Importantly, there was no interaction between incubation phase and time of day (homogeneous slopes), indicating that the daily variation in attentiveness was consistent in all phases of the incubation period. Furthermore, the pattern of attentiveness throughout the day, as typified by the slight decrease in the afternoon, was virtually identical for females in pairs and groups (ANCOVA test for homogeneity of slopes: Strategy*Time of day – $F_{1, 60} = 0.0017, P = 0.967, n = 35$ (pairs) and 29 (groups) nest watches).

![Figure 8.2. Daily variation in incubation attentiveness of females. The mean percentage (± s.e.) of time that females spent incubating in each phase of the incubation period (day 1-6, day 7-12, day 13-18) is plotted against the start time of the nest watch ($n = 130$ hr of observation at 29 nests). Attentiveness did not vary significantly between incubation phases, but did vary significantly with the time of day (ANCOVA: Incubation phase, $F_{2, 60} = 0.41, P = 0.667$; Time of day, $F_{1, 60} = 11.59, P = 0.001$; Incubation phase*Time of day, $F_{2, 58} = 2.08, P = 0.134$).]
Prior to investigating the effects of breeding strategy on incubation behaviour, attentiveness was corrected for the effect of time of day. This was achieved by regressing attentiveness against the start time of nest watch and using the residuals as an adjusted measure of attentiveness (Att\textsubscript{adj}) that was independent of the time of day. The means of the residuals were then calculated for each female from multiple nest watches within each nesting attempt (per clutch) and within each breeding season (per unit). In two-way analysis of variance (ANOVA), attentiveness did not differ significantly between females in pairs and groups, nor between 1998 and 1999 (Table 8.3, Fig. 8.3). Furthermore, attentiveness did not differ between strategies when confined either to first broods (2-factor ANOVA: Strategy - \( F_{1, 17} = 0.41, P = 0.53 \); Season - \( F_{1, 17} = 0.24, P = 0.63 \); Strategy*Season - \( F_{1, 17} = 0.55, P = 0.47, n = 21 \)) or to second broods (Mann-Whitney test: \( z = -0.15, P = 0.88, n = 8 \)).

Table 8.3. Influence of breeding strategy and season on incubation attentiveness. Analysis of Variance was conducted for nest watches pooled within nest attempts (per clutch) and within breeding seasons (per breeding unit). Unadjusted mean attentiveness per female is presented although all analyses used attentiveness corrected for the time of day (see text).

<table>
<thead>
<tr>
<th></th>
<th>Unadjusted mean attentiveness ± s.e. (%) (n)</th>
<th>ANOVA: ( DV = \text{Attentiveness}_{\text{adj}} )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>d.f.  MS  F  P</td>
</tr>
<tr>
<td>PER CLUTCH</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Season</td>
<td>1998 56.9 ± 3.4 (9) 1999 61.2 ± 1.5 (20)</td>
<td>1, 25 0.251 0.514 0.480</td>
</tr>
<tr>
<td>Group</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Strategy</td>
<td>Group 60.8 ± 2.2 (13) Pair 59.0 ± 2.0 (16)</td>
<td>1, 25 0.401 0.823 0.373</td>
</tr>
<tr>
<td>Season*Strategy</td>
<td>1, 25 0.247 0.506 0.483</td>
<td></td>
</tr>
<tr>
<td>PER BREEDING UNIT</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Season</td>
<td>1998 57.3 ± 3.6 (8) 1999 60.2 ± 1.9 (13)</td>
<td>1, 17 0.046 0.081 0.780</td>
</tr>
<tr>
<td>Group</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Strategy</td>
<td>Group 59.9 ± 2.8 (9) Pair 58.5 ± 2.4 (12)</td>
<td>1, 17 0.291 0.514 0.483</td>
</tr>
<tr>
<td>Season*Strategy</td>
<td>1, 17 0.218 0.385 0.543</td>
<td></td>
</tr>
</tbody>
</table>
Breeding biology

Figure 8.3. Effect of breeding strategy on female attentiveness per breeding unit. Attentiveness expressed as the standardized residuals (± s.e) to correct for daily variation in the percentage of time spent incubating (arcsine transformed). The number of females per category is given below the x-axis; the mean number of nest watches per female is given in parentheses above the error bars.

Duration of incubation bouts
Incubation bouts ($n = 404$) ranged from 1 to 40 minutes, though bouts were rarely less than 5 minutes. The mean of the average bout duration per female was $12.4 ± 0.85$ min at a rate of 2.85 bouts per hour ($n = 21$ breeding unit-years). Mean duration of incubation bouts ($\log_{10}$ transformed) was not significantly correlated with either day of incubation ($r = -0.18$, $P = 0.15$, $n = 64$) or time of day ($r = -0.03$, $P = 0.84$, $n = 64$). The mean duration of incubation bouts did not vary significantly with incubation phase or time of day in the same ANCOVA model that was applied to attentiveness (Fig. 8.4). Thus, it was not necessary to adjust bout duration to correct for the effect of time of day or days from laying. There was a non-significant trend for females in groups to have longer incubation bouts than females in pairs per nest attempt (Table 8.4). Incubation bouts were also marginally longer in 1998 than 1999 (Table 8.4). However, when multiple nest attempts in the same season were pooled, the trend for strategy was very weak and non-existent for season (Table 8.4). Incubation bouts during first broods were significantly longer in 1998 ($F_{1, 17} = 6.6$, $P = 0.02$, $n = 21$), but there was no significant difference between strategies ($F_{1, 17} = 1.82$, $P = 0.20$, $n =$
There was no significant difference in mean bout duration between pairs and groups in second broods in 1999 (Mann-Whitney test: $z = -1.42$, $P = 0.136$, $n = 8$).

**Figure 8.4.** Daily variation in mean duration of incubation bouts. The mean duration of incubation bouts ($\pm$ s.e.) in each phase of the incubation period (day 1-6, day 7-12, day 13-18) is plotted against the start time of each nest watch ($n = 130$ hr of observation at 29 nests). Incubation bout duration did not vary significantly between incubation phases or with the time of day (ANCOVA: Incubation phase, $F_{2, 60} = 0.73$, $P = 0.484$; Time of day, $F_{1, 60} = 0.017$, $P = 0.898$; Incubation phase*Time of day, $F_{2, 58} = 0.26$, $P = 0.77$).
Table 8.4. Influence of breeding strategy and season on the mean duration of incubation bouts. Analysis of Variance was conducted for nest watches pooled within nest attempts (per clutch) and within breeding seasons (per breeding unit). Unadjusted mean duration per female is presented although all analyses used log transformed data.

<table>
<thead>
<tr>
<th></th>
<th>Unadjusted mean bout duration ± s.e. (min) (n)</th>
<th>ANOVA: DV = Mean bout duration</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>d.f.</td>
</tr>
<tr>
<td><strong>PER CLUTCH</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Season</td>
<td>1998 12.4 ± 1.2 (9) 1999 10.7 ± 0.7 (20)</td>
<td>1, 25</td>
</tr>
<tr>
<td>Strategy</td>
<td>Group 12.4 ± 1.0 (13) Pair 10.3 ± 0.7 (16)</td>
<td>1, 25</td>
</tr>
<tr>
<td>Season*Strategy</td>
<td></td>
<td>1, 25</td>
</tr>
<tr>
<td><strong>PER BREEDING UNIT</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Season</td>
<td>1998 12.6 ± 1.3 (8) 1999 10.9 ± 0.8 (13)</td>
<td>1, 17</td>
</tr>
<tr>
<td>Strategy</td>
<td>Group 12.9 ± 1.1 (9) Pair 10.5 ± 0.9 (12)</td>
<td>1, 17</td>
</tr>
<tr>
<td>Season*Strategy</td>
<td></td>
<td>1, 17</td>
</tr>
</tbody>
</table>

*Contribution of males during incubation*

Males fed the incubating female at the nest 73 times and supplied 92 batches of nest material during nest watches. The mean rate of food provisioning per breeding unit (n = 21) was 0.56 ± 0.13 feeds/hr but rates up to 4 feeds/hr were recorded during individual nest watches. The mean rate of supplying nest material was 0.69 ± 0.20 visits/hr with a maximum rate of 6.5 visits/hr. There was much variation in the propensity of males to visit the nest during the incubation period. Males in five breeding units were not observed feeding the incubating female at the nest (n = 10 nest watches) and nest maintenance was not observed in four breeding units (n = 10 nest watches). However, males in only two breeding units (one of which was only observed for 1 nest watch) were completely absent from the nest during incubation.

Males were observed feeding females away from the nest and females often terminated incubating bouts upon hearing strident calls from the male nearby. As females were out of sight between incubating bouts, it was not possible to ascertain absolute rates of female provisioning during incubation. Thus, differences between males in their preference for feeding their partners on or away from the nest may
confound comparisons between breeding units. However, a reluctance to visit the nest during incubation was randomly distributed through the population as indicated by the percentage of breeding units in which males did not feed females at the nest (males in pairs – 25%, primary males in cooperative units – 33%, helpers – 33%; \( \chi^2 = 0.24, d.f. = 2, P = 0.89 \)), enabling comparisons to proceed with caution.

The mean rate of feeding the incubating female at the nest was similar in groups (0.48 ± 0.16 visits/hr, n = 9) and pairs (0.62 ± 0.20 visits/hr, n = 12) (Mann-Whitney z = 0.31, P = 0.76). When restricted to first broods, mean provisioning rate was close to parity (Mann-Whitney z = 0.09, P = 0.93, n = 8, 11). The mean provisioning rate of primary males in cooperative units (0.31 ± 0.11 visits/hr) was half that of males in pairs (0.62 ± 0.20 visits/hr), although this was not statistically significant (Mann-Whitney z = 0.67, P = 0.5, n = 9, 12). The disparity was also evident when only first broods were considered (Primary males: 0.38 ± 0.16 visits/hr; Pair males: 0.65 ± 0.20 visits/hr; Mann-Whitney z = 0.86, P = 0.39, n = 8, 11).

Helpers delivered 35% of the food items (n = 31) received by females at all cooperative nests (n = 9 units). Helpers were not observed feeding the female in two breeding units. In the remaining seven breeding units, the mean helper provisioning rate was 39 ± 12% of the total feeding contribution. The mean provisioning rate of helpers (0.18 ± 0.06 visits/hr) was less than that of primary males (0.31 ± 0.11 visits/hr), but the means did not differ significantly (\( t_{paired} = -1.74, P = 0.12, n = 7 \)). Helpers contributed 31.5% of batches of nest material (n = 54) at a mean rate per group of 0.25 ± 0.1 visits/hr. This accounted for 0% to 66% (mean: 29 ± 10%) of the total nest maintenance per breeding unit. The mean nest maintenance rate of helpers was less than half that of the primary male (0.66 ± 0.31 visits/hr), although this difference was not statistically significant (\( t_{paired} = -1.41, P = 0.20, n = 8 \)).

**Nestlings**

**Nestling period**

In broods of more than one, nestlings usually fledged on the same day, but delays of 24 – 36 hours between fledging events were recorded. Nestlings typically fledged during their 26th day post-hatching (n = 11) with a range from 22 – 23 days to 30 – 31 days (Table 8.5). Nestlings fledged one day earlier, on average, from cooperative
nests (25 –26 days, \( n = 7 \)) than nests of pairs (26 – 27 days, \( n = 4 \)) (Mann-Whitney \( z = 1.06, P = 0.29 \)).

Table 8.5. Duration of the nestling stage in 11 breeding units of the White-browed Treecreeper at Yarrara FFR. All dates are 1999, except where indicated.

<table>
<thead>
<tr>
<th>Breeding unit</th>
<th>Hatching date</th>
<th>Fledging date</th>
<th># fledglings</th>
<th>Nestling period (days)</th>
<th>Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>T2 (1998)</td>
<td>October 17</td>
<td>November 12</td>
<td>2</td>
<td>26 – 27</td>
<td>1 day</td>
</tr>
<tr>
<td>T6</td>
<td>September 20</td>
<td>October 14</td>
<td>3</td>
<td>25 – 26</td>
<td>1 day</td>
</tr>
<tr>
<td>T7</td>
<td>September 20</td>
<td>October 20</td>
<td>1</td>
<td>30 – 31</td>
<td>1 day</td>
</tr>
<tr>
<td>T17</td>
<td>September 23</td>
<td>October 17 / 18</td>
<td>2</td>
<td>24 – 26</td>
<td>2 days</td>
</tr>
<tr>
<td>T3</td>
<td>September 28</td>
<td>October 24</td>
<td>1</td>
<td>26 - 27</td>
<td>1 day</td>
</tr>
<tr>
<td>T13</td>
<td>September 28</td>
<td>October 24</td>
<td>2</td>
<td>26 - 27</td>
<td>2 days</td>
</tr>
<tr>
<td>T2</td>
<td>September 30</td>
<td>October 25</td>
<td>2</td>
<td>25 - 26</td>
<td>2 days</td>
</tr>
<tr>
<td>T11</td>
<td>October 4</td>
<td>October 28</td>
<td>1</td>
<td>24 - 25</td>
<td>1 day</td>
</tr>
<tr>
<td>T24</td>
<td>October 17 / 18</td>
<td>November 12*</td>
<td>1</td>
<td>25 - 27</td>
<td>2 days</td>
</tr>
<tr>
<td>T3 (2\textsuperscript{nd} brood)</td>
<td>November 18</td>
<td>December 10*</td>
<td>1</td>
<td>22 – 23</td>
<td>1 day</td>
</tr>
<tr>
<td>T12 (2\textsuperscript{nd} brood)</td>
<td>November 27</td>
<td>December 22*</td>
<td>2</td>
<td>25 – 26</td>
<td>1 day</td>
</tr>
</tbody>
</table>

\* Nestlings flushed from nest upon inspection.

Brood care

A total of 103 nest watches summing to 206 hours of observation were included in the analyses of brood care during the nestling stage. Nesting was monitored in nine breeding units in 1998 (10 nest attempts: \( n = 31 \) nest watches) and 15 breeding units (22 nest attempts: \( n = 72 \) nest watches) in 1999.

Brooding

Only the female was recorded brooding from a total of 337 brooding bouts (Pairs – 223; Groups – 114). Predictably, there was a very strong negative correlation between the percentage of time spent brooding (arcsine transformed) and the age of
the nestlings ($r = -0.843$, $P < 0.001$, $n = 103$ nest watches), declining from a mean of 51 ± 3% in days 1–8, to 24 ± 4% in days 9–16 to 2.8 ± 0.9% for nestlings older than 16 days. After day 12, the female rarely spent more than 20% of her time brooding (Fig. 8.5a). Breeding strategy had little influence on the rate of decrease in time spent brooding as nestlings aged (ANCOVA test for homogeneity of slopes: Strategy*Age of nestling – $F_{1, 99} = 1.13$, $P = 0.29$, $n = 61$ (pairs) and 42 (groups) nest watches).

In simple correlation, there was not a significant relationship between percentage of time spent brooding and time of day ($r = -0.084$, $P = 0.4$, $n = 103$). Yet, in partial correlation weighted by nestling age, a significant negative relationship between brooding and time of day emerged, although the amount of variation explained by the relationship was low ($r = -0.206$, $P = 0.037$, $n = 103$: Fig. 8.5b).

The slopes of an ANCOVA of time spent brooding versus nestling age (divided into 3 phases: 1–8 days, 9–16 days and >16 days) as the main factor and time of day as the co-variate were heterogeneous (Phase*Time of day – $F_{2, 97} = 3.21$, $P = 0.045$: Fig. 8.6). Thus, the manner in which females modified their brooding with the time of day changed as the nestlings aged and therefore each phase should be analysed separately.

Time of day was a significant factor in a linear regression confined to the period when brooding was most intense (day 1–8) (% time brooding = 1.03 – 0.00024*Time of day, $F = 9.60$, $P = 0.004$, $R^2 = 0.193$; Fig. 8.6). However, the significance of this regression was sensitive to the removal of two observations (highlighted in Fig. 8.5b) (% time brooding = 0.89 – 7.2 X 10^-5*Time of day, $F = 1.24$, $P = 0.27$, $R^2 = 0.007$). These observations refer to day 8 nest watches at nests 14 and 16 respectively, both of which were too high for direct verification of hatching date; therefore hatching was estimated from adult behaviour. An underestimation of nestling age by only 1–2 days would exclude these observations from the regression. Time of day was not a significant predictor of brooding behaviour when nestlings were aged 9–16 days in a quadratic regression model, which was superior to a linear model (% time brooding = -0.97 + 2.56*Time of day – 1.05 X 10^-6 *(Time of day)^2, $F = 1.28$, $P = 0.3$, $R^2 = 0.119$; Fig. 8.6).
Figure 8.5. Influence of (a) age of nestlings and (b) time of day on the percentage of time spent brooding by female White-browed Treecreepers at Yarrara FFR. The percentage of time brooding in (b) has been corrected for nestling age in partial regression. The solid dots in (b) indicate observations with high leverage on regression results (see text). Although each circle represents one nest watch, where brooding was not recorded, circles overlap ($n = 206$ hr of observation at 32 nests in 24 breeding unit-years).
Figure 8.6. Variation in brooding behaviour in each phase of nestling development as a function of time of day. The mean of the percentage time spent brooding (± s.e.) in each phase of the nestling period (day 1-8, day 9-16, day 16+) is plotted against the start time of each nest watch (n = 206 hr of observation at 32 nests).

The residuals from a linear regression of time spent brooding against the age of the nestlings were used as an adjusted measure of brooding (Brood_{adj}) to account for age-related decreases in brooding effort. Brood_{adj} per breeding unit did not differ significantly between females in pairs and groups, or between breeding seasons (Table 8.6, Fig. 8.7a). Furthermore, there was not a significant influence of strategy in the first 12 days of the nestling stage, when brooding was likely to be most critical (Table 8.6, Fig. 8.7b).
Table 8.6. Influence of breeding strategy and inter-season variation on percentage of time spent brooding by females. ANOVA results are presented for data inclusive of the entire nestling stage and for nestlings aged 1-12 days only. Unadjusted values for mean percent time spent brooding per female are presented, although all analyses used brooding corrected for nestling age (see text).

<table>
<thead>
<tr>
<th></th>
<th>Unadjusted mean brooding time ± s.e. (%) (n)</th>
<th>ANOVA: $DV = \text{Brood}_\text{adj}$</th>
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<tr>
<td>Season</td>
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<td>1, 20</td>
<td>0.045</td>
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<tr>
<td>1998</td>
<td>23.2 ± 4.7 (9)</td>
<td>25.3 ± 3.1 (15)</td>
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<td>1999</td>
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<td>Group</td>
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<td>1, 20</td>
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<td>0.500</td>
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<td><strong>DAY 1 – 12</strong></td>
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<td>1, 16</td>
<td>0.032</td>
<td>0.070</td>
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<tr>
<td>1998</td>
<td>37.9 ± 7.4 (6)</td>
<td>44.2 ± 4.8 (14)</td>
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<tr>
<td>1999</td>
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<td>Group</td>
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<td>1.092</td>
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<td>0.426</td>
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Figure 8.7. Effect of breeding strategy and season on time spent brooding by females per breeding unit, for (a) the entire nestling stage and (b) nestlings aged 1 – 12 days. Brooding is expressed as the standardized residuals (± s.e) from regressions to correct for nestling age-related decreases in brooding time (arcsine transformed). The number of females per category is given below the x-axis; the mean number of nest watches per female is given in parentheses above the error bars.
If helpers are relieving the female from caring for fledglings from the first brood, it might be expected that females at cooperative nests would be able to spend a greater proportion of their time tending to the second brood than females without helpers. In a 2-factor ANOVA restricted to 1999 data, there was not a significant effect of breeding strategy or brood number on Brood$_{adj}$, nor was there a significant interaction between these factors (Table 8.7, Fig. 8.8a). Limiting the model to the first 12 days of the nestling stage does not alter the ANOVA result (Table 8.7, Fig. 8.8b). Thus, there was no significant difference between strategies in the amount of time spent brooding in either the first or second broods. Nonetheless, there appears to be a strong trend in the direction predicted, with females in groups spending more time on the nest with the second brood than females in pairs, particularly when the nestlings have just hatched (Fig. 8.8b).

Table 8.7. Influence of breeding strategy and brood number on percentage of time spent brooding by females in 1999. ANOVA results are presented for data inclusive of the entire nestling stage and for nestlings aged 1-12 days only. Unadjusted values for mean percent time spent brooding per female are presented, although all analyses used brooding corrected for nestling age (see text).

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<td>brooding ± s.e. (%) (n)</td>
<td>d.f.</td>
<td>MS</td>
<td>F</td>
<td>P</td>
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<tr>
<td>Strategy</td>
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<tr>
<td>Group</td>
<td>28.9 ± 6.2 (11)</td>
<td>1, 18</td>
<td>0.150</td>
<td>0.344</td>
<td>0.565</td>
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<td>Pair</td>
<td>28.6 ± 6.3 (11)</td>
<td>1, 18</td>
<td>0.011</td>
<td>0.016</td>
<td>0.899</td>
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<tr>
<td>Brood number</td>
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<tr>
<td>First</td>
<td>19.8 ± 4.4 (14)</td>
<td>1, 18</td>
<td>6.5 X 10$^{-4}$</td>
<td>0.001</td>
<td>0.970</td>
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<td>Second</td>
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<td>1.005</td>
<td>2.305</td>
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<td>Strategy*Brood number</td>
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<td></td>
<td></td>
<td>brooding ± s.e. (%) (n)</td>
<td>d.f.</td>
<td>MS</td>
<td>F</td>
<td>P</td>
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<tr>
<td>Strategy</td>
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<tr>
<td>Group</td>
<td>45.1 ± 5.9 (11)</td>
<td>1, 16</td>
<td>0.776</td>
<td>1.152</td>
<td>0.299</td>
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<tr>
<td>Pair</td>
<td>42.0 ± 6.0 (9)</td>
<td>1, 16</td>
<td>0.011</td>
<td>0.016</td>
<td>0.899</td>
<td></td>
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<tr>
<td>Brood number</td>
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<td></td>
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</tr>
<tr>
<td>First</td>
<td>40.6 ± 6.1 (12)</td>
<td>1, 16</td>
<td>0.124</td>
<td>1.817</td>
<td>0.196</td>
<td></td>
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</tr>
<tr>
<td>Second</td>
<td>48.5 ± 4.9 (8)</td>
<td>1, 16</td>
<td>1.224</td>
<td>1.817</td>
<td>0.196</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Strategy*Brood number</td>
<td>1, 16</td>
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</tbody>
</table>
Figure 8.8. Effect of breeding strategy and brood number on time spent brooding by females in 1999, for (a) the entire nestling stage and (b) nestlings aged 1 – 12 days. Brooding time is expressed as the standardized residuals (± s.e) from regressions to correct for nestling age-related decreases in brooding time. The number of females per category is given below the x-axis; the mean number of nest watches per female is given in parentheses above the error bars.
Factors affecting nestling provisioning

A total of 1640 provisioning visits were observed, with 929 and 711 visits to nests of pairs and groups, respectively. Total provisioning per nest watch varied between 0 and 23.3 visits/hr with a mean of 8.1 ± 0.4 visits/hr ($n = 103$). Overall, the mean provisioning rate by females was 3.0 ± 0.2 visits/hr ($range: 0-11.3$ visits/hr) compared to 4.1 ± 0.2 visits/hr ($range: 0-11.5$ visits/hr) by primary males. At cooperative nests, the sum of the provisioning rate of all helpers averaged 2.4 ± 0.3 visits/hr ($range: 0-7.3$ visits/hr, $n = 42$ nest watches).

Total provisioning rate increased with the age of the nestlings but was not significantly related to the time of day the nest watch was conducted (Fig. 8.9). Further, there were no significant differences in total provisioning rate (adjusted for the age of nestlings) between nest watches that commenced prior to 10am, between 10am – 3pm and after 3pm (ANOVA: $F_{2, 100} = 0.031$, $P = 0.969$, $n = 57, 20$ and 26).

The number of nestlings present was not routinely checked when nest watches were conducted for a variety of logistic and ethical reasons. However, for a subset of 90 nest watches, brood size could be determined retrospectively from known hatching success, fledgling productivity and periodic nest inspections. Thus, a second regression was conducted that included brood size in addition to nestling age and time of day. After variation attributable to nestling age was removed, brood size was a significant predictor of the total provisioning rate to the brood (Table 8.8a). However, all three nest watches of broods with three nestlings (all at the same nest) had leverage values indicating that they may be exerting undue influence on parameter estimation (SPSS undated). When the model was refitted without these nest watches, brood size was not included as a significant predictor variable (Table 8.8b). Thus, a significant increase in overall provisioning appeared to be triggered in broods of three nestlings with no significant difference between broods of one and two nestlings. Observations of more broods of three nestlings are necessary to assess the generality of this conclusion.
Figure 8.9. Partial regression plots (standardized residuals) of total provisioning rate (Log$_{10}$ transformed) per nest watch ($n = 103$) as a function of (a) nestling age after controlling for time of day and (b) time of day after controlling for nestling age. Nestling age was the only parameter included in the forward stepwise linear regression model (Constant = 0.765 ± 0.039, $\beta = 0.011 \pm 0.003$, $F = 17.781$, $P < 0.001$, $R^2 = 0.141$).
Table 8.8. Stepwise linear regression of factors influencing the total provisioning rate (log$_{10}$ transformed) to White-browed Treecreeper broods. Nest watches at nests with 3 nestlings were included in model (a) ($n = 90$) but excluded in model (b) ($n = 87$).

(a)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>s.e.</th>
<th>t</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>0.512</td>
<td>0.107</td>
<td>4.788</td>
<td>&lt;0.001</td>
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<tr>
<td>Nestling age</td>
<td>0.013</td>
<td>0.003</td>
<td>4.667</td>
<td>&lt;0.001</td>
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<tr>
<td>Brood size</td>
<td>0.124</td>
<td>0.048</td>
<td>2.571</td>
<td>0.012</td>
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</table>

(b)

<table>
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<tr>
<th>Variable</th>
<th>Estimate</th>
<th>s.e.</th>
<th>t</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>0.758</td>
<td>0.041</td>
<td>18.356</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Nestling age</td>
<td>0.010</td>
<td>0.003</td>
<td>3.954</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Brood size</td>
<td>-</td>
<td>-</td>
<td>1.339</td>
<td>0.184</td>
</tr>
</tbody>
</table>

1 Time of day was not included as a significant predictor variable in either model (a) or (b).

Broods of two nestlings accounted for the majority (77%) of nest watches with known brood size. However, there were disproportionately more nest watches of 2-nestling broods at nests of pairs than for groups, while at the latter nest watches of broods of one or three nestlings were more frequent than expected ($\chi^2 = 21.25$, df. = 2, $P < 0.001$). Using Type III sum-of-squares ANOVA to compensate for the unbalanced design, the total provisioning rate was compared between strategies and brood size, excluding the 3-nestling nest (Table 8.9). There was not a significant main effect of brood size in this comparison. There was, however, a significant main effect of strategy and a significant interaction between strategy and brood size, suggesting each strategy should be considered in isolation.
Table 8.9. Influence of breeding strategy and brood size (1-nestling vs. 2-nestlings) on the total food provisioning rate (corrected for nestling age - see text) to the nestlings per breeding unit.

<table>
<thead>
<tr>
<th></th>
<th>d.f.</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
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<td>Strategy</td>
<td>1, 18</td>
<td>2.157</td>
<td>6.859</td>
<td>0.017</td>
</tr>
<tr>
<td>Brood size</td>
<td>1, 18</td>
<td>0.575</td>
<td>1.828</td>
<td>0.193</td>
</tr>
<tr>
<td>Strategy*Brood size</td>
<td>1, 18</td>
<td>2.870</td>
<td>9.129</td>
<td>0.007</td>
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</table>

For pairs, total provisioning rate per breeding unit was much higher at the only nest with one nestling (Prov$_{adj}$ = 1.48) than the mean of the 12 units with two nestlings (Prov$_{adj}$ = -0.039 ± 0.13). This counter-intuitive result probably reflects an artifact of the solitary datum at the one-nestling nest rather than a consistent effect of higher overall provisioning to single nestling broods. For groups, mean total provisioning rate was lower at single-nestling broods (Prov$_{adj}$ = -0.48 ± 0.36) than two-nestling broods (Prov$_{adj}$ = 0.10 ± 0.31), but this difference was not significant ($t_{7}$ = -1.24, $P = 0.256$). There was little difference in provisioning rates between groups and pairs with two nestlings ($t_{15}$ = -0.5, $P = 0.624$). Therefore, the significant main effect of strategy in the ANOVA (Table 8.9) is attributable to the difference in provisioning rates at broods with one nestling, which as mentioned, is probably not a representative value for pairs. Thus, it was decided to proceed with the remainder of the analysis using all 103 nest watches without including brood size as a co-variate, cognizant of the small influence increased brood size may have on provisioning, and mindful of the effect brood size might have at the only nest with three nestlings.

Comparison of nestling provisioning in pairs and groups

The rate of increase in provisioning as nestlings developed was similar in groups and pairs (ANCOVA test for homogeneity of slopes: $F_{1, 99} = 2.124$, $P = 0.148$; Fig. 8.10). However, whilst there was a significant negative correlation between provisioning rate and the percentage of time spent brooding by females in pairs ($r = -0.447$, $P$
<0.001, \( n = 61 \)), no such relationship was evident in groups (\( r = -0.099, P = 0.532, n = 42 \)).

![Graph showing total provisioning rate vs. age of nestlings for pairs and groups.]

**Figure 8.10.** Increase in total provisioning rate per nest watch (\( n = 103 \)) with nestling age, differentiated by breeding strategy. Linear regression lines are fitted for pairs (solid) and groups (dashed). The slopes of the regression lines did not differ significantly in ANCOVA.

Provisioning rates were controlled for nestling age by using residuals from regressions of provisioning rate (\( \log_{10} \) transformed) against age, and then calculating the mean residual (\( \text{Prov}_{\text{adj}} \)) per clutch and per unit (as for attentiveness). Separate regressions were fitted for total, female and primary male provisioning rates, generating three sets of residuals specific to the comparison of interest.

Total \( \text{Prov}_{\text{adj}} \) per breeding unit did not differ significantly between breeding seasons or strategies (Table 8.10). Although the mean adjusted provisioning rate for groups was less than pairs in 1998 and greater than pairs in 1999 (Fig. 8.11), the interaction between season and strategy was not significant (Table 8.10). Similar results were obtained when provisioning rate was analysed per clutch (Table 8.10).
Table 8.10. Influence of breeding strategy and season on total food provisioning rate to nestlings. Analysis of Variance was conducted for nest watches pooled within nest attempts (per clutch) and within breeding seasons (per breeding unit). Unadjusted values for mean provisioning rate are presented although all analyses used provisioning rate corrected for nestling age (see text).

| PER CLUTCH | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Unadjusted mean provisioning ± s.e. (visits/hr) (n) | ANOVA: \( DV = \text{Prov}_{adj} \) | | \( \text{df} \) | \( MS \) | \( F \) | \( P \) | |
| Season | 1998 | 7.3 ± 0.9 (10) | 1999 | 7.9 ± 0.8 (22) | 1, 28 | 0.406 | 0.715 | 0.405 |
| Group | | | | | | | | | |
| Pair | | | | | | | | | |
| Strategy | 8.2 ± 1.0 (14) | 7.4 ± 0.7 (18) | 1, 28 | 0.059 | 0.104 | 0.750 |
| Season*Strategy | | | | | | | | | |

| PER BREEDING UNIT | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Unadjusted mean provisioning ± s.e. (visits/hr) (n) | ANOVA: \( DV = \text{Prov}_{adj} \) | | \( \text{df} \) | \( MS \) | \( F \) | \( P \) | |
| Season | 1998 | 7.7 ± 0.9 (9) | 1999 | 8.2 ± 0.6 (15) | 1, 20 | 0.368 | 1.033 | 0.322 |
| Group | | | | | | | | | |
| Pair | | | | | | | | | |
| Strategy | 8.5 ± 0.9 (9) | 7.7 ± 0.6 (15) | 1, 20 | 0.074 | 0.207 | 0.654 |
| Season*Strategy | | | | | | | | | |

**Figure 8.11.** Influence of breeding strategy and season on total provisioning rate. Provisioning rate is expressed as the mean standardized residual per breeding unit (± s.e.) from regressions to correct for nestling age-related increases in provisioning. The number of breeding units per category is given below the x-axis; the mean number of nest watches per breeding unit is given in parentheses above the error bars.
In 1999, total provisioning rate did not differ significantly between first and second broods or between strategies (Table 8.11, Fig. 8.12). However, the standardized residual associated with nest 3 was large (-2.61). Removal of one nest watch at nest 3 (during which the nestling was not fed) overcame this anomaly. (Some reservation about this modification is expressed, as there was no *a priori* reason for excluding this nest watch.) When re-analysed, there was a trend for total provisioning to first broods to be greater than to second broods in both strategies (Table 8.11). The difference in total provisioning rate between strategies was negligible during first broods, but provisioning to second broods was considerably higher for groups (Fig. 8.12). Repeating the analysis based on a new provisioning rate – nestling age regression, fitted to the 1999 data only, did not alter the general trend of the results.

Table 8.11. Influence of breeding strategy and brood number on total food provisioning rate to nestlings in 1999. Analysis of Variance was conducted for all observations and then with an anomalous nest watch excluded from the analysis. Unadjusted mean provisioning rates are presented although all analyses used provisioning rate corrected for nestling age (see text).

<table>
<thead>
<tr>
<th></th>
<th>Unadjusted mean provisioning ± s.e. (visits/hr) (n)</th>
<th>ANOVA: ( DV = \text{Prov}_{\text{adj}} )</th>
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<td></td>
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<tr>
<td><strong>ALL OBSERVATIONS</strong></td>
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<tr>
<td>Strategy</td>
<td></td>
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</tr>
<tr>
<td>First</td>
<td>Group: 8.5 ± 1.2 (11)</td>
<td>1, 18</td>
</tr>
<tr>
<td></td>
<td>Pair: 7.4 ± 1.0 (11)</td>
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<tr>
<td>Brood number</td>
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<tr>
<td>First</td>
<td>9.3 ± 0.9 (14)</td>
<td>1, 18</td>
</tr>
<tr>
<td>Second</td>
<td>5.6 ± 0.8 (8)</td>
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<tr>
<td>Strategy*Brood number</td>
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<td></td>
</tr>
<tr>
<td>First</td>
<td></td>
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<tr>
<td>Second</td>
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<tr>
<td><strong>EXCLUDING OUTLIER</strong></td>
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<tr>
<td>Strategy</td>
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<tr>
<td>First</td>
<td>Group: 8.6 ± 1.1 (11)</td>
<td>1, 18</td>
</tr>
<tr>
<td></td>
<td>Pair: 7.4 ± 1.0 (11)</td>
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</tr>
<tr>
<td>Brood number</td>
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</tr>
<tr>
<td>First</td>
<td>9.4 ± 0.9 (14)</td>
<td>1, 18</td>
</tr>
<tr>
<td>Second</td>
<td>5.6 ± 0.8 (8)</td>
<td></td>
</tr>
<tr>
<td>Strategy*Brood number</td>
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<td>1, 18</td>
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</tbody>
</table>
Figure 8.12. Effect of breeding strategy and brood number on total provisioning rate in 1999, expressed as the mean standardized residual per nest attempt (± s.e) from regressions to correct for nestling age-related increases in provisioning. The solid square represents the revised mean for groups after removing the anomalous nest watch at nest 3. The number of breeding units per category is given below the x-axis; the mean number of nest watches per breeding unit is given in parentheses above the error bars.

Mean total Prov$_{adj}$ and mean Prov$_{adj}$ for primary males and females per breeding unit-year are shown in Figure 8.13. The presence of helpers did not significantly increase the total provisioning rate ($t = -0.012$, $d.f. = 22$, $P = 0.990$; Fig. 8.13a). Similarly, the provisioning rate of breeding males did not differ significantly in the presence of helpers ($t = 0.590$, $d.f. = 22$, $P = 0.561$; Fig. 8.13b). However, the provisioning rate of females was significantly lower in breeding units with helpers ($t = 4.094$, $d.f. = 22$, $P < 0.001$; Fig. 8.13c).
Breeding biology

(a) Total provisioning

(b) Primary male provisioning

(c) Female provisioning

Figure 8.13. The effect of breeding strategy on (a) total provisioning rate, and provisioning rates of the (b) breeding male and (c) breeding female in White-browed Treecreepers. Provisioning rate is expressed as the mean standardized residual per breeding unit-year (± s.e) from regressions to correct for nestling age-related increases in provisioning. For pairs \( n = 15 \), and for groups \( n = 9 \).

The gender differences were supported by paired comparisons of provisioning rates between females and breeding males, based on separate provisioning rate – nestling age regressions for pairs and groups, respectively. In pairs, there was no difference in \( \text{Prov}_{\text{adj}} \) between the sexes (\( t_{\text{paired}} = 1.358, d.f. = 14, P = 0.196 \)). However, primary
males in groups provided significantly more food to the nestlings than their female partners ($t_{paired} = 11.702$, $d.f. = 8$, $P < 0.001$).

**Provisioning by parents**

Provisioning by pairs (i.e. breeder-only care) increased by an average of 43% from the first week to the second week and by a further 48% in the third week and beyond (Table 8.12, Fig. 8.14). In the first week of the nestling stage, the provisioning rates of females and primary males in cooperative groups were equivalent to their counterparts in pairs (Table 8.12). However, due to the additional care of helpers, total provisioning was greater in groups (Table 8.12). A consequence of this was that the proportional contribution of the parents (in particular the female) was lower in groups than pairs (Fig. 8.14).

As nestlings entered their second week, total provisioning increased in pairs, due mainly to increased provisioning by the female (accounted for 71% of the increase in total provisioning), but remained relatively constant in groups, such that the discrepancy between the strategies evident in the first week dissipated (Fig. 8.14). The provisioning rate of females in groups also increased and although the proportional contributions of the female and primary male were still lower in groups relative to pairs, there were no significant differences in their absolute provisioning rates (Table 8.12).

From the third week forward, total provisioning rate was similar in groups and pairs (Fig. 8.14). However, helpers contributed 27.3 ± 5.5% of provisioning visits at cooperative nests during this phase. Thus, although females in groups actually increased their rate of provisioning by an average of 67% from the second to third weeks, it was still significantly lower than the mean provisioning rate of females without helpers (Table 8.12). Primary males in groups maintained a steady provisioning rate whilst their counterparts in pairs continued to slowly raise their provisioning effort, such that the provisioning rate of the latter was 26% higher, although the difference between them was not significant (Table 8.12).
Table 8.12. Comparison of the mean provisioning rate\(^1\) (± s.e.) per breeding unit-year for all breeding unit members (Total), the breeding male and the female, partitioned by nestling age. Sample size refers to number of breeding unit-years.

<table>
<thead>
<tr>
<th></th>
<th>Week 1 (n = 16)</th>
<th>Week 2 (n = 14)</th>
<th>Week 3+ (n = 19)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Pairs Groups</td>
<td>Pairs Groups</td>
<td>Pairs Groups</td>
</tr>
<tr>
<td>Total</td>
<td>5.2 ± 0.5</td>
<td>7.4 ± 0.6</td>
<td>11 ± 1.2</td>
</tr>
<tr>
<td></td>
<td>8.1 ± 1.3</td>
<td>7.8 ± 1.5</td>
<td>10.1 ± 1.5</td>
</tr>
<tr>
<td>Breeding male</td>
<td>3.6 ± 0.6</td>
<td>4.2 ± 0.6</td>
<td>5.8 ± 0.8</td>
</tr>
<tr>
<td></td>
<td>4.2 ± 0.8</td>
<td>4.0 ± 0.8</td>
<td>3.8 ± 0.5</td>
</tr>
<tr>
<td>Female</td>
<td>1.7 ± 0.2</td>
<td>3.2 ± 0.5</td>
<td>5.2 ± 0.6</td>
</tr>
<tr>
<td></td>
<td>1.1 ± 0.2</td>
<td>2.0 ± 0.7</td>
<td>3.4 ± 0.6</td>
</tr>
</tbody>
</table>

\(^1\) Provisioning rates were Log\(_{10}\) transformed prior to analyses.

Figure 8.14. Variation in parental provisioning with nestling age and breeding strategy. The figure depicts the mean provisioning rate for females, primary males and all extra-parental helpers combined, partitioned by nestling age. The mean proportional contribution of females, primary males and helpers is shown within the bars. The sample size above each bar is the number of breeding units that were used to calculate the mean provisioning rates per category.
Provisioning by helpers

A new regression was constructed for nestling age against the provisioning rate of the female, primary male and helper(s) (pooled for the one unit with >1 helper) in the nine cooperative breeding units only. The residuals were again used as a corrected measure of provisioning rate, this time in a mixed-model ANOVA including status (i.e. female, breeding male, helper) and breeding unit-year (Table 8.13). There was a non-significant trend ($P < 0.1$) for provisioning rate to differ according to the status of the provider. The rate of provisioning also varied significantly among breeding units but this among-unit variability differed between females, primary males and helpers (i.e. significant interaction). The reason for this was the failure of the helper in T12 to provide any food (Fig. 8.15). Removal of this nest from the analysis renders the interaction term non-significant, yet the dependence of provisioning rate on status is strengthened (Table 8.13). The significant among-group variation in provisioning rate persists in the remaining eight groups. This analysis highlights significant differences in provisioning rate between females, breeding males and helpers, and significant among-group variability in provisioning rate.

Table 8.13. Mixed-model ANOVA of the variation in provisioning rates among breeding units (random effect) and of the influence of reproductive status (fixed effect: female vs breeding male vs helper). All analyses used provisioning rate corrected for nestling age (see text).

<table>
<thead>
<tr>
<th></th>
<th>d.f.</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>ALL BREEDING UNITS</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Status</td>
<td>2, 16</td>
<td>6.174</td>
<td>2.745</td>
<td>0.094</td>
</tr>
<tr>
<td>Breeding unit</td>
<td>8, 96</td>
<td>1.897</td>
<td>3.463</td>
<td>0.002</td>
</tr>
<tr>
<td>Status*Breeding unit</td>
<td>16, 96</td>
<td>2.249</td>
<td>4.105</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td><strong>EXCLUDING T12</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Status</td>
<td>2, 14</td>
<td>4.163</td>
<td>4.496</td>
<td>0.031</td>
</tr>
<tr>
<td>Breeding unit</td>
<td>7, 78</td>
<td>1.882</td>
<td>3.099</td>
<td>0.006</td>
</tr>
<tr>
<td>Status*Breeding unit</td>
<td>14, 78</td>
<td>0.926</td>
<td>1.525</td>
<td>0.122</td>
</tr>
</tbody>
</table>
However, the pattern of provisioning by helpers was inconsistent between groups. There was significant variation between groups in the proportional contribution of helpers (relative to the parents) to provisioning (Kruskal-Wallis $H = 24.79$, $d.f. = 8$, $P = 0.002$; Fig. 8.15). In six of the nine breeding unit-years, the provisioning rate of the helper(s) was either greater than or nearly equal to the primary male and in most cases more than the female (Fig. 8.15a). In these groups, the helpers’ contribution accounted for between 32% and 44% of the overall provisioning effort (Fig. 8.15b). However, in three groups, the provisioning rate of the helper was much less than either of the parents: the helper contributed moderately in one group (22%), whilst in the remaining two groups, the helpers’ contribution to provisioning was small (8%) or non-existent (0%) (Fig. 8.15b).

**Cross-territorial feeding**

Only one instance of cross-territorial feeding – in which the same individual provides care at the nests of two or more different females – was observed. Early in the 1999 breeding season, the secondary male from T2 visited nest 3 in an adjacent territory several times (T3 – see Fig. 6.4). Initial attempts by the male to feed the incubating female with saltbush berries were rejected, but on one occasion the male arrived with a moth which she accepted and ate. This male was not observed feeding the nestlings at this or subsequent nests of the T3 female. Other examples of individuals appearing at nests outside their territories appeared to be accidental (during foraging) or antagonistic.
Figure 8.15. Variation in nestling provisioning by helpers in the nine cooperative groups. (a) Mean provisioning rate per individual (± s.e.) within each group per breeding season. As the comparison of interest is the contribution of helpers relative to the breeding pair, provisioning rate is not adjusted for nestling age. (b) Mean proportional contribution of helpers (± s.e.) to the total provisioning effort within each group. In T2 (1998) there were 3 helpers; their contribution is combined in these graphs. In all other groups, there was only one helper.
Diet

Identification of food items brought to the nest was difficult and size-biased. The majority (55%) of identified items were adult moths (Lepidoptera) of various species and sizes, but a wide array of invertebrates was taken. Frequently identified items included ants (Formicoidea), which probably also accounted for many of the unidentified small items, soft-bodied grubs (probably Lepidoptera and Coleoptera larvae), small beetles (Coleoptera) and brightly coloured saltbush berries (*Rhagodia spinescens*, *Chenopodium curvispicatum* and *Enchylaena tomentosa*). Other prey items that were identified less frequently, but nevertheless comprise part of the diet of White-browed Treecreepers, included grasshoppers and mantids (Orthoptera), stick-insects (Phasmatodea), dragonflies and damselflies (Odonata), butterflies (Lepidoptera), termites (Isoptera), adult flies (Diptera), bugs (Hemiptera), small spiders (Araneae), millipedes (Diplopoda) and worms (Oligochaeta).

Nestlings in their first week tended to be fed smaller and easily digestible prey, such as ants, small moths and grubs, though they were provided with some surprisingly large items (e.g. bigger moths) on occasions. As the nestlings grew, larger items and those with harder exoskeletons (e.g. beetles, grasshoppers, mantids, dragonflies and bugs) were more prevalent. Small food items were still delivered to older nestlings. Saltbush berries were an increasingly common component of the nestlings’ diet as they aged. Berries were identified only once during provisioning to nestlings in their first week, in contrast with 55 times for nestlings in their third week or older. Whilst there were more nest watches conducted in the third week and increased provisioning to older nestlings afforded more opportunity to identify food items, this imbalance is striking.

Post-fledging

Upon fledging, juveniles were clumsy flyers and weak climbers but were capable of moving from tree to tree and finding refuge in higher branches, where they tended to remain still for long periods. For about a week after fledging, whilst entirely dependent on parents or helpers for nutrition, juveniles remained in close proximity to the nest (within ≈100 m). As juveniles gained strength and mobility, they ventured further afield, often moving with their parents and/or helpers in small family groups.
Juveniles from the same brood usually remained in close association and were often ‘shepherded’ by a helper as they learnt to forage. Juveniles foraged successfully for themselves from about 7 - 10 days post-fledging. The latest a juvenile was observed being fed by a carer was 37 days post-fledging.

**Sweeping**

Pieces of sloughed reptile skin were often present in nests. These were probably residue from ‘sweeping’, an unusual behaviour that has only been described in Australian treecreepers (Noske 1982a) and Nuthatches (Sittidae) (Skutch 1999), but as yet, not for the White-browed Treecreeper. During sweeping, a bird holds a piece of material (usually reptile skin, a pebble or beetle carapace, sometimes a piece of plastic) in its bill and drags it in a side-to-side motion over the bark of the nest tree. The hollow entrance receives particular attention but some individuals sweep for several metres above and below the hollow and on all sides of the trunk. Bouts of sweeping may continue for several minutes or until the material disintegrates. Sweeping is performed by all members of a breeding unit, including helpers, and was observed at all stages of nesting, from construction through to the nestling stage. The purpose of this peculiar behaviour is uncertain. Noske (1982a) proposed that it might be to disrupt scent marks of potential mammalian competitors for nesting hollows. Similarly, it may be to confuse reptilian predators that hunt by olfactory cues.

**8.4 Discussion**

**The significance of multi-broodedness**

In many ways, the breeding biology of the White-browed Treecreeper is typical of a small Australian passerine: it has a small and stable clutch size, a long breeding season and the ability to raise more than one brood in the same season (Woinarski 1985, Yom-Tov 1987, Rowley & Russell 1991). In fact, the mean clutch size of the White-browed Treecreeper (1.93) was lower than predicted for an Australian passerine of the same weight (2.58) (from equations in Yom-Tov 1987). However, the mean clutch size was comparable with the Rufous Treecreeper and Red-browed
Breeding biology

Treecreepers, which were also below the predictions of Yom-Tov (2.55 and 2.58, respectively) but less than the Brown Treecreepers and White-throated Treecreeper (Table 8.14). Although the mean clutch size of the Brown Treecreepers was slightly higher than predicted (2.54), it appears that Climacteris treecreepers generally have smaller clutches than expected for Australian passerines of the same size.

The small clutch size of the White-browed Treecreeper is more likely to have evolved in response to food limitation (Lack 1947, 1948) than intensity of nest predation (Skutch 1949, Slagsvold 1982). Woinarski (1985) has argued that the small clutches of Australian foliage gleaning insectivores may arise from their stable but relatively poor year-round food supply, in contrast with the extreme seasonal fluctuations in food availability experienced by northern temperate birds. Noske (1986) has suggested Australian bark-foraging insectivores occupy a specialized foraging niche with a more limited food supply than foliage gleaners. Further, non-Hymenopteran invertebrates (e.g. moths, grubs, spiders), which are preferentially fed to nestlings, may be particularly difficult to locate. Thus, clutches may be small to limit the number of nestlings that must be fed simultaneously, reducing the risk that a temporary food shortage will result in nestling starvation. In contrast, the hypotheses of reduced clutch size due to predation intensity relate to open-nesting, single-brooded species whose main predators hunt by visual or aural cues (Slagsvold 1982, Major 1991). These explanations have little relevance to the White-browed Treecreeper, which are hollow-nesting, multi-brooded and most likely to be preyed upon by reptiles hunting by olfactory cues.

There was little variation in the clutch size of White-browed Treecreepers, with 84% of clutches consisting of two eggs. Thus, there is limited potential to adjust reproductive effort through variation in clutch size, in contrast with passerines in temperate regions of the northern hemisphere (Klomp 1970, Boyce & Perrins 1987, Daan & Tinbergen 1997). Adjustment of annual reproductive effort in Australian birds is primarily achieved through manipulation of the number of broods raised (Rowley & Russell 1991), which is facilitated by longer breeding seasons (Woinarski 1985, Wyndham 1986). The White-browed Treecreeper fits this life-history pattern. First clutches were initiated across three months in the two seasons studied. The breeding season, defined as the period during which at least some members of the
Table 8.14. Comparative nesting data for five species of Australian treecreepers.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean adult weight (g)</th>
<th>Social organisation</th>
<th>Mean clutch size</th>
<th>Breeding season (laying)</th>
<th>Incubation period (days)</th>
<th>Nestling period (days)</th>
<th>Multi-brooded?</th>
<th>Location of study</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>White-throated Treecreeper <em>Cromobates leucophaea</em></td>
<td>22.5</td>
<td>Non-cooperative</td>
<td>2.55</td>
<td>September – mid Novem.</td>
<td>23</td>
<td>26</td>
<td>Rarely</td>
<td>Northern NSW</td>
<td>Noske 1991</td>
</tr>
<tr>
<td>Brown Treecreeper <em>Climacteris picumnus</em></td>
<td>35.0</td>
<td>Co-operative</td>
<td>2.82</td>
<td>Late July – early Novem.</td>
<td>16</td>
<td>21 – 26</td>
<td>Occasionally</td>
<td>Northern NSW</td>
<td>Noske 1991</td>
</tr>
<tr>
<td>Rufous Treecreeper <em>Climacteris rufa</em></td>
<td>34.6 (male)</td>
<td>Co-operative</td>
<td>1.94</td>
<td>August – January</td>
<td>17</td>
<td>28</td>
<td>Frequently</td>
<td>South-west WA</td>
<td>Rose 1996 Luck 2000</td>
</tr>
<tr>
<td>Red-browed Treecreeper <em>Climacteris erythrops</em></td>
<td>22.8</td>
<td>Co-operative</td>
<td>2.0</td>
<td>Late August – late Decem.</td>
<td>18</td>
<td>25</td>
<td>Yes</td>
<td>Northern NSW</td>
<td>Noske 1991</td>
</tr>
<tr>
<td>White-browed Treecreeper <em>Climacteris affinis</em></td>
<td>22.3 (male)</td>
<td>Co-operative</td>
<td>1.93</td>
<td>Late August – mid Novem.</td>
<td>18</td>
<td>26</td>
<td>Yes</td>
<td>North-west Victoria</td>
<td>This study</td>
</tr>
<tr>
<td></td>
<td>21.6 (female)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Breeding biology

population are involved in rearing offspring, is considerably longer, spanning six months from August to February. Yet, a brood can be raised to nutritional independence in only 90 days. The long breeding season enables a second brood to be raised in favourable conditions and compensates for failed nesting attempts because there is the opportunity for replacement clutches.

Rainfall is a fundamental proximate determinant of the timing of breeding in many birds living in unpredictable or semi-arid environments (Boag & Grant 1984, Ford 1989, Lloyd 1999). In 1999, 61% more rain fell to the beginning of August and 43% more rain in the three months preceding August - the interval in which rainfall is most likely to act as a cue for the onset of breeding - than in 1998 (Fig. 8.16). August rainfall in 1998 was 36% below average, but was 25% above average in 1999. The asynchronous pattern of laying observed in 1998 (Fig. 8.16) may have been induced by spasmodic and low rainfall before the breeding season, leading to low insect abundance and poor conditions for breeding. Individuals may therefore have adopted a “wait-and-see” approach, in which they delayed breeding until conditions improved, in an attempt to coincide the nestling and fledgling stages with maximum insect abundance, thereby optimizing reproductive success (Lack 1954, Ford 1989). Variation in the degree to which individuals delayed breeding would produce the asynchronous pattern of laying observed. This “wait-and-see” strategy relies on a long breeding season. Further, a long breeding season enables individuals that nest early, despite poor conditions, to re-nest if their first attempt fails.

Consistent and above average rain during the winter of 1999 appeared to trigger a population-wide breeding response, leading to earlier and synchronised laying (Fig. 8.16). Multi-broodedness then permits individuals to increase their reproductive effort should the early signals prove correct in heralding favourable conditions. A long breeding season is necessary for - but does not guarantee - multiple broods. Thus, increased reproductive effort in White-browed Treecreepers results from a nexus of early nesting, multi-broodedness and a long breeding season, triggered by favourable climatic conditions. Reproductive success is ultimately optimized by spreading effort across several smaller nesting attempts in one season rather than concentrating a large effort into a single nesting attempt (Payne 1977).

There was considerable variation in the date of laying and expression of multi-broodedness in individual White-browed Treecreepers in response to environmental
Breeding biology

stimuli. This supports Daan & Tinbergen’s (1997) assessment that environmental effects may interact with variation in life history traits via ‘phenotypic plasticity’, in which a single genotype can produce a range of phenotypes that optimizes an individual’s reproductive effort. A caveat of the application of this hypothesis to this study is that I assume a causative relationship between rainfall, insect abundance and food availability (e.g. see Woinarski & Cullen 1984, Zack & Ligon 1985, Frith et al. 1997).

Figure 8.16. Laying date of the first clutch in relation to annual cumulative rainfall. Rainfall data (solid lines) relates to Meringur (34° 24' S, 141° 20' E – 7 km W of the study plot). Dashed line represents mean annual rainfall at Mildura (34° 23' S, 142° 08' E – approximately 70 km E of Yarrara) between 1946 and 1996 (CBOM, 2000). Annual rainfall at Meringur in 1998 (231.8 mm) was 22% below average and in 1999 (349.9 mm) was 18% above average.

Duration of nesting

The mean incubation period of the White-browed Treecreeper (18 days) was about three days longer than predicted by the regression of Yom-Tov (1987) for all Australian passerines (15.1 days) and by Rahn et al. (1975) for an altricial bird (15.2
days) of the same weight. The 26-day nestling period was nearly 10 days longer than predicted by Yom-Tov (1987) for the average Australian passerine, corrected for body weight. However, the duration of the incubation and nestling stages was similar to other Climacteridae (Table 8.14).

The lengthy incubation and nestling stages of Australian treecreepers is typical of hollow-nesting species, which generally have longer nesting cycles than open nesting species (Woinarski 1985). Noisy and conspicuous nestlings in open nests are particularly vulnerable to predators, which has probably favoured selection for accelerated nestling development and early fledging in open-nesting species. For example, the nestling period of small to medium-sized, open-nesting insectivores appears to be especially abbreviated in comparison with the 25-28 day nestling period in treecreepers: 11-12 d in the Rufous Whistler (Bridges 1994); 12-13 d in the Grey-headed Robin (Frith & Frith 2000); 14 d in the Leaden Flycatcher (Tremont & Ford 2000) and 14.3 d in the Willie Wagtail (Goodey & Lill 1993). The protection from predators afforded by nesting in hollows alleviates the necessity for nestlings to develop rapidly. This eases the provisioning burden on parents (see below), who may benefit through energy conservation. Furthermore, nestlings are more advanced when they fledge and therefore more likely to survive. These benefits are offset by the relative scarcity of suitable nest sites compared with the options available to open-nesting species. However, only 2-3% of Australian passerines nest in hollows (Saunders et al. 1982); consequently, it is not surprising that Yom-Tov’s (1987) equations underestimate development times of treecreepers.

**Diet**

The diversity of food items brought to the nest was greater than previously reported for the White-browed Treecreeper from stomach contents analyses (Lea & Gray 1936, Barker & Vestjens 1990). A high proportion of prey brought to the nest were soft-bodied, particularly adult moths, which presumably could not be detected in stomach contents analysis. When compared with the numerical dominance of ants in the diet of most adult treecreepers (Noske 1986; personal observation), this suggests moths were selectively fed to nestlings, even allowing for error due to a size-bias in prey identification.
Nestlings were often fed saltbush berries, particularly in the latter stages of nesting. Adults also consumed saltbush berries occasionally. Saltbush berries have the capacity to meet the daily water demands and 50% of the energy requirements of arid-zone honeyeaters (Prinzinger & Schleucher 1998). As treecreepers rely on their food intake to satisfy their water demands, saltbush berries were probably an important water source for nestlings and adults alike, particularly during the hot and dry summer months.

**Provisioning rates among Australian treecreepers**

The mean rate of total provisioning across all nest watches at White-browed Treecreeper nests was 8.1 visits per nest per hour, which appears to be typical of the smaller treecreepers [e.g. Red-browed Treecreeper: 9.6 visits/hr and White-throated Treecreeper: 8.7 visits/hr (Noske 1991)]. As the majority of nests contained two nestlings, provisioning by White-browed Treecreepers is at the lower limit of the 4 - 12 meals per nestling per hour considered standard for small passerines (Skutch 1976), and lower than recorded for many small Australian insectivores [e.g. White-fronted Chat (Major 1991), Purple-crowned Fairy-wren (Rowley & Russell 1993) and Willie Wagtail (Goodey & Lill 1993)].

Provisioning rates recorded for the Brown Treecreeper (17.9 visits/hr) (Noske 1991) and Rufous Treecreeper (21.8 visits/hr) (Luck 2001) are considerably higher than for the White-browed Treecreeper. These comparisons use the raw means of nest watches, which may be confounded by factors that affect provisioning rate, such as nestling age, number of nestlings and time of day. However, using the regression models in Luck (2001) for the Rufous Treecreeper and in Table 8.8a for the White-browed Treecreeper, a specific comparison can be made between these two species. For example, the provisioning rate at a nest containing two 23-day old nestlings at 9am on a day of 25˚ is predicted to be 25.7 visits/hr for the Rufous Treecreeper, more than double the predicted rate of only 10.5 visits/hr for the White-browed Treecreeper.

The higher provisioning rates of the Rufous Treecreeper and Brown Treecreeper may be related to the difference in body weight between these two species and the other treecreepers (Table 8.14). At fledging, juvenile Rufous Treecreepers and Brown
Breeding biology

Treecreepers are undoubtedly heavier than other treecreepers in Table 8.14 (Noske 1982a, Luck 2000). Given that the duration of the nestling period is equivalent in all species, nestlings of the heavier species will have higher energetic demands to reach fledging weight within the nestling period. This is achieved by higher overall provisioning to the nestlings in the larger species. Unfortunately, no data is available on the breeding behaviour of the Black-tailed Treecreeper, the largest of the treecreepers.

**Division of labour between the sexes**

The interaction between mating system, gender differences in morphology and the roles of the sexes in breeding and parental care can be summarized by two general syndromes. Polygamy, sexual dimorphism or dichromatism and a distinct division of labour during breeding comprises the first syndrome (Krebs & Davies 1993, Ryan 1997). The second syndrome is characterised by monogamy, monomorphism and biparental care (Wickler & Seibit 1977, Krebs & Davies 1993). The differences in the syndromes are distilled in the generalization that males of sexually dimorphic and polygamous species are less inclined to provide direct care at the nest than monomorphic and monogamous species (Verner & Willson 1969). Clearly, the syndromes represent opposite ends of a continuum and many exceptions have been well documented (e.g. Major 1991, Clarke & Clarke 1999).

How well does the White-browed Treecreeper fit the patterns described above? They are socially monogamous and sexually dichromatic. Complex courtship and precopulation displays suggest there is some competition between males for mates. Both males and females participated in nest construction but insufficient data was collected to ascertain skew in their respective contributions. However, incubating and brooding was the sole responsibility of the female. At nests without helpers, males and females provisioned the nestlings equally but a male-bias in provisioning was evident when helpers were present. Both sexes were observed to defend territory boundaries against conspecifics and the nest from intruders. Thus, whilst there was division of labour and substantial asymmetry in several aspects of breeding behaviour, both parents invested heavily in parental care.
Bi-parental care is consistent with the putatively monogamous mating system but at odds with their sexual dichromatism and complex mating displays. It may be that sexual dichromatism in treecreepers has not evolved in response to sexual selection but serves some other unidentified purpose. Alternatively, genetic studies may reveal the mating system is not strictly monogamous. Under these conditions, there may be competition between males for mating opportunities that promotes selection for dichromatism. In a departure from the syndromes discussed above, Krebs & Davies (1993) contend that monogamy may be forced on birds due, in part, to strong competition among males for mates. In this situation, monogamy and dichromatism would not necessarily represent components of different mating systems but would be complementary.

**Effect of breeding strategy on nesting behaviour**

If helpers provide functional assistance to the breeding pair, it is predicted that the nesting behaviour of breeders with helpers should differ from that of unassisted pairs such that the burden of parental care on the breeders is relaxed without reduction in nestling fitness. It is predicted that the impact of helpers on the nesting behaviour of the breeding pair will be accentuated during second broods, when the burden of simultaneous care for two broods can be carried by a larger number of adults.

Female attentiveness during incubation may be a function of the amount of time the female must spend foraging and therefore could be expected to be higher in cooperative groups, if helpers augment provisioning to incubating females (e.g. Noske 1991, Langen & Vehrencamp 1999). This expectation was not met in this study. Although helpers accounted for about 40% of the provisioning visits to incubating females and also made a substantial contribution to nest maintenance, food delivery to the incubating female was not higher at cooperative nests. Female attentiveness did not differ between groups and pairs, nor was there an interaction with brood number as might be expected if females with helpers were able to devote more time to incubation during the second brood. Thus, it may be that primary males have the most to gain from the helpers’ contribution during incubation. The possibility that primary males may be able to reduce their level of care during the
incubation stage when assisted by helpers, with implications for energy conservation, increased body condition and longevity, deserves further study and attention.

The amount of time females spent brooding was negatively correlated with nestling age. However, neither the overall time spent brooding, nor the rate of decrease as nestlings aged, was influenced by breeding strategy. This suggests helpers do not decrease the brooding workload for females, although females with helpers may be able to reduce their provisioning commitment whilst brooding. A slightly different picture emerges when second broods are examined in isolation. There was a trend for females in groups to spend more time brooding during second broods than females without helpers (Fig. 8.8), as expected if helpers absorb some of the provisioning workload. However, additional data are needed to confirm this trend because the differences between breeding strategies were not significant, although there was a high probability that biologically significant differences could have been overlooked (i.e. low power).

White-browed Treecreepers are similar to many other cooperatively breeding species, in that total provisioning to the nestlings is not dependent on breeding strategy, which in this case is a surrogate for group size (reviews in Brown 1987, Stacey & Koenig 1990, Emlen et al. 1991, Crick 1992). This implies that either helpers do not feed the nestlings, or parents with helpers reduce their own provisioning effort to compensate for the contribution of the helpers (Hatchwell 1999). The first option can be rejected from empirical observation leaving compensatory reductions in care by the parents as the logical explanation.

Total provisioning rate increased with nestling age, as the energetic requirements of the nestlings increased. The total calorific value of food delivered to the nestlings probably increased by more than the increase in provisioning rate because the average size of food items also increased as nestlings aged. Pairs showed a (non-significantly) steeper increase in provisioning rate with nestling age than groups, due to females in pairs switching their care from brooding to provisioning during the second week of the nestling stage. Females in groups also reduced their commitment to brooding but a complementary increase in provisioning was not detected. This suggests females with helpers could afford more time to forage for their own benefit in order to replenish body condition that may have deteriorated during the current nesting attempt or build up fat reserves for subsequent nesting attempts.
Total provisioning was consistently, but not significantly, higher to first broods than second broods in both pairs and groups. This is consistent with the hypothesis that the ability to provide for nestlings will be strained during second broods when there are more mouths to feed on the territory. One way in which helpers may increase the reproductive success of groups is by buffering this decrease in provisioning between first and second broods. Again, the evidence for this was indicative rather than significant, but as predicted, there was a smaller decrease in provisioning to second broods in groups than in pairs. This difference takes on greater merit when one considers that the re-nesting duration is significantly shorter in cooperative groups (Chapter 9) and thus fledglings from the first brood are less likely to have reached nutritional independence.

Taken in isolation, each of these factors does not suggest that helpers provide significant functional assistance to the breeding pair. However, the synergistic effects of slightly higher brooding attentiveness and total provisioning rate during second broods, together with a shorter re-nesting period between broods, may represent significant practical assistance. Importantly, these differences suggest mechanisms by which helpers may increase nestling fitness.

**Parental investment strategies**

Parental investment in breeding represents a trade-off between the benefits of increasing fitness for the current brood and the costs for future reproduction (Williams 1966a, Daan et al. 1996). Compensatory reductions in care reflect this trade-off because breeder fitness and future fecundity may be enhanced indirectly through energy savings or prolonged survival (Tidemann 1986, Crick 1992, Wright & Dingemanse 1999) or directly through accelerating the nesting cycle (Russell & Rowley 1988, Langen & Vehrencamp 1999). Hatchwell (1999) predicts that breeders in cooperative groups will show compensatory reductions in care when the level of breeder-only care is high, and conversely, when breeder-only care is low, breeders will maintain their level of care such that helper care will be additive. I suggest that a logical extension of this behavioural flexibility is that individuals should regulate their provisioning strategy in relation to nestling age and resource requirements within a nesting cycle.
To examine this proposition, the provisioning rate of pairs was used as an estimate of breeder-only care, a crude currency of the reproductive costs incurred by White-browed Treecreepers during the nestling stage. Breeder-only provisioning progressively increased each week, so reproductive costs were assumed to increase as nestlings developed and their energetic demands increased (Table 8.15). Thus, breeders in cooperative groups are predicted to maintain their level of care early in the nestling stage when costs are lower and hence, the helpers contribution will be additive. As nestlings age and reproductive costs increase, parents with helpers are able to reduce their relative costs through compensatory reductions, with negligible impacts on brood fitness.

The patterns observed in the week-by-week analysis of provisioning rates support Hatchwell’s (1999) predictions. However, the compensatory mechanism involved male and female White-browed Treecreepers employing different provisioning strategies as reproductive costs increased (Table 8.15). When reproductive costs were relatively low, parents with helpers maintained their provisioning effort (in comparison to parents without helpers) and therefore, the helpers’ contribution was additive. As costs associated with providing for the brood increased, parents with helpers reduced their provisioning effort relative to those without help, although absolute rates of provisioning increased in both strategies. However, females in cooperative groups showed a greater degree of compensatory reduction than males, who appeared to only partially compensate for the contribution of helpers. Thus, considerable plasticity in provisioning strategy was evident, with parents switching from non-compensatory to compensatory as the level of breeder-only care increased.

What advantage does such flexibility in provisioning strategy convey to the primary breeders? This question implies that additive care during the first week of the nestling stage produces significant fitness benefits to the brood. This may be related to the necessity for the female to spend 50% of her time brooding in the first week, irrespective of breeding strategy, which impairs her ability to provide food to the nestlings. Helpers appear to offset this shortfall - first week nestlings in cooperative nests are fed at a rate equivalent to second week nestlings in the absence of helpers - whilst the female maintains her brooding attentiveness. Thus, the fitness benefits of maintaining their level of investment are probably greater for parents than the relatively low costs of provisioning during the first week.
Table 8.15. Plasticity in the provisioning strategy of White-browed Treecreepers in cooperatively breeding groups.

<table>
<thead>
<tr>
<th>Relative reproductive costs (Total provisioning in pairs)</th>
<th>Week 1</th>
<th>Week 2</th>
<th>Week 3+</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low (5.2 visits/hr)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Moderate (7.4 visits/hr)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>High (11.0 visits/hr)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total provisioning</td>
<td>Groups &gt;&gt; Pairs</td>
<td>Groups = Pairs</td>
<td>Groups = Pairs</td>
</tr>
<tr>
<td>Primary male provisioning</td>
<td>Groups = Pairs</td>
<td>Groups = Pairs</td>
<td>Groups &lt; Pairs</td>
</tr>
<tr>
<td>Female provisioning</td>
<td>Groups = Pairs</td>
<td>Groups = Pairs</td>
<td>Groups &lt;&lt; Pairs</td>
</tr>
<tr>
<td>Helpers additive?</td>
<td>Helpers additive</td>
<td>Helpers not additive</td>
<td>Helpers not additive</td>
</tr>
<tr>
<td>Parental compensation?</td>
<td>No parental compensation</td>
<td>Female partially compensates</td>
<td>Male doesn’t compensate</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Female compensates</td>
<td>Male partially compensates</td>
</tr>
</tbody>
</table>

There was no evidence that nestling starvation was less frequent in groups than pairs (see Chapter 10), which indicates that the additional care of the helpers during the first week may not be necessary for nestling survival. Nonetheless, there may be fitness benefits to the brood even though starvation rates are not affected. For example, the growth rate of nestlings in cooperative nests may be faster during this early period resulting in larger chicks that have enhanced post-fledging survival and recruitment to the adult population (Garnett 1981, Magrath 1991, Mumme 1992, Hatchwell & Russell 1996). Similarly, chicks that receive more food at this early stage may fledge earlier (Caffrey 2000).

This does not resolve why parents change their investment strategy as the nestlings develop, which probably relates more to the fitness of the parents than the brood. When the level of care is high, parents may achieve significant energetic savings through a modest reduction in provisioning trips. Parents may then obtain fitness benefits by diverting these energetic savings into either a subsequent brood or replenishing their own energy reserves. No detrimental effect on the success or productivity of the current brood is correlated with this reduction in care because provisioning by helpers supplements the nutritional requirements of the nestlings in cooperative groups. The parents’ provisioning strategy, particularly that of females,
represents a clear shift in the trade-off between reproductive costs associated with the current brood and future reproduction and survival.

There was much variation in many of the nesting behaviours within and between nest watches at the same nest. This emphasizes the requirement for multiple nest watches of considerable duration at each nest to collect reliable data. Breeding units were observed for an average of 4.3 nest watches during the nestling stage in this study but the number of nest watches per breeding unit ranged from one to seven, introducing the possibility of sampling bias error in the results. However, there was no significant difference in the mean number of nest watches per breeding unit between groups and pairs.

**Variation in helper provisioning**

Considerable variation in the helpers’ proportional contribution to nestling provisioning was observed at White-browed Treecreeper nests (Fig. 8.16). The amount of care provided by helpers is partially determined by the needs of the breeders and the costs to the helper (Cockburn 1998, Heinsohn & Legge 1999) and will vary within and between species (Brown 1978, Emlen 1982b, Cockburn 1998). A major component of the breeders’ needs is determined by brood size: increased resource requirements of larger broods may solicit an increased provisioning effort from all group members, including helpers (e.g. Tidemann 1986, Heinsohn 1995, Luck 2000) or prompt breeders to recruit additional helpers (Reyer & Westerterp 1985). Although a significant increase in the total provisioning rate from single nestling broods to broods with two nestlings was not detected in this study, it is possible that subtle variation in breeder demand related to brood size accounts for some the variation in the proportional contribution of helpers. However, a significant increase in total provisioning to broods of three was apparent. The increase in the proportional provisioning contribution (and absolute provisioning rate) of the helper in T6 in 1999 (Fig. 8.16) may have been due to the large brood of three nestlings, and consequently, a greater demand for assistance to feed the brood.

Costs of nestling provisioning to the helper will depend on the additional energy expenditure and exposure to predators required to gather food for the brood, which may reduce body condition or survival (Clutton-Brock 1991, Crick 1992). These
Breeding biology

costs will be less for helpers that forage more efficiently, which, in turn, may be related to age and experience (Brown 1987, Heinsohn et al. 1988, Langen 1996). Thus, some of the between-group variation in helper contributions may be attributable to differences in the age of helpers and hence foraging efficiency and costs incurred whilst helping. However, there was no evidence to support this hypothesis in White-browed Treecreepers. The provisioning rates of several first-year helpers (e.g. T1 and T11) were equivalent to the primary male or more experienced helpers at other nests (Fig. 8.16a). Thus, first-year birds were capable of provisioning as effectively as older individuals, suggesting there were not age-related differences in foraging efficiency.

A third source of variation in helpers’ provisioning effort may arise from the relatedness of helpers to the brood. Enhanced indirect fitness (kin selection) is now widely accepted as one of the primary benefits of helping in many species (Brown 1987, Emlen 1997, Komdeur & Hatchwell 1999 but see Jamieson 1989, Wright et al. 1999). Kin selection theory predicts that individuals will preferentially provision more closely related nestlings when there is a choice of potential recipient broods (e.g. Curry 1988, Emlen & Wrege 1988, Komdeur 1994a) and/or reduce provisioning rate or likelihood of provisioning to nestlings with lower relatedness (e.g. Clarke 1984, Mumme 1992, Komdeur 1994a: but see Rabenold 1985, Dunn et al. 1995, Magrath & Whittingham 1997). Thus, a positive correlation between provisioning rate and relatedness is expected. However, Cockburn (1998) suggests that males are more likely to help for direct fitness benefits, in which case provisioning patterns would be less affected by kin recognition and selection.

Provisioning by helpers in the Yarrara population of White-browed Treecreepers followed the expectations of kin selection theory with higher provisioning (relative to the parents) shown by helpers feeding more closely related kin. Unfortunately, in the absence of genetic data or long-term genealogies, the assessment was diminished by assumptions of relatedness in several group-years. Relatedness could only be assigned confidently for those helpers that joined groups during the study (i.e. T1, T11 and T12). Amongst these three groups, the lowest proportional contribution to provisioning (0%) was by the helper with the lowest relatedness (half-sib at T12). In contrast, the two helpers with ‘confirmed’ full-sib relationships (T1 and T11) fed the nestlings at equivalent rates to the parents (Fig. 8.16). The relationship between
provisioning and kinship was variable amongst those groups for which relatedness could not be confirmed (Fig. 8.16). The helper and primary male in T3 fed the nestlings at similar rates in both years, consistent with the assumed full-sib relationship. Helper investment in T2 was confounded by variation in group size between seasons, but the proportional contribution in 1999, when the solitary helper was assumed to be only a quarter-sib, was low relative to other groups. The contribution of the helper in T6 (assumed full-sib in both years) varied from very low to high. Assuming the contribution of helpers increases fledgling productivity (Chapter 9), indirect fitness benefits may play a significant role in maintaining helping behaviour in White-browed Treecreepers (see Chapter 10). Thus, the degree of relatedness between the helper and the brood may be important in explaining variation in provisioning rates between groups.

Finally, helper quality may vary as a function of individual variability, independent of age, kinship or parental inducements. That is, there may be a tendency for helpers to fix their level of alloparental behaviour according to their ability (Heinsohn & Legge 1999). This may be manifest in variation in the extent of care or variation in types of help provided. For example, in one group (T12), the only tangible assistance furnished by the yearling male was as a ‘shepherd’ for recently fledged juveniles, though his contribution to nest and/or territorial defence was not quantified. Alloparental care by philopatric yearlings was similarly confined to the post-fledging period in the Gray Jay *Perisoreus canadensis*, although as a species-wide trait rather than individual variants (Waite & Strickland 1997).

**Is helping behaviour adaptive?**

One of the most challenging issues for researchers of cooperative breeding species is presented by the ‘unselected’ hypothesis for the evolution and maintenance of helping behaviour by non-breeding auxiliaries (Jamieson & Craig 1987, Jamieson 1989, 1991, Craig 1991 cf. Ligon & Stacey 1989, 1991, Emlen et al. 1991, White et al. 1991). This hypothesis argues that the provisioning of nestlings by auxiliaries, that is, ‘helping behaviour’, is the unselected by-product of the universal stimulus-response mechanism, in which all altricial birds respond to the begging calls and gaping mouths of nestlings by feeding them. In other words, helping behaviour *per se* is not an adaptive response that has been modified by processes of natural
selection, but is an unselected outcome of selection for parental care that arises as a consequence of non-dispersing birds gaining access to begging nestlings (Jameison 1991). To refute the unselected hypothesis, one must demonstrate that helping behaviour is a flexible response that varies according to need (Heinsohn & Legge 1999) or that helping behaviour has been modified in ways that enhance the fitness of helpers (Emlen et al. 1991).

There are several lines of evidence to suggest that helping in White-browed Treecreepers is not merely misdirected parental care but is selectively ‘fine-tuned’ to increase the fitness of the helper. First, not all non-breeding White-browed Treecreepers that were resident in cooperative territories provisioned nestlings. This refers not only to ‘floating’ females, which may have been prevented from provisioning by extraneous inhibiting factors (e.g. female – female antagonism) but also to one helper (T12) who frequently visited the nest, and therefore was repeatedly exposed to the begging stimulus but was never observed provisioning. Second, there were many instances of helpers provisioning incubating females and bringing nest material to the nest, which represent significant modifications from the ‘hard-wired’ response to the stimulus of begging chicks.

Third, of the 1640 observed provisioning visits, not one instance of cross-territorial feeding of nestlings was detected, despite the clustering of nests in adjacent territories (Fig. 6.5). If helpers were randomly feeding any nestling they encountered, the rate of cross-territorial feeding would have been much higher. It is unlikely that territorial defence prevented cross-territorial feeding because several individuals were observed foraging on or near nest trees in adjacent territories, indicating there were opportunities for stimulus-response provisioning of unrelated nestlings. Cross-territorial feeding is common in other Australian treecreepers (e.g. Noske 1991, Luck 2000) but has been interpreted as a mechanism by which helpers assess habitat quality and breeding vacancies in nearby territories (Luck 2000), similar to the dispersing forays of non-breeding Acorn Woodpeckers Melanerpes formicivorus (Mumme et al. 1990). Finally, the variation in helper provisioning described in the preceding section illustrates the flexibility in helpers’ response to the needs of the brood, and provides weak evidence for the preferential provisioning of close kin.

Thus, I suggest that helping behaviour in White-browed Treecreepers is facultative and adaptive. However, I have only compared the outcome of the selection process
(i.e. current expression of helping behaviour) to that expected in the absence of selection (i.e. the instinctive stimulus-response feeding mechanism). In the next chapters, I shall examine the current utility of helping behaviour in terms of its impact on the fitness of both breeders and helpers and explore several mechanistic hypotheses that have been presented to account for the current expression of helping behaviour in the White-browed Treecreeper.

**Conclusions**

As is characteristic of many Australian passerines that inhabit regions with variable climates, the White-browed Treecreeper regulates its reproductive effort by variation in the number of clutches laid within a breeding season rather than clutch size, which is small and invariant. Rainfall may be the proximate environmental cue that stimulates breeding. The incubation (~18 days) and nestling (~26 days) durations are longer than expected for an altricial passerine, due largely to the relative protection from predators provided by nesting in hollows. Both parents participate in caring for the brood, although incubation and brooding is the sole responsibility of the female. The rate of provisioning nestlings increases with nestling age, but is relatively low compared to other small and medium insectivores. Males and females provision the nestlings equally in pairs, but the males make a larger proportional contribution in cooperative groups. Helpers contribute to all facets of the nesting effort, save incubation and brooding.

Taken over the entire nestling stage, the overall rate of nestling provisioning was not influenced by breeding strategy (i.e. group size). Thus, breeders in cooperative groups showed compensatory reductions in provisioning investment, which may impart fitness benefits to the breeders through enhanced future fecundity (including expeditious re-nesting) or survival. However, the investment strategy of breeders in cooperative groups showed considerable plasticity within a nesting cycle, as a function of the costs of reproduction (as ascertained from breeders without helpers) versus the fitness benefits of parental care. Variation in the helpers provisioning effort appeared to be associated with relatedness to the brood and breeder need. Thus, increases in indirect fitness and parental inducements may be important factors in determining the level of helper investment.
Chapter 9

Effect of helpers on reproductive success of the White-browed Treecreeper
9.1 Introduction

A primary aim of this research is to document the breeding biology of the White-browed Treecreeper (Chapters 6-8) and to provide the first quantitative estimates of the reproductive success of a population of this species. This is the objective of this chapter. An assessment of the effect of helpers on the reproductive success of this cooperatively breeding species is intrinsic to this process.

The most conspicuous way in which helpers may increase productivity in a given nesting attempt is by feeding the incubating female, nestlings and fledglings. In some species, this may increase the amount of food received by nestlings, thereby reducing the incidence of starvation (Emlen 1990, Reyer 1990, Boland et al. 1997) or increasing their growth rate (Mumme 1992). Alternatively, compensatory reductions in provisioning by the parents may result in no net increase in food delivery despite the assistance of helpers (Tidemann 1986, Hatchwell 1999, Langen & Vehrencamp 1999; and see Chapter 8). However, parents may benefit from significant energetic savings and hence increased survivorship and future reproductive success (Crick 1992). Helpers may also increase nesting success through participation in predator vigilance and repulsion, thereby reducing nest predation (Rabenold 1990, Woolfenden & Fitzpatrick 1990, Innes & Johnston 1996, Boland 1998). Further, helpers may improve territory defence or acquisition, enabling maintenance of larger or better quality territories (Brown 1978, Emlen 1978, Langen & Vehrencamp 1998). In multi-brooded species, helpers may assume nutritional responsibility for nestlings or fledglings, thereby releasing the parents (particularly the breeding female) to re-nest in a shorter time, and often with greater success than would be possible without helpers (Russell & Rowley 1988, Ligon & Ligon 1990a, Langen & Vehrencamp 1999).

The effect of helpers is most commonly assessed by correlational analysis of productivity versus group size. In some cases, increases in productivity with group size are pronounced (Rowley & Russell 1988, Rabenold 1990, Emlen & Wrege 1991), others show subtle but consistent increases (Curry & Grant 1990, Woolfenden & Fitzpatrick 1990), whilst several studies have not been able to confidently assign productivity gains to increasing group size (Ligon & Ligon 1990a, Marzluff & Balda 1990, Zahavi 1990). Of more concern is the increasing awareness of the potential for circularity between group size and productivity (Nias 1986, Magrath & Yezerinac...
Reproductive success

1997, Cockburn 1998, Legge 2000). The influence of factors that potentially confound the relationship between group size and productivity, such as territory size or parental experience, limits the value of correlational studies that do not account for them.

Experimental studies that remove helpers from groups in a natural setting, thereby theoretically controlling for confounding variables, tend to find lower reproductive success in experimentally diminished groups suggesting a positive effect of helpers (Brown et al. 1982, Mumme 1992, Komdeur 1994b), although this conclusion is not universal (Leonard et al. 1989). However, removal experiments may themselves be confounded by group size effects rather than testing for an effect of help *per se* (Cockburn 1998). A third approach utilizes natural variation in either the amount of help provided to the brood in groups of the same size (Davies 1990, Komdeur 1994b, Macgrath & Yezerinac 1997) or group size at the same territory across years (Walters 1990, Caffrey 2000, Legge 2000). Once again, the results are ambiguous; only Davies (1990) and Komdeur (1994) concluded that helpers increase the reproductive success of the breeding pair.

In this study, experimental manipulation of group size was precluded by the conservation status of the White-browed Treecreeper, field work was not conducted for long enough to encounter year-to-year variation in group size in a large number of territories, and non-helping non-breeding resident males were not detected. Therefore, a comparative approach contrasting cooperative groups with unassisted pairs was the only option available to assess the effect of helpers on reproductive success and productivity. This approach involved four steps:

1. Quantify reproductive success and productivity per breeding unit and compare between cooperative groups and unassisted pairs.

2. Deconstruct reproductive productivity into components and compare between breeding strategies.

3. Identify mechanisms by which helpers may increase productivity or components thereof.
4. Examine the influence of extrinsic factors on reproductive success and productivity, and hence assess their potential to confound the relationship between breeding strategy and productivity.

The study was fortuitously conducted over two years of contrasting rainfall, which enabled variation in reproductive success to be compared between a ‘good’ and ‘poor’ year. The interaction between climate and any effect of helpers may provide insights into the environmental circumstances under which selection for cooperative breeding may have occurred in White-browed Treecreepers.

9.2 Methods

Field methods

The reproductive success of all breeding units encountered within the study plot (Fig. 6.1), and whose territories overlapped the core area, was monitored in 1998 and 1999. Detection and monitoring of nests was described in Chapters 6-8. A breeding attempt was considered successful if at least one nestling fledged from the nest and was consistently observed outside the nest for two weeks post-fledging. Where more than one nestling was present up to the anticipated fledging date, the number of fledglings was confirmed by colour-banding and monitoring of family groups, simultaneous sightings of fledglings, or independent sightings of sexually dichromatic fledglings within the natal territory. Successful nests were subsequently checked for second broods, and unsuccessful breeding units were monitored afresh as they often re-nested in a different hollow.

Reproductive success

Reproductive success was estimated at the population (all nests monitored) and sub-population (within breeding strategies) level as the proportion of breeding units that successfully reared at least one fledgling. Reproductive success was also calculated using the Mayfield method, to avoid over-estimates of nesting success that may otherwise result when nests are detected at various stages of development (Mayfield
Reproductive success

Mayfield reproductive success is derived from a daily rate of nest mortality, which is calculated by dividing the number of nests predated, abandoned or otherwise destroyed by the number of nest-days a group of nests was under observation, a period termed *exposure* (Mayfield 1975). Thus, the daily survival probability for a given set of nests is one minus the daily mortality rate.

The probability of a nest surviving a particular stage of nesting is determined by raising the daily survival probability to the power of the number of days in that stage. Survival probabilities were calculated separately for the incubation, nestling and total nesting periods. Incubation and nestling durations were assumed to be 18 and 25 days, respectively (Chapter 8). Failed nests were assigned an exposure of 50% of the interval between nest visits, except when the interval exceeded 7 days whereupon an exposure of 40% of the interval was used (Miller & Johnson 1978).

**Productivity**

Indices of productivity measure the number of fledglings produced per breeding attempt and thus consolidate clutch / brood size, brood reduction (due to infertile eggs, starvation, sibling rivalry or accidents) and overall success. Whereas measures of reproductive success generally refer to a population of breeding units, productivity can be calculated and compared between individual breeding units. Breeding units that held a territory but (apparently) did not attempt to breed, or prepared a nest but failed to lay a clutch, were excluded from productivity calculations. Four measures of productivity were determined per breeding unit:

1. Average number of fledglings per nesting attempt per season (Flg/N).
2. Average number of fledglings per successful nest per season (Flg/SN).
3. Total number of fledglings per season, summed across multiple broods (Flg/S).
4. Total number of fledglings per adult (parents and helpers) per season (Flg/Ad/S).
Components of productivity

The extent of investment in reproduction and the success of the respective nesting stages determine overall fledgling productivity. Deconstructing overall productivity into its component parts may elucidate the mechanisms by which particular breeding units produce more fledglings. Several of these components measure the proportional success of transition from one stage of nesting to the next. The number of breeding units that contributed to each of these indices varied because nests were located at various stages of development. The components of productivity calculated were:

1. Clutch size (# eggs)
2. Hatching success (%) – ratio of hatchlings to eggs laid per nest.¹
3. Nestling success (%) – ratio of fledglings to hatchlings per nest.¹
4. Fledgling success (%) – ratio of fledglings to eggs laid per nest.
5. Number of clutches – total number of clutches laid per season, including replacement clutches after unsuccessful nest attempts.
6. Number of broods attempted – number of clutches laid per season, excluding replacement clutches after unsuccessful nest attempts.
7. Renesting period (days) – interval between fledging and laying date of the next brood.

Potential correlates of reproductive success

Breeding strategy

Group size of cooperative groups varied little, consisting of a breeding pair and one male helper in 14 of 15 group-years (Chapter 6). Thus, there was little variation in group size that could not be explained by breeding strategy alone. Therefore, breeding strategy was deemed a surrogate for group size and treated as a dichotomous variable (i.e. group versus pair) to assess the effect of helpers.

¹ If clutch size was unknown, two eggs were assumed. If it could not be determined whether a depleted brood suffered mortality during the incubation or nestling stage, the loss was partitioned equally between the stages.
Parental experience

Parental experience, defined as previous attempts to breed, could not be unequivocally determined for each individual because the breeding history of individuals could only be traced for two years, and it was possible (but unlikely) that putatively novice breeders in 1999 may have had undetected failed nests early in the 1998 season. However, if ‘parental experience’ is redefined to equate to 1998 breeding success, all members of breeding units in 1999 could be categorized accurately. Therefore, ‘parental experience’ or previous breeding success was only considered as a correlate of reproductive success for 1999 data. This a reasonable compromise in lieu of better data but individuals that may have bred successfully prior to 1998 may be incorrectly classified as previously ‘unsuccessful’. Individuals were categorized as either previously successful or not previously successful. For females, previous success was defined as fledging at least one offspring in 1998. For males, previous success was defined as attending a successful nest in 1998, either as a parent or helper.

Territory size

Territory size was considered an analogue of territory quality, on the basis that larger territories provide greater access to resources (Ligon & Ligon 1990a). Territory size for 11 breeding units was estimated using RANGES V software (Kenward & Hodder 1996). Of the indices calculated, minimum convex polygons using 95% of available position fixes per breeding unit (MCP95%) were the most reliable estimate of territory size (Chapter 6). To correct for the sampling bias between breeding units, territory size (MCP95%) was regressed against the number of position fixes per breeding unit, and the residuals (MCP95%res) used as a corrected measure of territory size (Chapter 6).

Foraging resources

Treecreepers appeared to use tree dominance (density of tree basal area) as a proximate environmental cue for habitat selection during foraging (Chapter 4). Therefore, I used tree dominance to assess variation among territories in the amount of available foraging substrate. Data were collected by the wandering quarter method.
for estimating tree density (Catana 1963). This is an adaptation of the point-centered quarter method (Chapter 2), whereby a starting point is randomly chosen and the nearest tree within a pre-determined 90° angle of inclusion is taken as the starting point for measurements. Successive tree-to-tree distances are measured to the closest tree in the 90° inclusion zone, which is repeatedly re-orientated to the original compass points after each distance measure (Fig. 9.1). Twenty-five trees were included in each wandering quarter transect. Tree species and diameter at breast height (DBH) were recorded for each tree encountered to enable tree dominance to be calculated.

The study plot was stratified into 25 4-ha sub-units and the starting point of one wandering-quarter transect was randomly located within each sub-unit. The direction of the transect (NE, SE, SW or NW) was selected to maximize the likelihood of remaining within the designated sub-unit. The map of White-browed Treecreeper territories (Fig. 6.5) was superimposed over the location of the wandering quarter transects and each transect allocated to a single territory. This method enabled a larger proportion of each White-browed Treecreeper territory to be sampled than would have been possible with equal effort using plot-based methods but each transect was small enough to be constrained within a single territory.

In 21 of the 25 wandering-quarter transects, the spatial distribution of trees (all species combined, including dead standing trees) was random (following Catana 1963). Therefore, density was estimated, without correction for aggregation, as $A / (d_x)^2$ where $A$ is the unit area (100 m$^2$) and $d_x$ is the mean of the 25 tree-to-tree distances per transect. Tree dominance per unit area (cm$^2$ / 100 m$^2$) was derived as the product of tree density and mean tree basal area, where basal area = $\pi \times (DBH / 2)^2$. Values from multiple transects within the same territory were averaged to produce a single estimate of tree dominance per territory.
Figure 9.1. Operation of the wandering-quarter method (adapted from Catana 1963).

Rainfall

Rainfall data was provided by staff at the Meringur post-office (34° 24' S, 141° 20' E), 7 km W of the study plot, which is an official recording station for the Commonwealth Bureau of Meteorology.

Laying date

Laying date (see Chapter 8) was examined as a correlate of the number of young fledged per season, scaled to the median laying date within each season to remove the significant influence of year-to-year variation (Chapter 8).

Data analysis

Mayfield reproductive success

The Mayfield method produces a single estimate of reproductive success for the nests under observation, lacking any estimate of population variance. Johnson (1979) presents a method for deriving variance estimates of the mortality rate, enabling comparisons between nesting stages or sub-populations. Johnson’s technique
involves calculating the ratio of the differences of the daily mortality rates to their standard errors and compares this to the normal deviate (Geering and French 1998). Using this method, daily mortality rates during the incubation stage were compared to those of the nestling period, firstly across all nests and then separately for nests of pairs and groups, and nests in 1998 and 1999. Daily mortality rates during the incubation and nestling stages and for the total nesting period were then compared between years and between breeding strategies using the same technique.

**Effect of helpers**

For all comparisons between breeding strategies, ‘breeding unit-year’ was used as the unit of replication to avoid pseudo-replication stemming from breeding units that might contribute two non-independent data points per season from discrete nesting attempts. Thus, for those response variables that relate to each nesting attempt (e.g. Flg/N, Flg/SN, clutch size, hatching success, nestling success), the values from multiple nesting attempts were averaged so that each breeding unit contributed only one data point per season. Fledgling success was calculated as the total number of young fledged to the total number of eggs laid per season. Data from 1998 and 1999 were not pooled as 6 of the 11 breeding units changed breeding strategy and/or group membership in that interval. However, interactions between breeding strategy and year were examined and analyses conducted independently for each year where appropriate.

Chi-square tests were used to compare frequencies (i.e. reproductive success) between strategies. The effect of helpers on continuous response variables (i.e. productivity indices) was examined by including breeding strategy as a fixed factor in standard parametric tests (ANOVA, ANCOVA, t-tests) where the assumptions of normality and homogeneous variance were met. Non-parametric tests (Mann-Whitney U-test, Wilcoxon sign test) were used to compare variables that did not meet parametric assumptions after appropriate transformations were applied, provided the response populations were drawn from similar distributions.
Productivity modelling

Multi-variate regression techniques were used to model the effects of selected environmental and demographic factors on the number of fledglings per breeding unit per season (Flg/S) and the number of fledglings per adult per season (Flg/Ad/S). The aim was to partition the variation in productivity between the effect of helpers (i.e. breeding strategy) and the influence of season, territory size (MCP95%res), foraging resources (tree dominance) and laying date (scaled to median date per season). A sub-set of 20 group-years from 10 territories was available for this analysis.

As each breeding unit was represented twice in the data (1998 and 1999), there was potential for dependency within breeding units between seasons (Legge 2000). To overcome this using modelling procedures, Cockburn (1998) recommends including ‘breeding unit’ as a random variable in a mixed model to control for parental ability. Thus, I constructed a model that included breeding unit as a random effect, breeding strategy and season as fixed factors and laying date, territory size and tree dominance as co-variates (Bennington & Thayne 1994). Following the modelling strategy of Legge (2000), I used the residual maximum likelihood (REML) procedure in GenStat 5 (VSN 2000) to assess the change in deviance when the random effect of breeding unit was excluded from the full linear mixed model. For both Flg/S and Flg/Ad/S, omitting breeding unit from the full model resulted in a non-significant change in deviance. Thus, there was no evidence for intra-group dependency between seasons, and breeding unit was dropped from further analyses. The modelling approach implemented for Flg/S and Flg/Ad/S differed from this point forward.

The effect of the predictor variables on the number of fledglings per season was examined using ordinal logistic regression (Hosmer & Lemeshow 2000) because the number of fledglings corresponds to an ordinal categorical response, ranging from 0 to 4 fledglings. The significance of predictor variables (and relevant interactions) was assessed by examining the change in deviance when the variable of interest was removed from the full model (i.e. backwards elimination). Using a logit link function, the output of ordinal regression describes the probability of the response variable falling in each ordinal category, given the significant predictor variables (Legge 2000).
Reproductive success

A generalized linear model was constructed, using the REML procedure in GenStat 5, to examine the influence of the predictor variables on the number of fledglings per adult per season. The significance of the predictor variables was assessed by the change in deviance when individual terms were dropped from the full model.

Laying date

Variation in laying date between breeding strategies was examined using a linear mixed model that also included breeding unit as the random effect. The influence of laying date on the productivity of individual nest attempts (Flg/N) was examined further by including laying date as the co-variate in an ordinal regression, with breeding strategy as the main effect.

9.3 Results

Reproductive success

Observed reproductive success

A total of 41 nesting attempts in 26 breeding unit-years were monitored during the study. This comprised fourteen nesting attempts by 11 breeding units in 1998, and 27 attempts by 15 breeding units in 1999. Overall, 61% of observed nesting attempts produced at least one fledgling, with no significant difference in reproductive success of nesting attempts between seasons (Yates $\chi^2 < 0.01, P = 0.94$). Groups appeared to have higher nesting success, pooled across both seasons, but the discrepancy was not significant (Yates $\chi^2 = 2.45, P = 0.12$) (Fig. 9.2a). Similarly, whilst the difference between strategies in success per nest attempt was minimal in 1998 (Fisher’s 2-tail exact test, $P = 1.0$), a trend was evident for groups to experience higher nesting success in 1999 (Fisher’s 2-tail exact test, $P = 0.11$; Fig. 9.2a). Offspring fledged from 18 of the 26 (69%) first nests of the season, which was higher than the observed reproductive success of 47% for replacement or second brood clutches (7 from 15 nests), although the frequency distribution of successful nests between first and second clutches was not significantly different (Yates $\chi^2 = 1.20, P = 0.274$).
Reproductive success

At least one chick per season fledged from 81% of all breeding units observed. Variation between seasons was negligible, with 100% of groups and 76.5% of pairs producing at least one fledgling per season (Fisher’s 2-tail exact test, \( P = 0.263 \)) (Fig. 9.2b).

**Figure 9.2.** Observed reproductive success of White-browed Treecreeper breeding units at Yarrara, 1998-99. The percentage of (a) successful (fledged ≥1 offspring) nesting attempts and (b) successful breeding seasons is shown for pairs, groups and all breeding units combined. The number of (a) nests and (b) breeding units per category is indicated above each bar.

**Mayfield reproductive success**

The Mayfield estimate of the probability of nest survival through the incubation stage was 85.7%. The daily probability of mortality was higher during the nestling stage; consequently, the probability of nest survival from hatching to fledging was only 65.5%. The Mayfield survival probability over the entire nesting period – from laying to fledging – was 55.7%. This trend for higher daily probabilities of mortality during the nestling stage, and therefore lower survival of nests than during the incubation stage, was evident across all sub-sets of nests examined (Fig. 9.3). In fact, for nests of pairs and all nests in 1999, daily probability of mortality during the nestling stage was more than twice that experienced during incubation. However, the extent of variation in daily mortality probability was such that no significant differences between the incubation and nestling stages were found (using Johnson’s (1979) normal deviate technique) in pairwise comparisons of the nests of pairs or groups, nor for all nests in 1998 or 1999.
The probability of survival during the incubation stage was only 6.6% lower for pairs than groups and was relatively stable across both seasons (Fig. 9.3). However, the mean probability of daily mortality during the nestling stage was four times higher for pairs (0.025 ± 0.008) than groups (0.006 ± 0.004), a significant difference following Johnson’s technique (z = 2.18, P = 0.030). This translates into a 33% better chance that nests of groups will survive from hatching to fledging (Fig. 9.3). The daily probability of nestling mortality increased from 0.012 ± 0.007 in 1998 to 0.019 ± 0.006 in 1999 with a commensurate decrease in the probability of survival (Fig. 9.3). However, this increase was not statistically significant (z = 0.73, P = 0.53).

When restricted to the first nest of the season, the daily probability of nest mortality during the nestling stage was 0.017 ± 0.01 (47% survival) in 1998, decreasing to 0.007 ± 0.005 (74% survival) in 1999 (z = 0.94, P = 0.35). By comparison, the probability of survival through the nestling stage for second nests in 1999 was only 38%, which was significantly less than for first nests of the same season (z = 2.1, P = 0.032).

Over the entire nesting period, the daily probability of mortality was significantly higher for pairs (0.019 ± 0.005) than for groups (0.006 ± 0.004) (z = 2.04, P = 0.042). Consequently, the probability of fledging at least one chick per nest was 77% for groups, compared to 44% for pairs, over both years combined (Fig. 9.3).
Figure 9.3. Mayfield estimates of probability of nest survival (± 95% CI) during the incubation and nestling stages and for the entire nesting period for pairs and groups, and for all nests in 1998 and 1999, and in both years combined. (n = 41 nests)

Productivity

Seasonal variation in productivity

An average of one fledgling was produced per nesting attempt (Table 9.1). A mean of 1.64 offspring fledged per successful nest (i.e. excluding those nests in which the entire clutch or brood was lost) (Table 9.1). The mean seasonal productivity of 1.58 fledglings per breeding unit (Table 9.1) was higher than the fledgling productivity per nest because several units raised two broods in 1999. Two fledglings per season was the most common outcome per breeding unit, although four fledglings were produced by a single breeding unit on two occasions (Fig. 9.4). In contrast, seasonal fledgling productivity was zero in four of the 26 breeding unit-years (Fig. 9.4). On a per capita basis, 0.65 fledglings were produced per adult - including helpers - attending the nest per season (Table 9.1).

<table>
<thead>
<tr>
<th></th>
<th>Mean (± se)</th>
<th>95% CI</th>
<th>Min - Max</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fledglings / nest</td>
<td>1.0 ± 0.14</td>
<td>0.71 – 1.29</td>
<td>0 - 3</td>
<td>41</td>
</tr>
<tr>
<td>Flg / successful nest</td>
<td>1.64 ± 0.11</td>
<td>1.41 – 1.87</td>
<td>1 - 3</td>
<td>25</td>
</tr>
<tr>
<td>Fledglings / season</td>
<td>1.58 ± 0.21</td>
<td>1.15 – 2.01</td>
<td>0 - 4</td>
<td>26</td>
</tr>
<tr>
<td>Flg / adult / season</td>
<td>0.65 ± 0.08</td>
<td>0.48 – 0.81</td>
<td>0 – 1.33</td>
<td>26</td>
</tr>
</tbody>
</table>

However, these results relate only to breeding units that laid a clutch, disregarding units that may have held a territory but either did not attempt to breed or in which a nest was built but no eggs laid. If four units that did not breed in 1998 but were detected breeding in 1999 (Fig. 9.4) and another unit that was present on the study plot but did not lay a clutch in either season (T33) were included in the analysis, the mean number of fledglings per territory per season falls to 1.28 ± 0.20. Further, per capita productivity decreases to 0.53 ± 0.08 fledglings per season.

The total number of young fledged in the study plot more than doubled from 1998 to 1999 (Fig. 9.5). This was a function of an increase in the number of units breeding (+36%) and an increase in mean productivity of 0.685 fledglings per breeding unit (+58%) in 1999, though the latter was not statistically significant ($t_{24} = 1.49$, $P = 0.15$).

A significant increase in seasonal productivity (Flg/S) was evident in a matched-pair comparison for those units that attempted to breed in both seasons (Wilcoxon signed rank test: $z = -2.13$, $P = 0.033$, $n = 11$; Fig. 9.4). However, three of these breeding units gained helpers in 1999 (Fig. 9.4; Chapter 6) which may obscure seasonal differences in productivity.

A comparison of seasonal productivity (Flg/S) within breeding strategies did not reveal a difference between seasons, but as sample sizes were small, the results are predisposed to Type II errors (Mann-Whitney U-tests: Pairs - $z = 0.57$, $P = 0.57$, $n = 8, 9$; Groups - $z = 1.61$, $P = 0.11$, $n = 3, 6$).
Figure 9.4. Number of young fledged within each territory in 1998 (top) and 1999 (below). Territories in which no attempt to breed was detected or in which pairs were not established are denoted by an asterisk. Cooperatively breeding units are indicated by filled bars and pairs by open bars.
Reproductive success

**Figure 9.5.** Fledgling productivity within the Yarrara study plot, 1998 – 1999. Error bars designate ± 1 s.e.

**Relationship between breeding strategy and productivity**

For both seasons combined, there was a non-significant trend for groups to have greater productivity per nest attempt (Table 9.2). The magnitude of the difference between breeding strategies increased in 1999. The mean number of fledglings per nest attempt was not significantly higher for groups in 1998 but in 1999 almost twice as many young were fledged per nest attempt from group nests (Table 9.2). The mean number of fledglings per nest attempt did not differ significantly between seasons within either pairs or groups (Table 9.2). However, the trend between seasons differed between breeding strategies. The number of fledglings per nest increased by 21% from 1998 to 1999 for groups but decreased in pairs by 28%. The decrease in pairs is related to the high rate of failure in their second nest attempts in 1999, compared with their 1998 nesting success. Thus, the reduction in the number of fledglings per nest must be placed in the context of a slight rise in their seasonal productivity over the same period (Fig. 9.6). In contrast to productivity per nesting attempt, there was no indication of significant variation in the number of fledglings per successful nest related to either breeding strategy or season (Table 9.2).
Table 9.2. Mean productivity per breeding unit in 1998, 1999 and for both seasons pooled. Mann-Whitney U-tests were used to compare productivity between breeding strategies in 1998, 1999 and for seasons pooled, and between seasons for pairs and groups respectively.

<table>
<thead>
<tr>
<th></th>
<th>Mann-Whitney P values:</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Between strategies:</td>
<td>Between seasons:</td>
<td>Between seasons:</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>pairs only</td>
<td>groups only</td>
</tr>
<tr>
<td>Fledglings/nest</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1998</td>
<td>1.00 ± 0.31</td>
<td>1.17 ± 0.44</td>
<td>0.672</td>
<td>0.686</td>
</tr>
<tr>
<td>1999</td>
<td>0.72 ± 0.15</td>
<td>1.42 ± 0.20</td>
<td>0.016</td>
<td></td>
</tr>
<tr>
<td>Seasons pooled</td>
<td>0.85 ± 0.16</td>
<td>1.33 ± 0.19</td>
<td>0.074</td>
<td></td>
</tr>
<tr>
<td>Flg/success nest</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1998</td>
<td>1.50 ± 0.22</td>
<td>1.33 ± 0.33</td>
<td>0.655</td>
<td>0.447</td>
</tr>
<tr>
<td>1999</td>
<td>1.71 ± 0.18</td>
<td>1.83 ± 0.31</td>
<td>0.804</td>
<td></td>
</tr>
<tr>
<td>Seasons pooled</td>
<td>1.61 ± 0.14</td>
<td>1.67 ± 0.24</td>
<td>0.970</td>
<td></td>
</tr>
<tr>
<td>Flg/adult/season</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1998</td>
<td>0.56 ± 0.15</td>
<td>0.36 ± 0.02</td>
<td>0.210</td>
<td>0.568</td>
</tr>
<tr>
<td>1999</td>
<td>0.67 ± 0.14</td>
<td>0.89 ± 0.16</td>
<td>0.360</td>
<td></td>
</tr>
<tr>
<td>Seasons pooled</td>
<td>0.62 ± 0.10</td>
<td>0.71 ± 0.14</td>
<td>0.803</td>
<td></td>
</tr>
</tbody>
</table>

† $n$ (1998) = 8 (except $n$ (Flg/SN) = 6); $n$ (1999) = 9 (except $n$ (Flg/SN) = 7).

In a two-factor ANOVA, there was a trend for groups to have greater seasonal productivity per breeding unit (Table 9.3a). As neither season, nor strategy*season, were significant, season was removed and a one-way ANOVA conducted on the data pooled across both seasons. This revealed a significant effect of breeding strategy on seasonal productivity (Table 9.3b). In 1998, the number of young fledged per breeding unit was similar for groups and pairs (Mann-Whitney $z = 0.33$, $P = 0.74$; Fig. 9.6) but it was significantly higher for groups in 1999 (Mann-Whitney $z = 2.0$, $P = 0.045$; Fig. 9.6). This increase in productivity in groups was reflected in an 150% increase in per capita productivity (Flg/Ad/S) between 1998 and 1999 (Table 9.2). However, per capita productivity did not differ significantly between strategies in either season (Table 9.2).
Reproductive success

Figure 9.6. Mean number of fledglings (± s.e.) per breeding unit per season in 1998 and 1999 for pairs and cooperative groups, respectively. Different letters indicate differences between groups and pairs in Mann-Whitney tests within each year.

Table 9.3. Effect of breeding strategy on seasonal productivity per breeding unit \(^1\) at Yarrara, 1998 - 1999.

<table>
<thead>
<tr>
<th>Test of effect</th>
<th>Mean Flg/S ± s.e. (n)</th>
<th>d.f.</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) 2-factor ANOVA</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Strategy</td>
<td>Pair 1.24 ± 0.20 (17)</td>
<td>1, 22</td>
<td>0.421</td>
<td>3.391</td>
<td>0.079</td>
</tr>
<tr>
<td></td>
<td>Group 2.22 ± 0.40 (9)</td>
<td>1998</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>1999</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Season</td>
<td>1.18 ± 0.23 (11)</td>
<td>1, 22</td>
<td>0.320</td>
<td>2.574</td>
<td>0.123</td>
</tr>
<tr>
<td></td>
<td>1.87 ± 0.31 (15)</td>
<td>1998</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>1999</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Strategy*Season</td>
<td>1.18 ± 0.23 (11)</td>
<td>1, 22</td>
<td>0.240</td>
<td>1.175</td>
<td>0.290</td>
</tr>
<tr>
<td></td>
<td>1.87 ± 0.31 (15)</td>
<td>1998</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>1999</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>b) One-way ANOVA</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Strategy</td>
<td>1.24 ± 0.20 (17)</td>
<td>1, 24</td>
<td>0.696</td>
<td>5.405</td>
<td>0.029</td>
</tr>
<tr>
<td></td>
<td>2.22 ± 0.40 (9)</td>
<td>1998</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>1999</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^1\) Transformation used: \(\sqrt{(Flg/S + 0.5)}\)
Reproductive success

Components of productivity

Clutch size was almost always two (Table 9.4), with only three clutches of one egg (two of which were laid by the same female in different years) and one clutch of three eggs recorded. Most eggs produced hatchlings: mean hatching success per breeding unit was 84%. Mean nestling success per breeding unit was considerably lower (60%) (Table 9.4). The 15% decline in nestling survival between 1998 and 1999 (Table 9.5) appears counter to the general increase in productivity observed in 1999 (Fig. 9.5). This can be attributed to numerous second brood attempts that failed in the nestling stage in 1999. Thus, only 50% of eggs laid per nest per breeding unit ultimately produced fledglings (Table 9.4).

More breeding units laid two clutches per season than a single clutch (Table 9.4). Many of these were replacement clutches following complete failure of the first nest attempt. However, a second clutch was laid following a successful first nest in 10 of the 26 breeding unit-years (38.5%), all of which were in 1999. Thus, an average of 1.38 broods was attempted per season was per breeding unit (Table 9.4). Twenty days typically elapsed between successful fledging of the first brood and egg laying for the second brood (Table 9.4).


<table>
<thead>
<tr>
<th>Component</th>
<th>Mean (± se)</th>
<th>95% CI</th>
<th>Min - Max</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clutch size</td>
<td>1.95 ± 0.05</td>
<td>1.84 – 2.05</td>
<td>1 - 3</td>
<td>38</td>
</tr>
<tr>
<td>Hatching success (%)</td>
<td>84.15 ± 4.92</td>
<td>74.20 – 94.09</td>
<td>0 - 100</td>
<td>41</td>
</tr>
<tr>
<td>Nestling success (%)</td>
<td>59.91 ± 7.38</td>
<td>44.95 – 74.87</td>
<td>0 - 100</td>
<td>37</td>
</tr>
<tr>
<td>Fledgling success (%)</td>
<td>50.00 ± 7.35</td>
<td>35.13 – 64.87</td>
<td>0 - 100</td>
<td>39</td>
</tr>
<tr>
<td># clutches laid</td>
<td>1.58 ± 0.10</td>
<td>1.37 – 1.78</td>
<td>1 - 2</td>
<td>26</td>
</tr>
<tr>
<td># broods attempted</td>
<td>1.38 ± 0.10</td>
<td>1.18 – 1.59</td>
<td>1 - 2</td>
<td>26</td>
</tr>
<tr>
<td>Renesting period</td>
<td>20.0 ± 3.12</td>
<td>12.8 – 27.2</td>
<td>7 - 35</td>
<td>9</td>
</tr>
</tbody>
</table>
Effect of breeding strategy on components of productivity

There was no significant variation in mean clutch size or hatching success between breeding strategies or seasons (Table 9.5). The increase in the hatching success of groups between years (25%) was probably an artifact of the small sample in 1998, which may have exaggerated fluctuations in hatching success. The percentage of hatchlings that were successfully reared to fledglings per nest attempt (nestling success) was significantly higher at nests of groups, particularly in 1999 when it was approximately double that of pairs (Table 9.5). This culminated in significantly higher fledgling success for nests attended by groups (Table 9.5). Thus, groups were more proficient in converting eggs into fledglings due primarily to greater efficacy during the nestling stage.

There was significant variation in number of clutches laid and second broods attempted between the two years of the study (Table 9.5). White-browed Treecreepers were more inclined to attempt a second brood in 1999 than in 1998, irrespective of breeding strategy. Thus, the increase in the number of clutches laid in 1999 reflects an increased propensity for multi-broodedness rather than an increase in failure of first nests, which actually declined slightly from 27% to 20%. However, neither the number of clutches laid, nor the number of broods attempted, varied significantly between breeding strategies (Table 9.5). The renesting period between broods was significantly shorter in groups than pairs (Table 9.5). In fact, the slowest re-nesting interval for groups (range 7 – 21 days) was still two days shorter than the fastest pair (range 23 - 35 days).
Table 9.5. Components of productivity in pairs and groups of the White-browed Treecreeper in 1998, 1999 and for both seasons pooled. Mann-Whitney U-tests were used to compare variables between breeding strategies, and between seasons for pairs and groups, respectively.

<table>
<thead>
<tr>
<th></th>
<th>Pairs mean ± se†</th>
<th>Groups mean ± se¶</th>
<th>Mann-Whitney P values:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Between strategies:</td>
<td>Between seasons: pairs only</td>
<td>Between seasons: groups only</td>
</tr>
<tr>
<td>Clutch size 1998</td>
<td>1.88 ± 0.13</td>
<td>1.83 ± 0.17</td>
<td>1.000</td>
</tr>
<tr>
<td>1999</td>
<td>2.00 ± 0.00</td>
<td>2.00 ± 0.13</td>
<td>0.545</td>
</tr>
<tr>
<td>Seasons pooled</td>
<td>1.95 ± 0.06</td>
<td>1.93 ± 0.10</td>
<td>0.764</td>
</tr>
<tr>
<td>Hatching % 1998</td>
<td>75.00 ± 12.27</td>
<td>66.67 ± 22.05</td>
<td>0.675</td>
</tr>
<tr>
<td>1999</td>
<td>88.89 ± 7.35</td>
<td>91.67 ± 8.33</td>
<td>0.799</td>
</tr>
<tr>
<td>Seasons pooled</td>
<td>82.35 ± 6.95</td>
<td>83.33 ± 9.32</td>
<td>0.829</td>
</tr>
<tr>
<td>Nestling % 1998</td>
<td>61.90 ± 15.31</td>
<td>88.89 ± 11.11</td>
<td>0.327</td>
</tr>
<tr>
<td>1999</td>
<td>41.67 ± 10.21</td>
<td>79.17 ± 10.03</td>
<td><strong>0.028</strong></td>
</tr>
<tr>
<td>Seasons pooled</td>
<td>50.52 ± 8.89</td>
<td>82.41 ± 7.41</td>
<td><strong>0.024</strong></td>
</tr>
<tr>
<td>Fledgling % 1998</td>
<td>50.00 ± 15.67</td>
<td>61.00 ± 20.11</td>
<td>0.528</td>
</tr>
<tr>
<td>1999</td>
<td>36.11 ± 7.35</td>
<td>71.00 ± 9.50</td>
<td><strong>0.007</strong></td>
</tr>
<tr>
<td>Seasons pooled</td>
<td>42.65 ± 8.24</td>
<td>67.67 ± 8.61</td>
<td><strong>0.041</strong></td>
</tr>
<tr>
<td># clutches laid 1998</td>
<td>1.25 ± 0.16</td>
<td>1.33 ± 0.33</td>
<td>0.792</td>
</tr>
<tr>
<td>1999</td>
<td>1.78 ± 0.15</td>
<td>1.83 ± 0.17</td>
<td>0.799</td>
</tr>
<tr>
<td>Seasons pooled</td>
<td>1.53 ± 0.12</td>
<td>1.67 ± 0.17</td>
<td>0.509</td>
</tr>
<tr>
<td># broods att’d 1998</td>
<td>1.00 ± 0.00</td>
<td>1.00 ± 0.00</td>
<td><strong>0.011</strong></td>
</tr>
<tr>
<td>1999</td>
<td>1.56 ± 0.18</td>
<td>1.83 ± 0.17</td>
<td><strong>0.049</strong></td>
</tr>
<tr>
<td>Seasons pooled</td>
<td>1.29 ± 0.11</td>
<td>1.56 ± 0.18</td>
<td>0.296</td>
</tr>
<tr>
<td>Renest period* 1999</td>
<td>28.0 ± 2.55</td>
<td>13.6 ± 2.86</td>
<td><strong>0.014</strong></td>
</tr>
</tbody>
</table>

† n (1998) = 8 (except n (Nestling %) = 7); n (1999) = 9.
* Data for 1999 only, n (pairs) = 4; n (groups) = 5.

Breeding strategy and the success of second broods

The productivity of first and second broods was compared between strategies to examine the hypothesis that helpers increase the productivity of second brood attempts (1999 only). The proportion of first nest attempts that were successful was higher for groups than pairs (Table 9.6), though this did not differ from the null
hypothesis of random nest success (Fisher’s exact test $P = 0.23$). Nor did the mean number of fledglings from the first nest attempt of 1999 differ significantly between breeding strategies (Pairs: $1.11 \pm 0.31$, Groups: $1.83 \pm 0.31$; Mann-Whitney $z = 1.39$, $P = 0.17$, $n = 9, 6$).

Pairs and groups showed an equal propensity to attempt a second brood if the first nest of the season was successful (Table 9.6). However, groups were more successful than pairs in fledging young from their second brood (Table 9.6) though the lack of statistical power in this test resulted in a non-significant trend (Fisher’s exact test $P_{1\text{-tail}} = 0.08$). However, productivity of second broods was significantly higher for cooperative groups ($1.00 \pm 0.45$ flg/nest) compared with pairs ($0.00 \pm 0.00$ flg/nest) (Mann-Whitney $z = 1.94$, $P_{1\text{-tail}} = 0.026$, $n = 5, 5$).

Table 9.6. Re-nesting by White-browed Treecreepers, and success ($\geq 1$ fledgling) of second broods. $S =$ success, $F =$ failure

<table>
<thead>
<tr>
<th>Sequence of nests</th>
<th>1998</th>
<th>1999</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Pairs</td>
<td>Groups</td>
<td>Pairs</td>
</tr>
<tr>
<td>S</td>
<td>4</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>F</td>
<td>2</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>FS</td>
<td>2</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>SF</td>
<td>5</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>SS</td>
<td></td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>FF</td>
<td>1</td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>First nest S</td>
<td>4</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td>Renest after S</td>
<td>0</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>Success after S</td>
<td>-</td>
<td>-</td>
<td>0</td>
</tr>
</tbody>
</table>

Causes of nest failure and brood reduction

Predation (sudden disappearance of entire nest contents) was the main cause of complete nest failure (34%), although abandonment was detected during both the incubation and nestling stages (Table 9.7). Nests of pairs were more likely to be preyed upon than nests attended by groups (Yates’ $\chi^2 = 3.21$, $P = 0.073$; Table 9.7). Between 17% - 22% of all nests detected, and 28% - 36% of successful nests, suffered partial brood reduction (Table 9.7). Assuming (i) that all unknown partial
losses were due to nestling starvation and (ii) a clutch of two for the two nests with unknown clutch sizes, brood depletion due to nestling starvation occurred at a maximum of 17.5% of all nests detected and 28% of nests that were successful. Excluding nests that suffered total loss, there was no difference in the frequency of brood reduction between pairs and groups (Yates’ $\chi^2 = 0.014, P = 0.90$) or in the prevalence of egg sterility (Yates’ $\chi^2 = 0.58, P = 0.44$) or nestling starvation (Yates’ $\chi^2 = 0.42, P = 0.52$) (Table 9.7).


<table>
<thead>
<tr>
<th>Cause of failure / reduction</th>
<th>Pairs</th>
<th>Groups</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nests detected</td>
<td>26</td>
<td>15</td>
<td>41</td>
</tr>
<tr>
<td>Complete nest failure</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Predation</td>
<td>13 (50%)</td>
<td>3 (20%)</td>
<td>16 (39%)</td>
</tr>
<tr>
<td>Egg abandonment</td>
<td>1 (4%)</td>
<td>-</td>
<td>1 (2.5%)</td>
</tr>
<tr>
<td>Nestlings abandoned / starvation</td>
<td>-</td>
<td>1 (7%)</td>
<td>1 (2.5%)</td>
</tr>
<tr>
<td>Partial brood reduction</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sterile eggs</td>
<td>-</td>
<td>2 (13%)</td>
<td>2 (5%)</td>
</tr>
<tr>
<td>Nestling starvation</td>
<td>2 (8%)</td>
<td>1 (7%)</td>
<td>3 (7.5%)</td>
</tr>
<tr>
<td>Unknown</td>
<td>1-3 (4%-11%)</td>
<td>1 (7%)</td>
<td>2-4 (5%-10%)</td>
</tr>
</tbody>
</table>

1 Clutch size was unknown in two nests that fledged only one chick. Therefore, because it was impossible to determine whether the original broods had been reduced, a range is given.

Natal dispersal

Natal dispersal is difficult to verify and quantify (Walters 2000). In 1998, 12 of the 13 fledglings in the study plot were banded. Juvenile White-browed Treecreepers appeared to follow one of three distinct pathways in their first year: (i) disperse once nutritionally independent ($\approx 40–50$ days), (ii) delay dispersal for some time ($\approx 6 - 8$ months) or (iii) remain in their natal territory for the next breeding season. Gender and social composition of the natal breeding unit appeared to influence the dispersal behaviour of young birds (Table 9.8). Of the seven males that fledged in 1998, the three from cooperative nests had disappeared by late summer, presumably having
dispersed. One of these was re-sighted in June (7 months post-fledging) ≈ 0.7 km from his natal nest. In contrast, three of the four male fledglings from nests of pairs remained in their natal territory for the following breeding season and subsequently assisted at the nests of their parents. This observation forms the basis of the supposition that helpers were the progeny of the breeding pair.

Four of the six female fledglings had disappeared well before the end of summer (one was re-sighted in May ≈ 2.5 km from its natal nest) whilst the other two remained on their natal territories for extended periods of six to eight months. However, all females had dispersed or perished by the commencement of the 1999 breeding season. Unfortunately, as field work ceased in mid-February 2000, no attempt was made to colour-band fledglings during the 1999 season on ethical grounds, precluding a similar assessment for the 1999 cohort.

### Table 9.8. Dispersal behaviour of 13 fledglings from the 1998 breeding season.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Breeding strategy of natal nest</th>
<th>Total fledglings</th>
<th>Disperse when nutritionally independent</th>
<th>Delay dispersal until winter</th>
<th>Natal philopatry (become helpers)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>Cooperative</td>
<td>3</td>
<td>3&lt;sup&gt;a&lt;/sup&gt;</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Pair</td>
<td>4</td>
<td>1&lt;sup&gt;b&lt;/sup&gt;</td>
<td></td>
<td>3</td>
</tr>
<tr>
<td>Female</td>
<td>Cooperative</td>
<td>1</td>
<td>1</td>
<td></td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Pair</td>
<td>5</td>
<td>4&lt;sup&gt;c&lt;/sup&gt;</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> One fledgling re-sighted 0.7 km from natal nest on 15/6/99.

<sup>b</sup> Individual not banded, assumed dispersed or perished.

<sup>c</sup> One fledgling re-sighted 2.5 km from natal nest on 11/5/99.

### Parental experience and reproductive success

Confirmed previous breeding success was used as a surrogate for parental experience. The success of individual nest attempts in 1999 was higher for previously successful females (69% success, $n = 13$ nests) than females without previous breeding success (50% success, $n = 14$ nests) but this did not depart from expectations of the null hypothesis ($Yates \chi^2 = 0.39$, $P = 0.54$). The average number of fledglings per nest attempt did not differ from the null hypothesis of equal productivity for parents with and without previous reproductive success (Mann-
Whitney U-tests: Females: \( z = 0.85, P = 0.40, n = 7, 8 \); Males: \( z = 0.87, P = 0.39, n = 6, 9 \). Similarly, seasonal productivity did not depart from the expectations of the null hypothesis of no difference between parents with previous success and those assumed to be novice breeders (Females: \( z = 0.80, P = 0.43, n = 7, 8 \); Males: \( z = 0.81, P = 0.42, n = 6, 9 \); Fig. 9.7). The propensity to undertake a second brood following a successful first nest was identical for experienced and novice females (83%, \( n = 6, 6 \)). However, the distribution of previously successful breeders was skewed towards groups, for both males and females (Fisher’s exact test: Females \( P = 0.041 \), Males \( P = 0.028 \); Fig. 9.7).

![Figure 9.7](image-url)

*Figure 9.7.* Mean (± s.e.) number of offspring fledged in 1999 by previously successful (experienced) and unsuccessful (novice) individuals. The number of individuals in each category is indicated above the bars.

Therefore, to separate the effects of experience and strategy, previous reproductive success and current breeding strategy were entered as explanatory variables in an ordinal logistic regression of the number of fledglings produced in 1999. For both females and males, the number of fledglings was significantly affected by breeding...
Reproductive success

strategy (Females: $\chi^2 = 4.74$, $d.f. = 1$, $P = 0.029$; Males: $\chi^2 = 5.00$, $d.f. = 1$, $P = 0.025$) but not by previous reproductive success (Females: $\chi^2 = 0.45$, $d.f. = 1$, $P = 0.5$; Males: $\chi^2 = 0.72$, $d.f. = 1$, $P = 0.4$). Groups were most likely to fledge 2 to 4 offspring for the season whereas pairs were most likely to fledge 0 to 2 young, irrespective of previous reproductive success.

Perhaps a more elegant and powerful approach is to simply compare productivity between previously successful and unsuccessful parents currently breeding in unassisted pairs, and between groups and pairs for previously successful parents only. For pairs, experienced individuals did not perform better than previously unsuccessful or primiparous birds (Table 9.9; Fig. 9.7). Previously successful females performed better in groups than their counterparts in pairs though the difference was not statistically significant (Table 9.10; Fig. 9.7). Experienced males achieved significantly greater productivity per nest attempt breeding in groups than pairs which translated into a strong trend for higher seasonal productivity when breeding in groups (Table 9.10; Fig. 9.7).

### Table 9.9.  Mann-Whitney U-tests comparing productivity of previously successful individuals with previously unsuccessful individuals breeding in pairs in 1999.

<table>
<thead>
<tr>
<th></th>
<th>Mean fledglings / nest attempt</th>
<th>Fledglings / season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$z$</td>
<td>$P$</td>
</tr>
<tr>
<td>Females (n = 2, 7)</td>
<td>0.175</td>
<td>0.861</td>
</tr>
<tr>
<td>Males (n = 3, 6)</td>
<td>1.234</td>
<td>0.217</td>
</tr>
</tbody>
</table>

### Table 9.10.  Mann-Whitney U-tests comparing productivity of previously successful individuals breeding in pairs with individuals breeding in groups in 1999.

<table>
<thead>
<tr>
<th></th>
<th>Mean fledglings / nest attempt</th>
<th>Fledglings / season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$z$</td>
<td>$P$</td>
</tr>
<tr>
<td>Females (n = 2, 5)</td>
<td>1.496</td>
<td>0.135</td>
</tr>
<tr>
<td>Males (n = 3, 6)</td>
<td>2.032</td>
<td>0.042</td>
</tr>
</tbody>
</table>
Variation in territory quality

The extent of variation in canopy tree dominance within the 25 wandering-quarter transects was relatively small (mean (± s.e.) = 412.5 ± 23.4 cm² / 100 m², co-efficient of variation = 28.3%). There was not significant variation in tree dominance among the 15 White-browed Treecreeper territories for which I had data (F₁₄ = 0.54, P = 0.86; mean (± s.e.) = 416.2 ± 22.6 cm² / 100 m²). A negative correlation between territory size and tree dominance would be expected if territory size increased to compensate for lower habitat quality (i.e. foraging resources). The absence of significant correlation between tree dominance and territory size (MCP95%res) (r = 0.291, P = 0.385, n = 11) suggests territory size is a reasonable surrogate for access to foraging resources and hence habitat quality.

Tree dominance was compared between territories of groups and pairs in 1998 and 1999 separately, due to the change in strategy in some territories between seasons. There was little difference between strategies in 1998 (t₈ = 0.24, P = 0.82: mean dominance ± s.e.: Pairs = 440.5 ± 39.1 cm² / 100 m², n = 7; Groups = 421.4 ± 58.4 cm² / 100 m², n = 3). In 1999, average tree dominance was marginally higher in territories of groups (460.2 ± 43.3 cm² / 100 m², n = 6) than pairs (386.8 ± 23.7 cm² / 100 m², n = 8) but this difference was not significant (t₁₂ = -1.53, P = 0.15).

Models of the effect of potential correlates of fledgling productivity

Seasonal productivity

Laying date, breeding strategy, season, tree dominance and territory size were included in the full ordinal regression model of the number of fledglings per season per breeding unit. Laying date was the only significant variable identified during backwards elimination (χ² = 5.624, d.f. = 1, P = 0.018). However, the change in deviance associated with the removal of breeding strategy from the full model was almost significant (χ² = 3.542, d.f. = 1, P = 0.06), indicating that the effect of helpers on seasonal productivity was substantial, after accounting for other potential correlates of reproductive success. Removal of tree dominance, territory size, season or the season*strategy interaction term did not result in a significant or near-significant change in model deviance (all P values > 0.1). Thus, these co-variates
Reproductive success

appear to have little effect on seasonal productivity over and above the impacts of laying date and breeding strategy.

A final ordinal regression model of seasonal productivity was built that included laying date and breeding strategy as the predictor variables (Table 9.11). The shape of the regression curves are the same for pairs and groups, but the position of the graph is shifted to the right for cooperative groups by 25 days. Thus, for both strategies, the earlier laying commenced, the greater the probability of producing two fledglings rather than one or none (Fig. 9.8). Breeding units that commenced laying early, particularly groups, had a greater probability of producing four fledglings as it maximized their opportunity for multiple broods. Pairs that were very late (≥30 days after the seasonal median) had a 50% probability of complete breeding failure and a 90% probability of producing no more than one fledgling for the season (Fig. 9.8a). Pairs that commenced laying on the median laying date had a 50% probability of fledging one offspring for the season, whereas groups that commenced nesting on the same date had a 50% probability of fledging two young (Fig. 9.8). For pairs, the laying date at which the probability of one fledgling is equal to the probability of two fledglings is 12 days before the season median, whereas for groups, the same point is 13 days after the season median.

Table 9.11. Ordinal logistic regression model of the effects of laying date (scaled to seasonal median) and breeding strategy on seasonal productivity of the White-browed Treecreeper. Model fit: $\chi^2 = 6.73$, $d.f. = 2$, $P = 0.035$.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>s.e.</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Threshold</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fledglings = 0</td>
<td>-3.444</td>
<td>1.114</td>
<td>0.002</td>
</tr>
<tr>
<td>Fledglings = 1</td>
<td>-0.848</td>
<td>0.719</td>
<td>0.238</td>
</tr>
<tr>
<td>Fledglings = 2</td>
<td>1.424</td>
<td>0.760</td>
<td>0.061</td>
</tr>
<tr>
<td>Fledglings = 3</td>
<td>1.914</td>
<td>0.857</td>
<td>0.025</td>
</tr>
<tr>
<td>Location</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Laying date</td>
<td>-0.0567</td>
<td>0.031</td>
<td>0.068</td>
</tr>
<tr>
<td>Strategy$^1 = Pair$</td>
<td>-1.440</td>
<td>0.919</td>
<td>0.117</td>
</tr>
</tbody>
</table>

$^1$ Parameter estimate for Groups = 0
Figure 9.8. Predictions from the ordinal regression model of the probability of fledging 0, 1, 2, 3 or 4 offspring per season, versus laying date, for (a) pairs and (b) groups. Laying date is scaled to the seasonal median. Standard errors of the predictions are excluded for simplicity (see Table 9.11 for errors associated with parameter estimates).
Reproductive success

Per capita productivity

The number of fledglings per attending adult per season was not significantly affected by any of the five variables entered into the general linear model, at a critical $\alpha$ level of 0.05. Of the five variables modelled, the largest change in deviance was associated with the removal of laying date from the full model ($\chi^2 = 3.61, d.f. = 1, P = 0.057$). This reiterates the importance of the timing of nesting for maximizing reproductive success for all individuals involved. There was a weak trend for tree dominance ($\chi^2 = 2.73, d.f. = 1, P = 0.099$) to affect per capita productivity. Territory size, breeding strategy and season were all non-significant. A hierarchical partition was conducted in parallel with this analysis and corroborated the relative influence of the predictor variables on per capita productivity.

Effect of breeding strategy on laying date

The random effect of breeding unit in the linear mixed model of laying date was not significant ($\chi^2 = 0.35, d.f. = 1, P = 0.55$). Thus, laying date was not dependent on the identity of the breeding unit, irrespective of other factors. Although mean laying date (scaled to seasonal median) for groups (-3.9 ± 2.4) was more than eight days earlier than for pairs (4.5 ± 4.6), the effect of breeding strategy was not significant in the linear mixed model ($\chi^2 = 1.28, d.f. = 1, P = 0.26$). Thus, groups do not commence breeding significantly earlier than pairs, or vice-versa.

The laying dates of individual nest attempts were also scaled to the median for all nest attempts within each season (rather than for the first nest of the season as above). In a two-way analysis of variance of laying date that included breeding strategy and nest outcome (success/failure) as main effects, successful nests were initiated significantly earlier than unsuccessful nests but there were not significant differences between breeding strategies (Table 9.12).

In the ordinal regression model of the effect of breeding strategy and laying date on productivity of individual nest attempts (Fig. 9.9), laying date was a significant explanatory variable of the number of fledglings per nest (Table 9.13). However, the effect of breeding strategy was not significant (Table 9.13).
Table 9.12. Two-way Analysis of Variance of the effect of breeding strategy and nest outcome (success/failure) on laying date of the White-browed Treecreeper at Yarrara, 1998 - 1999. Laying date was scaled to the median laying date for all nest attempts within a season.

<table>
<thead>
<tr>
<th>Test of effect</th>
<th>Laying date mean ± s.e. (n)</th>
<th>d.f.</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Pair</td>
<td>Group</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Strategy</td>
<td>8.2 ± 5.9 (25)</td>
<td>0.0 ± 6.9 (15)</td>
<td>1, 36</td>
<td>105.4</td>
<td>0.154</td>
</tr>
<tr>
<td>Nest outcome</td>
<td>-4.7 ± 5.0 (25)</td>
<td>21.6 ± 7.0 (15)</td>
<td>1, 36</td>
<td>3713.4</td>
<td>5.440</td>
</tr>
<tr>
<td>Strategy*Outcome</td>
<td></td>
<td></td>
<td>1, 36</td>
<td>309.8</td>
<td>0.454</td>
</tr>
</tbody>
</table>

Figure 9.9. Fledgling productivity as a function of laying date for pairs and groups of the White-browed Treecreeper at Yarrara, 1998 - 1999. The lines of best fit are fitted according to a linear regression.
Table 9.13. Ordinal logistic regression model of the effects of laying date (scaled to seasonal median) and breeding strategy on productivity per nest attempt of the White-browed Treecreeper. Model fit: $\chi^2 = 12.84, \text{d.f.} = 2, P = 0.002$.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>s.e.</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Threshold</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fledglings = 0</td>
<td>-1.326</td>
<td>0.572</td>
<td>0.021</td>
</tr>
<tr>
<td>Fledglings = 1</td>
<td>-0.017</td>
<td>0.530</td>
<td>0.974</td>
</tr>
<tr>
<td>Fledglings = 2</td>
<td>3.509</td>
<td>1.066</td>
<td>0.001</td>
</tr>
<tr>
<td>Location</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Laying date</td>
<td>-0.038</td>
<td>0.013</td>
<td>0.003</td>
</tr>
<tr>
<td>Strategy$^1$ = Pair</td>
<td>-0.804</td>
<td>0.648</td>
<td>0.215</td>
</tr>
</tbody>
</table>

$^1$ Parameter estimate for Groups = 0

Thus, laying date is a significant factor in determining fledgling productivity at both the seasonal and individual nest level. Laying date does not differ significantly between breeding strategies, although the mean laying date for groups was earlier than for pairs in both seasons. Breeding strategy is an important factor in determining seasonal fledgling productivity, once the influence of laying date has been taken into account. However, at the nest level, the effect of breeding strategy on the number of fledglings produced is not significant, once variation due to laying has been accounted for. The key to unlocking this conundrum is the laying date of second broods in 1999. Groups commenced their second broods significantly earlier than pairs ($t_8 = 2.62, P = 0.03$) by an average of 17 days (Fig. 9.10). Thus, the productivity of second broods was greater for groups (given their earlier commencement date), and hence seasonal productivity was higher. However, a pair that commenced a nest (first or second attempt) at the same time as a group, would likely have equivalent productivity for that nest attempt.
9.4 Discussion

Reproductive success of the White-browed Treecreeper

This is the first study to quantify the reproductive success of the White-browed Treecreeper. The mean annual productivity of 1.58 fledglings per breeding unit, or 0.65 fledglings per attending adult, reflects a reproductive strategy characterised by low annual fledgling productivity, high adult survival, and long breeding seasons that is typical of Australian passerines (Rowley & Russell 1991). Recruitment of fledglings into the adult population will be lower again, although extended parental care in group-living species may moderate juvenile mortality (Russell 2000). The low annual productivity of White-browed Treecreepers is a product of small clutches, a long nesting cycle and a moderate rate of nest success (61% of observed nests successful; 56% Mayfield probability of nest survival). Failure of nests was more likely during the nestling stage than during incubation. The rate of nest success falls within the range observed for many Australian passerines (Ford 1989). The mean egg to fledgling success rate of 50% detected in this study is very close to the mean value of 45% for 14 species of Australian temperate passerines listed by Rowley and Russell (1991).
I was able to compare the reproductive success of the White-browed Treecreeper with four other Australian treecreepers, although temporal and geographic differences between the studies limits the precision of the comparisons (Table 9.14). In general, the nest success of treecreepers appears to be slightly higher than for the average Australian passerine. The average nest success of the five species of treecreeper was 68% compared to 45% for 19 species of Australian passerines in Rowley and Russell (1990b) and 39% for a woodland community of 21 species in south-east Victoria (Berry 2001). This difference is probably largely due to the protection from predators afforded to treecreepers by nesting in hollows (Nice 1957, Nilsson 1986). For example, open-nesting forest species often suffer high levels of nest predation, resulting in nest success as low as 13% for the Rufous Whistler (Bridges 1994) and 18% for the Leaden Flycatcher (Tremont & Ford 2000).

Nesting success was lower in this study than in all other studies of Australian treecreepers, except for one population of the Brown Treecreeper (Table 9.14). Higher rates of nest predation appeared to be the major cause of the lower nest success in this study. In contrast to the present study, Noske (1991) documented higher mortality during incubation than the nestling stage, for both the Brown Treecreeper and White-throated Treecreeper. He attributed the losses to egg abandonment in response to detection by predators but did not provide estimates of the proportion of nests actually preyed upon. Such anticipatory abandonment was rare in the White-browed Treecreeper. However, the proportion of nestlings that fledged was lower for the White-browed Treecreeper (60%) than reported by Noske (1991) for either the Brown Treecreeper (78%) or the non-cooperative White-throated Treecreeper (75%), suggesting predation of nestlings may have been more intense in this study. Noske (1991) did not detail productivity per successful nest or estimate losses from starvation, making it difficult to ascertain the relative importance of starvation and predation. A comparison of reproductive success between the sympatric populations of the White-browed Treecreeper and Brown Treecreeper at Yarrara FFR would provide a more insightful analysis of their relative susceptibility to nest predation.

The number of fledglings per nest attempt was also lower for the White-browed Treecreeper than in the two other studies of treecreepers with available data. This is probably a reflection of nest success because the number of fledglings per successful
nest for the White-browed Treecreeper was identical to the Rufous Treecreeper and only slightly less than the Brown Treecreeper (Table 9.14). This suggests that partial brood losses were similar in all three studies.

Annual fledgling productivity of the White-browed Treecreeper was mid-range of the reported values for Australian treecreepers (Table 9.14). This is despite a smaller mean clutch size and lower nest success than most other treecreepers. In fact, the product of mean clutch size and nest success (i.e. productivity per clutch in the absence of brood reduction) was lower for the White-browed Treecreeper (1.18 flg/clutch) than any of the other treecreeper species (range: 1.48 – 1.73 flg/clutch). This underscores the importance of multiple broods for increasing annual productivity because annual productivity was greater than productivity per clutch in only the Rufous Treecreeper and White-browed Treecreeper – the two species for which multi-broodedness was most common.

**Effect of helpers on reproductive success**

The effect of helpers varied between seasons. In 1998, there was no difference between groups and unassisted pairs in any of the measures of reproductive success or productivity. In 1999 however, both the success of individual nesting attempts and the number of young fledged per nesting attempt and per season were significantly higher for cooperative groups than pairs. In particular, groups were more successful in their attempts to raise a second brood (60% success) than pairs, in which all five attempts failed. Groups of Rufous Treecreepers were also more successful in rearing second broods (Luck 2000). Thus, the White-browed Treecreeper appears to be another example in which helpers augment the fitness of the breeding pair by increasing their reproductive success (e.g. Rowley 1965, Brown 1978, Rowley and Russell 1990a, Emlen and Wrege 1991, Noske 1991, Dickinson *et al.* 1996, Langen & Vehrencamp 1999). However, per capita productivity did not differ significantly between breeding strategies in either season. In fact, in 1998 pairs experienced slightly higher annual productivity per participating adult than groups.

<table>
<thead>
<tr>
<th>Species</th>
<th>Social organisation</th>
<th>Nesting success</th>
<th>Flg / nest</th>
<th>Flg / success nest</th>
<th>Flg / season / breeding unit</th>
<th>Location of study</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>White-throated Treecreeper</td>
<td>Non-cooperative</td>
<td>68%</td>
<td>-</td>
<td>-</td>
<td>1.31</td>
<td>Northern NSW</td>
<td>Noske 1991</td>
</tr>
<tr>
<td>Cormobates leucophaea</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brown Treecreeper Climacteris</td>
<td>Co-operative</td>
<td>48%</td>
<td>1.31</td>
<td>1.79</td>
<td>1.36</td>
<td>Northern NSW</td>
<td>Noske 1991</td>
</tr>
<tr>
<td>picumnus</td>
<td></td>
<td>73%</td>
<td></td>
<td></td>
<td>2.00</td>
<td></td>
<td>a Walters et al. 1999</td>
</tr>
<tr>
<td>Rufous Treecreeper Climacteris</td>
<td>Co-operative</td>
<td>78%</td>
<td>1.27</td>
<td>1.64</td>
<td>2.1</td>
<td>South-west WA</td>
<td>Luck 2000</td>
</tr>
<tr>
<td>rufa</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Red-browed Treecreeper</td>
<td>Co-operative</td>
<td>74%</td>
<td>-</td>
<td>-</td>
<td>1.1</td>
<td>Northern NSW</td>
<td>Noske 1991</td>
</tr>
<tr>
<td>Climacteris erythrops</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>White-browed Treecreeper</td>
<td>Co-operative</td>
<td>61%</td>
<td>1.0</td>
<td>1.64</td>
<td>1.58</td>
<td>North-west</td>
<td>This study</td>
</tr>
<tr>
<td>Climacteris affinis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Victoria</td>
<td></td>
</tr>
</tbody>
</table>
It has long been recognised that simple correlational relationships between group size and reproductive success may be misleading due to circularity between group size and success. Larger groups may be a consequence, rather than the cause, of higher reproductive success because groups may occupy better quality habitat or consist of better quality or more experienced breeders (Lack 1968, Brown 1978, 1987, Cockburn 1998). In this study, the influence of territory size and quality, parental experience and pair quality did not appear to confound the relationship between breeding strategy and fledgling productivity. Certainly, variation in productivity due to breeding strategy and the timing of nesting (laying date), which was probably in response to variation in climatic conditions, was of much greater importance. Moreover, a positive effect of helpers on seasonal productivity remained, even after accounting for variation due to the timing of nesting. Nonetheless, the effect of some of these potential correlates of reproductive success, and how they were assessed in this study, deserves closer attention.

**Parental experience**

Experienced parents did not achieve significantly higher reproductive success or productivity than birds that, to my knowledge, had not previously bred successfully. As expected, the distribution of previously successful parents was significantly skewed towards cooperative groups because groups were usually formed through the retention of offspring in their natal territory. Yet, in ordinal regression modelling, breeding strategy was a significant explanatory variable whereas previous reproductive success only accounted for a negligible amount of variation in seasonal productivity. Accordingly, comparisons of reproductive success of individuals with similar breeding histories revealed a trend for increased productivity when helpers were present.

It is not inevitable that successful breeders will form cooperative groups because male offspring sometimes disperse, and dispersal is customary for females. Consequently, the effect of parental experience on productivity should be most striking in pairs. However, no difference in the productivity of previously successful and putatively unsuccessful White-browed Treecreepers was detected. Thus, the enhanced reproductive success of groups did not appear to be dependent on, or
confounded by, prior breeding experience. In his study of the Rufous Treecreeper, Luck (2000) similarly did not find significant differences in reproductive measures between first year birds and parents with experience.

These results contrast with several studies on cooperatively breeding birds in which breeding or helping experience has been linked to enhanced reproductive success through improved nest site selection (Komdeur 1996, Hatchwell et al. 1999), expeditious nest construction (Van Bael & Pruett-Jones 2000), increased attentiveness during incubation (Komdeur 1996), longer breeding seasons (Magrath 2001) or increased likelihood of successfully raising two broods (Russell & Rowley 1988). In addition, there is a wealth of empirical evidence from non-cooperative species that individuals become more proficient at breeding as they age and gain experience (Sæther 1990, Robertson & Rendell 2001). Thus, the apparent lack of age-specific variation in reproductive success in the White-browed Treecreeper may reflect the short duration of this study or the inadequacy of previous reproductive success as a surrogate for age and experience. Age-specific variation may have been detected had I had knowledge of the full life-history of individuals. Previous reproductive success does not account for adaptive behaviour in response to failed nesting attempts (e.g. Boulton 1999). Furthermore, helping experience at successful nests may be more profitable for future productivity than failed breeding experience (Komdeur 1996, Hatchwell et al. 1999) but I could not assess prior helping experience for birds new to the study plot in 1999.

Nest site selection and nest building appear to be particularly responsive to breeding experience (Komdeur 1996, Hatchwell et al. 1999, Van Bael & Pruett-Jones 2000). It may be that in hollow-nesting birds, the importance of experience in nest construction is diminished relative to open-nesting species. For the White-browed Treecreeper at least, hollows were selected from those available according to specific criteria but the attributes of those hollows selected did not affect nest success (Chapter 8). Furthermore, White-browed Treecreepers build uncomplicated, unstructured nests consisting merely of a shallow cup or pad of locally abundant and easily obtained materials (Whitlock 1910, Howe 1921, Chapter 8). Finally, the duration over which previous reproductive success was assessed may have been too short to detect the full effects of experience. Two or more breeding seasons may be
Reproductive success

required before experience accrues productivity benefits to a breeding bird (Rowley & Russell 1990a, Walters 1990, Robertson & Rendell 2001).

Habitat quality

Satisfactorily controlling for habitat quality is difficult (Ligon & Stacey 1989). It is impossible to measure all habitat variables that may potentially be correlates of reproductive success. I used mean tree dominance, in concert with territory size, as indicators of habitat quality within each territory. Tree dominance was the most important variable in the model of habitat use developed for the White-browed Treecreeper in the Yarrara district (Chapter 4) and provides a measure of the amount of arboreal foraging substrate available to the treecreepers. Territory size served as a surrogate for other components of habitat quality, representing proportional access to resources. However, it is possible that the use of these coarse variables may have overlooked fine scale heterogeneity in resource availability such as variation in the shrub layer, which may influence productivity through its effect on insect abundance and provision of cover.

There was little evidence in this study for an independent effect of territory size or tree dominance on seasonal fledgling productivity, nor was there evidence for a confounding effect of territory size or tree dominance on the relationship between breeding strategy and reproductive productivity. It is salient that groups did not have significantly larger territories than pairs (Table 6.3) and tree dominance was not greater in the territories of groups. In contrast, an effect of breeding strategy on reproductive success was detected even when habitat quality, laying date, season and variation between individual breeding units were included in the ordinal logistic regression. Thus, there appeared to be intrinsic value for White-browed Treecreepers to breed in cooperative groups, that was not related to variability in habitat quality or parental quality. The regression approach used here concurs with many other studies that have controlled for habitat quality either experimentally or statistically and reported a positive effect of helpers on reproductive success (e.g. Grey-crowned Babbler Pomatostomus temporalis (Brown et al. 1982), Dunnock Prunella modularis (Davies 1990), Florida Scrub-jay Aphelocoma coerulescens (Mumme 1992), White-throated Magpie-jay Calocitta formosa (Innes & Johnston 1996, Langen &

Yet, when one considers the breadth of examples in which no effect of helpers could be shown after controlling for territory and parental quality (review in Cockburn 1998), it is doubtful that a unifying relationship between reproductive success, territory quality and the effect of helpers exists. Much as the adaptive explanations of helping may be best explained on a species by species basis (Ligon & Stacey 1989), the interaction between environment, demography and reproductive success is probably also species-specific. For example, the confounding influence of territory size on reproductive success in the Laughing Kookaburra *Dacelo novaeguineae* (Legge 2000) was predicated on larger groups occupying larger home ranges, a condition that was not evident in this population of White-browed Treecreepers.

Habitat quality is often correlated with the existence or abundance of a critical resource such as a key foraging resource (Langen & Vehrencamp 1998), abundance of prey (Komdeur 1992), specific nesting requirement (Walters 1990) or food storage facilities (Stacey & Ligon 1987). However, White-browed Treecreepers did not appear to be reliant on a single critical resource. The availability and quality of nest sites is one potentially critical resource. Whilst there was variation between territories in the quality and abundance of nest hollows (Chapter 8), nest success was not affected by hollow quality and it is therefore unlikely that hollow quality could account for variation in reproductive productivity. Moreover, the inclusion of breeding unit as a random variable in the modelling procedure should have accounted for any systematic bias in reproductive productivity due to quality of nest sites.

Habitat quality is unlikely to affect productivity if there is little variation in habitat quality between territories (Stacey & Ligon 1987, Pribil 1998). The extent of variation in habitat quality between territories at Yarrara FFR was probably insufficient to induce differences in productivity. That is, all territories contained relatively ‘high quality’ habitat and therefore breeding units were not constrained by availability of resources in any territories. Territory 33 may be the exception that proves this rule, as the established pair failed to breed in either season, ostensibly due to the lack of a suitable nest hollow. While this explains why productivity was not confounded by territory quality in this study, it does not discount the importance of
Reproductive success

habitat quality in determining reproductive success. The effect of habitat quality on productivity would best be explored through comparisons with other study areas (e.g. degraded remnants, Wyperfeld NP).

Relationship between climate, laying date and effect of helpers

It is a central tenet of avian breeding ecology that the timing of nesting should maximize reproductive success by synchronizing nestling and fledgling stages with peaks in food availability (Lack 1954), avoiding temperature extremes, minimizing exposure to predators (Martin 1987) and allowing sufficient time for multiple nest attempts (Ford 1989, Rowley & Russell 1990a). It follows that in environments with an unpredictable climate, the timing of reproduction must be flexible in order to respond to variability in breeding conditions (Ford 1989). The increases in the number of White-browed Treecreeper units breeding, the total number of fledglings produced, and the propensity for second broods suggest that higher autumn and winter rainfall in 1999 created environmental conditions conducive to breeding. As predicted by theory, laying date was a key factor in explaining variation in fledgling productivity of White-browed Treecreeper breeding units (Martin 1987). However, increased rainfall is also likely to influence breeding success in insectivorous birds independent of laying date, by stimulating plant growth and therefore arthropod abundance (Nix 1976). Hence, it is possible that both the earlier laying dates and increased productivity were correlated with the favourable climatic conditions of 1999, although earlier laying was not necessarily causative of increased productivity.

The relative productivity of groups and pairs cannot be divorced from the prevailing climatic conditions. Climate has frequently been proposed as an influential selective agent in the evolution of cooperative breeding. Cooperative breeding was originally proposed as an adaptation to environments with unpredictable climates that are prone to large fluctuations in resource availability (Rowley 1965, Harrison 1969). This “irregular climate” hypothesis has been dismissed in contemporary discussions (Dow 1980a, Clarke 1995, Cockburn 1996). More recently, the aseasonality of some Australian environments, and in particular the absence of a severe winter, has been emphasized as conducive to the evolution of cooperative breeding (Ford et al. 1988, Arnold & Owens 1999, but see Cockburn 1996). In this study, I was able to compare
the current utility of cooperative breeding under contrasting climatic conditions. Under the better conditions of 1999, groups fledged significantly more offspring than pairs but groups were not more successful in the more stressful conditions of 1998. This interaction between breeding strategy, productivity and climate concurs with the traditional “irregular climate” hypothesis that cooperative breeding may have evolved as a mechanism to exploit irregular favourable breeding conditions (Rowley 1965, 1976, Harrison 1969).

This conclusion assumes that the variation in rainfall experienced during this study (50% annual differential) is representative of inter-annual variation over the longer term. Annual variation in rainfall at Mildura from 1946 to 1996 (CBOM 2000) suggests that the climate is irregular in this region, with the 90th percentile for annual rainfall (412.7 mm) more than twice the 10th percentile (179.2 mm). However, cooperative breeding in the White-browed Treecreeper did not evolve over the last 50 years and it is uncertain whether annual variation was as irregular over an evolutionary time scale.

The “irregular climate” hypothesis is not mutually exclusive of the “aseasonal” hypothesis. North-west Victoria does not currently experience harsh winters (in July, the coolest month, the mean maximum temperature is 15.3°C and the mean minimum temperature is 4.4°C), and there is relatively little variation between seasons for several key climate indicators (co-efficient of variation in mean monthly values (1946 – 1996): rainfall = 16.1%; maximum temperature = 25.8%; minimum temperature = 42.6%). It is possible that an aseasonal climate set the stage for the evolution of cooperative breeding through increased longevity and sedentariness and hence formation of prolonged family alliances (Ford et al. 1988, Arnold & Owens 1999). However, the fitness advantages of cooperative breeding, and hence its evolution and maintenance in the population, may have been realized through productivity increases achieved in the irregular and infrequent good years.

Contrary to this hypothesis, some cooperatively breeding species tend to breed independently in favourable conditions and form groups in response to poor breeding conditions (Emlen & Demong 1980, Ligon & Ligon 1990a, Noske 1991, Du Plessis et al. 1995). Further, in a recent review of 10 cooperatively breeding species and data from his own work on the White-browed Scrubwren *Sericornis frontalis*, Magrath (2001) argued that group size has a larger positive effect on reproductive success.
under poor breeding conditions, whether caused by unfavourable environmental conditions or young, inexperienced breeders. The results from this study do not support this model. The proportion of units breeding independently did not change significantly between seasons and it certainly did not increase in the wetter year. The effect of helpers on fledgling productivity was positive during the better environmental conditions but neutral during the poorer season, contrary to the expectations of Magrath’s model. However, the sample size was too small to test for a differential effect of group size between experienced and novice breeders (sensu Magrath 2001).

Whether the composition of breeding units was directly driven by climate remains untested because the annual probability of natal philopatry is unknown. The dispersal patterns of young birds, and consequently the social composition of breeding units, are likely influenced by the availability of breeding positions and the relative costs and benefits of dispersal versus philopatry (Emlen 1984, 1997, Stacey & Ligon 1987). However, as natal dispersal in male White-browed Treecreepers occurs by the end of summer, it is improbable that autumn and winter rainfall acts as a proximate environmental cue for philopatry. Group composition is more likely influenced by the relative reproductive success of pairs and groups in the previous breeding season and survival during the non-breeding season, both of which may be influenced by climate. Thus, the demographic composition of the breeding population is unlikely to be directly driven by climatic variability but could be affected by the residual impact of climate on reproductive success.

**How do helpers increase reproductive success?**

Breeding strategy and laying date were the most important correlates of seasonal fledgling productivity. The mechanisms by which helpers may have assisted breeders in increasing the number of fledglings produced can be examined using the components of productivity. There was no difference between pairs and groups of White-browed Treecreepers in their propensity to attempt second broods, but groups renested more rapidly and had greater nest success in their second broods than pairs. The difference in the success of second broods accounts for most of the overall difference in productivity between breeding strategies.
The differences in productivity between breeding strategies emerged when climatic conditions (i.e. above average rainfall) stimulated earlier breeding, thereby enhancing the opportunity for multiple broods. In high rainfall years, productivity is more likely to be limited by female fecundity and the time available to raise young to independence rather than food availability. The key mechanism by which White-browed Treecreeper groups were able to capitalize on good breeding conditions was a reduction in the interval between nesting attempts (akin to Russell & Rowley 1988, Ligon & Ligon 1990, Clarke 1995, Malan et al. 1997, Langen & Vehrencamp 1999). Thus, groups commenced their second broods earlier, and hence were more likely to be successful (Martin 1987) in raising two broods within one breeding season, whereas pairs were only able to fledge a single brood.

The compensatory reductions in parental care by the female in cooperative groups (Chapter 8) were pivotal to the reduction in renesting interval. Females in groups were able to reduce their contribution to the first brood, relative to pairs, towards the end of the nestling stage. Thus, females with helpers probably achieved significant energetic savings and maintained superior body condition during this period, which enabled them to re-lay sooner (Martin 1987). Furthermore, females with helpers were able to recommence nesting when the fledglings from the first brood were younger because there were more adults to feed the dependent juveniles. Whether this occurred through a division of labour in which helpers assume responsibility for the first brood fledglings whilst the breeders renest (Rowley & Russell 1990a, Langen & Vehrencamp 1999, Van Bael & Pruett-Jones 2000), or a general dilution of the overall workload across all members of the group remains unclear. Nonetheless, it appears helpers do ‘lighten the load’ of breeders (sensu Crick 1992), facilitating increased reproductive success in groups relative to pairs under favourable breeding conditions.

There was little difference between strategies during incubation but nestling survival was significantly higher for groups, due primarily to lower probability of predation of the entire brood. However, in those nests that were successful, the number of fledglings per nest did not differ significantly between strategies, and brood reduction attributable to starvation was similar for groups and pairs.

These results infer that helpers increased the probability of success of individual nest attempts through reducing the rate of nest predation under conditions in which food
availability was not limiting. White-browed Treecreepers were observed chasing away unfamiliar conspecifics and interspecifics from near their nests and on one occasion a pair repeatedly dive-bombed and harassed a snake until it left their immediate vicinity. These observations suggest individuals are capable of active nest defence and therefore helpers have the potential to reduce nest predation through increased vigilance and nest defence (e.g. Bertram 1978, Rabenold 1990, Innes & Johnston 1996, Boland 1998). Moreover, the disparity in nest success between strategies was accentuated for second broods when parents without helpers may have been preoccupied with dependent fledglings, leaving the nest undefended and vulnerable to predators for longer periods.

The primary mechanism by which helpers increase reproductive success may explain the inconsistency of my results with the model presented by Macgrath (2001) to explain variation in group-size effects within a species. Macgrath (2001) attributed group-size effects to the incompetence of novice female breeders (e.g. later nesting, inferior provisioning skills) leading to reduced reproductive success compared with more experienced breeders. Analogously, food is likely to be scarce under poor environmental conditions, irrespective of breeder experience. Thus, helpers may compensate for the lack of parenting skills (or low food availability), such that group-size effects are manifest in the increased success of individual nest attempts only under poor conditions.

The group-size effect that I detected for the White-browed Treecreeper was primarily due to a reduction in the interval between first and second broods, resulting in an increase in the number of successful breeding attempts in a season. However, multiple broods are contingent on favourable breeding conditions. Therefore, positive group-size effects were expressed only during better breeding conditions. It may be that under severe environmental conditions (i.e. considerably worse than 1998), group-size effects become evident again, for reasons outlined by Macgrath (2001). However, given extreme environmental conditions, adult mortality is likely to increase, creating breeding vacancies and opportunities for independent breeding. Such demographic conditions are inconsistent with a rise in the incidence of cooperative breeding, although groups that do persist may enjoy greater reproductive success.
Conclusions

The data presented here clearly demonstrate that the effect of helpers on reproductive success of White-browed Treecreepers is variable, both temporally and within a population. Nestling survival, nest success and fledgling productivity were higher for groups than pairs in only one of the two seasons of the study. There was a meaningful effect of helpers on seasonal productivity after accounting for the influence of potentially confounding correlates such as habitat quality and parental experience. Seasonal productivity was significantly influenced by the timing of nesting (i.e. laying date), but laying date did not differ significantly between pairs and groups. Groups that commenced nesting early in the season were able to successfully rear two broods, whereas a successful second brood was not raised in the absence of helpers. It is argued that helpers augment reproductive success by reducing the burden of parental care on the breeding pair enabling them to renest earlier, thereby increasing the probability of success of second broods, and by assisting in nest defence and predator vigilance.

It is significant that the fitness advantages of cooperative breeding emerged during the better breeding conditions induced by higher rainfall in 1999, when opportunities for multiple broods increased. However, no advantage of cooperative breeding, in terms of increased reproductive success, was evident in 1998, when environmental conditions were less favourable. This concurs with the “irregular climate” theory (Rowley 1965, 1976, Harrison 1969) that cooperative breeding enables reproductive success to be maximised during infrequently encountered favourable breeding conditions. However, it does not fundamentally contradict the view that aseasonal environments facilitated the evolution of cooperative breeding (Ford et al. 1988, Arnold & Owens 1999).
Chapter 10

Cooperative breeding in the White-browed Treecreeper
10.1 Introduction

Cooperative breeding is characterized by the ostensibly paradoxical behaviour of individuals caring for young that are not their own. To reconcile this conundrum with the principles of natural selection, researchers have sought adaptive explanations for two essential components of cooperative breeding: (a) why do some birds delay dispersal and remain on their natal territory instead of attempting to breed independently, and (b) why do philopatric birds help? While delayed dispersal is usually a pre-requisite for helping, helping does not inevitably follow philopatry (Clarke 1995, Cockburn 1998). The adaptive basis of helping behaviour may therefore be independent of that for delayed dispersal.

The objective of this chapter is to integrate the results of the preceding four chapters into an assessment of the current utility of cooperative breeding in the White-browed Treecreeper. The underlying theme of this synthesis is to evaluate the factors that may have limited, or promoted, the incidence of cooperative breeding in the Yarrara population. I propose two primary questions:

1) What are the fitness consequences of retaining offspring as helpers for the breeding pair?

2) Why do some offspring delay dispersal and what benefits do they gain from helping?

I conclude by examining possible evolutionary pathways to cooperative breeding in the White-browed Treecreeper.

10.2 Cooperative breeding theory

The search for a unifying explanation for delayed dispersal in cooperatively breeding species has stimulated vigorous debate over the last 20 years. Juvenile birds must choose between dispersal and attempting to breed independently, or delaying dispersal and foregoing breeding in the short-term to remain in the relative safety of its natal territory. Stacey and Ligon (1991) expressed this trade-off as a general equation of fitness inequality defined by (benefits of philopatry – costs of philopatry) versus (benefits of dispersal – costs of dispersal). This equation has traditionally been
Cooperative breeding

presented in terms of either the ‘ecological-constraints’ to independent breeding versus the ‘benefits-of-philopatry’ of delayed dispersal. The ecological constraints model has focused on the costs associated with independent breeding, such as: the risk of mortality during dispersal (Emlen 1982a); intraspecific competition for rare breeding vacancies in a stable environment (i.e. habitat saturation sensu Selander (1964)) and the inability of birds to breed in marginal habitat (Koenig & Pitelka 1981); a shortage of mates (Emlen 1982a, Pruett-Jones & Lewis 1990) or the prohibitive cost of producing young in harsh environments (Emlen 1982a). The ‘benefits-of-philopatry’ model asserts that staying at home often provides a net benefit to the lifetime reproductive success of an individual (Stacey & Ligon 1987, 1991). This arises when there is extreme variation in territory quality, thereby encouraging prospective breeders in high quality territories to remain at home, replete with the advantages of group-living and the possibility of inheriting their natal territory (e.g. Ligon et al. 1991, Komdeur 1992, 1996, Hatchwell et al. 1999, Shaw & Shewry 2000).

However, the ecological constraints and benefits of philopatry models could be considered to differ only in the relative emphasis they place on the costs of dispersal as opposed to the benefits of staying (Hatchwell & Komdeur 2000). Recently, a consensus has emerged that the competing models can be encompassed within a generalist constraints approach that stresses the rate of turnover of breeding opportunities (Koenig et al. 1992, Emlen 1997, Hatchwell & Komdeur 2000). The key factor that determines the extent of cooperative breeding within a species, or population, is predicted to be the rate at which breeding vacancies arise, which is governed by the rate of population growth (difference between adult mortality and reproductive rate) and hence the existence or absence of a non-breeding surplus (sensu Brown 1987). However, all these models approach dispersal from the perspective of the offspring. In contrast, Cockburn (1996, 1998) emphasized the role of the breeders in either tolerating offspring as helpers as a mechanism to maximize their lifetime reproductive success or expelling offspring in situations where the costs of retaining helpers are prohibitive.

The framework for explanations of alloparenting behaviour is not as cohesive. One adaptive explanation that has received strong support is kin selection theory (Hamilton 1964) - an increase in the inclusive fitness of helpers derived from
increased production of non-descendent kin (Clarke 1984, Brown 1987, Smith 1990, Emlen 1997). This is predicated on three ground-rules: (i) that cooperative groups have greater reproductive success than unassisted pairs under certain ecological or demographic conditions, (ii) that helpers are closely related to the young they assist, and (iii) that the alloparental care provided by helpers contributes to the increased productivity of groups (Williams 1966b, Lack 1968, Brown 1978, 1987). However, growing scepticism of these three tenets has led to re-evaluations of the importance of kin selection in helping and challenges to the adaptive basis of helping behaviour (Jamieson 1989, 1991, Craig 1991, Dunn et al. 1995, Magrath & Whittingham 1997, Heinsohn & Legge 1999, Wright et al. 1999).

Alternatively, helping may have direct fitness benefits whereby the survivorship of individuals is enhanced by the benefits of group-living or the future probability of breeding is increased (Emlen et al. 1991, Clarke 1995, Cockburn 1998). Direct fitness benefits negate the importance of increased reproductive productivity and kinship in adaptive explanations of helping.

10.3 Fitness consequences for the breeding pair

The major quantifiable fitness benefit of helpers to breeding White-browed Treecreepers was an increase in annual fledgling productivity, due to expeditious re-nesting and enhanced success of second broods. Female, and to a lesser extent male, White-browed Treecreepers with helpers probably realized energetic savings due to compensatory reductions in provisioning. In other cooperative breeding species, such reductions have been correlated with increased breeder survival (Austad & Rabenold 1986, Tidemann 1986, Russell & Rowley 1988, Crick 1992). A powerful comparison of breeder survival was not possible in this study, but differences in the incidence of the disappearance of breeders suggest survival may be higher in cooperative groups. The future component of the breeders’ fitness may be enhanced if kin that remain as helpers are more successful when they eventually obtain a breeding position than offspring that disperse in their first year (Emlen 1984, Walters et al. 1992, Komdeur 1996, Hatchwell et al. 1999). Further research comparing the lifetime reproductive success of offspring that remain as helpers with those that disperse and attempt to breed independently would provide valuable insights to this fitness component.
Cockburn (1996) contends that the best way for breeders to insure against total lifetime reproductive failure may be to extend parental care to include the provision of a breeding territory (also see Russell 2000). This may be achieved by sharing mating opportunities with offspring [i.e. reproductive skew theory (Emlen 1982b, 1997, Vehrencamp 1983a, 1983b, Pusey & Packer 1997)] or territory inheritance. Either way, it begs the question as to the role played by parents in facilitating philopatry as a means for securing a minimum level of lifetime reproductive success (Cockburn 1996, 1998). Under this scenario, the threshold number of helpers that will benefit breeders is likely to be low – an excess of helpers would decrease breeder fitness if reproduction was shared among many individuals and the territory cannot be inherited by multiple offspring. Furthermore, productivity gains from many helpers are likely to be modest given the low fecundity and relatively long nesting cycle of the White-browed Treecreeper. Therefore, above a certain group size, breeder fitness is increased by expelling offspring from their territory once they reach independence. The small group size, patrilineal territory inheritance and dispersal of young males when helpers were already present were consistent with Cockburn’s view that the role of the breeders may be greater than previously recognized. However, although parents may be able to evict juveniles, they cannot force them to stay and the impetus for delayed dispersal must still come from the juveniles.

The fitness advantages of cooperative breeding for White-browed Treecreepers must be reconciled with the fact that the majority of breeding units comprised unassisted pairs. This may occur in populations that are expanding in recently colonized habitat (e.g. Komdeur 1992) or in which net population growth is negative (e.g. Austad & Rabenold 1986), neither of which applies to the White-browed Treecreeper population at Yarrara. Therefore, assuming that breeders have the capacity to expel offspring, it follows that the cost-benefit trade-off for breeders must not always favour retention of offspring as helpers. Perhaps I have placed an over-emphasis on the unusually good breeding conditions of 1999 at the expense of considering fitness benefits of breeding as an unassisted pair during more typical, and stressful, environmental conditions [e.g. mitigating the impacts of food limitation (Martin 1987)]. As Macgrath (2001) points out, the adaptive significance of breeding in groups depends on how frequently birds breed in conditions that favour cooperative breeding.
Clarke (1995) warns that significant ecological events (e.g. unusually wet or dry years) can have major implications for the conclusions that can be drawn from studies in unpredictable climatic regions. This study coincided with the end of a prolonged period of below average rainfall (i.e. pre-1999). If cooperative breeding is density-dependent (e.g. Komdeur 1992), the high proportion of pairs in the breeding population in 1998 may reflect high adult mortality and low reproduction in the years preceding my investigations, creating many opportunities for independent breeding and reducing the non-breeding surplus from which helpers are drawn.

10.4 Why delay dispersal?

Constraints to independent breeding

A fundamental result from this study was that fledgling productivity exceeded adult mortality, generating an excess of potential breeders relative to breeding positions available – the “non-breeding surplus” in the parlance of Brown (1987). That several of these surplus individuals delayed dispersal rather than attempting to breed independently, suggests suitable breeding habitat was limited. Within the study plot, virtually all available habitat was occupied by established breeding units, which prevented surplus individuals from founding new territories. Unoccupied pockets of Belah woodland, or habitat in the adjacent mallee woodland or farmland, were presumably of such poor quality that individuals preferred to delay dispersal than colonize low quality habitat. Furthermore, there was no evidence of partitioning of existing territories among group members (i.e. territorial budding) (e.g. Woolfenden & Fitzpatrick 1990). Breeding vacancies in established territories were rare and were filled promptly when they did arise.

Thus, independent breeding at Yarrara appears to be constrained by the saturation of suitable habitat with established territories and intense competition for breeding vacancies (sensu Selander 1964, Koenig & Pitelka 1981). This may have promoted natal philopatry, as has been suggested for the closely related Red-browed Treecreeper (Noske 1991) and Rufous Treecreeper (Luck 2000). For the White-browed Treecreeper, the specific ecological constraint is probably a satisfactory food supply (i.e. dominance of foraging trees), which given the homogeneity of habitat in the study plot, is governed by minimum area requirements. In short, there simply is
not enough space for an increase in the number of breeding territories. However, in some parts of the woodland, the ecological constraint on establishing breeding territories may be the availability of nest sites (Chapter 7).

However, evidence of habitat saturation is not necessarily evidence that it was the cause of delayed dispersal in White-browed Treecreepers. It does not explain why philopatry was not observed in females, as they face the same shortage of breeding vacancies (Cockburn 1998). It does not explain why surplus individuals delay dispersal rather than pursuing an alternative strategy, such as floating (Koenig et al. 1992). It does not explain why surplus individuals of non-cooperative species, confronting similar constraints to independent breeding, do not delay dispersal (Koenig et al. 1992, Smith 1994). Finally, philopatry and helping may have led to habitat saturation through enhanced productivity, not the other way round, introducing ambiguity in the direction of causality among habitat saturation, philopatry and enhanced productivity (Austad & Rabenold 1986, Zack 1990). Therefore, alternative explanations for philopatry should be explored.

A male-biased sex ratio has been suggested to lead to a shortage of female mates promoting male philopatry, particularly in populations in which only a moderate fraction of breeding units have helpers (Rowley 1965, Brown 1987). Although some species may be able to manipulate the sex ratio of offspring to bias the helping sex (Ligon & Ligon 1990b, Komdeur et al. 1997), in general, male-biased sex ratios in the adult population are a consequence, rather than a cause, of male philopatry (Emlen et al. 1986). This appears to be the case for White-browed Treecreepers, in which the ratio of male to female fledglings was equal. The sex ratio of all adults banded in the study plot was very close to equal, with transitory and “floating” females complementing the slight male-bias in the sex ratio of breeding units. The persistence of non-breeding, non-helping “floating” females in the population indicates potential mates are available for male helpers. Thus, there is no evidence that a shortage of breeding partners may discourage males from attempting to breed independently.

The high mortality associated with inter-patch dispersal may have, in the main, restricted dispersing individuals to their natal habitat patch, leading to the retention of the non-breeding surplus within a limited area of suitable habitat and hence habitat saturation. Thus, the costs of dispersal may have promoted philopatry directly
through a constraint on independent breeding (Emlen 1982a) as well as indirectly through facilitating habitat saturation. The weakness of this argument is that it should apply equally to females and males, whereas delayed dispersal appeared to be confined to males.

**Benefits of philopatry**

Fledgling productivity per season was not significantly affected by variation in territory quality or territory size, nor by territory identity, when included as a random effect. In addition, I could not identify a critical resource that may engender variation in territory quality sufficient to entice individuals to remain in high quality natal territories whilst forfeiting the opportunity to breed independently. This suggests that the central tenet of Stacey and Ligon’s (1987, 1991) ‘benefits of philopatry’ hypothesis for delayed dispersal – that variation in territory quality renders territory identity the primary determinant of lifetime reproductive success – does not hold for the White-browed Treecreeper population at Yarrara.

However, there was significant variation in the reproductive success of individuals living in groups of different sizes (i.e. between breeding strategies), such that group size itself may be the crucial benefit obtained from philopatry (Stacey & Ligon 1991). Moreover, the among-territory co-efficients of variation in total fledglings per territory and mean number of fledglings per season per breeder, exclusive of the effect of breeding strategy, were 69.8% and 54.4%, respectively. These values are concordant with the examples used by Stacey and Ligon (1991) to demonstrate high among-territory variance in fitness-related parameters in cooperatively breeding species to show that lifetime reproductive success is dependent on the particular territory in which an individual eventually breeds. Stacey and Ligon (1991) contend that such variation is not consistent with the ‘ecological-constraints’ hypothesis, and is sufficient incentive for offspring to delay independent reproduction in order to increase their chances of breeding in their natal territory. Although this provides a satisfactory explanation for philopatry in the White-browed Treecreeper above that of habitat saturation, the quandary remains that productivity could not be linked to variation in habitat quality *per se*.
Cooperative breeding

There are several possible reasons for this. First, the sample size of breeding territories was small and the duration of my study was short. Thus, my assessment of the benefits of philopatry is based on surrogate variables, such as habitat quality and reproductive success, rather than a direct appraisal of the dispersal decisions of young birds from contrasting territories. The treecreeper’s perspective of habitat quality may differ from my interpretation of their behaviour. It would also be educative to know if the extent of among-territory variation in demographic variables persists over a longer time-span.

Second, the benefits of philopatry model is most likely to apply when there is extreme variation in habitat quality. In this study, variation in habitat quality was low, suggesting that all territories were ‘high’ quality and thus, not a fair test of the hypothesis. When applied on a larger scale across several populations, variation in habitat quality may be an important determinant of dispersal strategies. Third, the strongest test of the benefits of philopatry model should occur in non-saturated habitats (e.g. Zack & Ligon 1985b, Austad & Rabenold 1986, Ligon et al. 1991, Komdeur 1992, Walters et al. 1992). Therefore, it would be instructive to investigate the social organisation and reproductive success of a second population of White-browed Treecreepers under a less constrained set of environmental and demographic conditions. A good candidate for such a comparison would be the population at Wyperfeld NP, which persists at a lower density than at Yarrara.

Other dispersal strategies are available to male juveniles that cannot obtain a breeding territory, such as ‘floating’ or ‘roaming’. That a considerable proportion of male offspring prefer to delay dispersal, or forego dispersal entirely, implies that they do obtain intrinsic benefits from philopatry even in the absence of extreme variation in territory quality. In particular, inheritance of the breeding position (e.g. Koenig & Stacey 1990, Rabenold 1990, Magrath & Whittingham 1997, Kokko & Johnstone 1999), or replacement of a breeder in an adjacent territory (e.g. Ligon & Ligon 1990a, Walters 1990) may be more profitable for securing a breeding than the alternative strategies that involve dispersal. Individuals from adjacent territories regularly fill male breeding vacancies in other treecreeper species (Noske 1991, Luck 2000). One instance of putative inheritance of a natal territory by a helper was recorded during this study.
Cooperative breeding

It appeared that dominance hierarchies within family groups influenced the decision to stay or disperse. When helpers were present in the natal breeding unit, male juveniles were less likely to delay dispersal compared to the male offspring of pairs. This is consistent with Stacey and Ligon’s (1991) assertion that dispersal strategies will vary within populations, with those individuals with little chance of inheriting their natal territory choosing to disperse, even from good quality territories. Therefore, from the juveniles’ perspective, territory quality in homogeneous, saturated habitat may not be determined by habitat attributes or breeding success, but by the social composition of the natal breeding unit and the probability of territory inheritance given their position in the dominance hierarchy.

That some female White-browed Treecreeper juveniles delay dispersal until just prior to the following breeding season (when they are probably dispelled by the breeding female) implies that there may also be advantages to philopatry that are not related to territory inheritance. These are most likely to be associated with group living and may include: enhanced survival of individuals through more effective predator detection (Bertram 1978) and hence greater foraging efficiency (Pulliam 1973), greater access to resources due to larger and better defended territories (Craig 1984, Woolfenden & Fitzpatrick 1990, Legge 2000) or acquiring the experience and skills necessary for efficient foraging (Heinsohn 1991b) or breeding (Komdeur 1996, Hatchwell et al. 1999).

How relevant is each of these benefits of group living for the White-browed Treecreeper? Increases in group size may enhance detection of snakes and forest raptors (e.g. Collared Sparrowhawk *Accipiter cirrhocephalus* and Brown Goshawk *Accipiter fasciatus*) due to the “many eyes” maxim. An increase in foraging efficiency through shared vigilance usually relates to flocking birds (Lima 1990) but White-browed Treecreepers do not congregate in large flocks, so would not be expected to gain substantial increases in foraging efficiency from group living. However, species that forage on tree-trunks face a unique situation in that their foraging substrate also provides their refuge from predators. Lima (1992) showed that vigilance amongst Downy Woodpeckers *Picoides pubescens* decreased in the presence of other birds, implying that foraging efficiency in trunk-foraging birds may be positively correlated with group size. More data on the respective survivorship of individuals in groups and pairs is required to properly assess this postulate in
Cooperative breeding
treecreepers, although the positive correlation between survival and group size in male Rufous Treecreepers (Luck 2000) provides preliminary support.

The absence of a significant relationship between breeding strategy and territory size of the White-browed Treecreeper suggests group living per se does not enhance access to resources or larger territories. However, an individual that is an accepted member of a breeding unit probably has better access to foraging resources and less antagonism than a floating or roaming individual in hostile territories. This may encourage philopatry in those individuals unable to obtain a breeding position. Although the foraging niche of treecreepers is specialized, the observation that juveniles are able to forage independently and disperse after only a few months suggests the skills required for efficient foraging are readily achievable and do not require prolonged learning in a group setting. Similarly, group living did not appear to be obligatory to acquire the skills necessary for successful breeding.

Thus, habitat saturation, brought about through high adult survival and high quality territories, results in a low rate of turnover of breeding vacancies, constraining opportunities for independent breeding. On the other hand, among-territory variance in reproductive parameters is high, due largely to the differences in productivity between breeding strategies, which may confer intrinsic benefits to individuals that remain in their natal territories. However, the casual relationship between philopatry and productivity (and therefore high among-territory variance) remains ambiguous.

**Sex bias in dispersal**

Although the synergy of extrinsic constraints to independent breeding and intrinsic benefits of philopatry offers one explanation for delayed dispersal, it remains perplexing that this strategy is not exploited by both sexes. Given that male White-browed Treecreepers are socially dominant and incestuous matings appear to be eschewed, females are unlikely to secure a breeding position through inheritance of their natal territory (e.g. Woolfenden & Fitzpatrick 1986). Therefore, it may be more profitable for females to disperse. This is consistent with Greenwood’s (1980) more general model of mating systems, in which dispersal is predicted to be female-biased to minimize inbreeding in those systems where the male reproductive strategy is based on defence of resources and attraction of a mate (e.g. White-browed
Cooperative breeding

Treecreeper). Females may benefit from dispersal by assessing several potential mates before settling (Greenwood 1980).

Female-biased dispersal may also stem from conflict between resident females and the inability of females to share reproduction (i.e. plural breeding, nest sharing or polygyny) because it leads to an unsustainable and sub-optimal brood size within the territory (Chao 1997). In support of this hypothesis, non-breeding females were routinely expelled from territories before the breeding season, suggesting the female-bias in dispersal may be determined more by parental aggression than the free will of the offspring. In addition, the small brood size and low reproductive rate of the White-browed Treecreeper suggests larger broods may not be achievable, which provides an impetus for the expulsion of secondary females.

10.5 Why do philopatric males help?

The role of kin selection

An increase in the inclusive fitness of individuals, derived from increased production of non-descendent kin, has often been postulated as the selective mechanism for helping behaviour (e.g. Clarke 1984, 1989, Dickinson et al. 1996, Emlen 1997, Langen & Vehrencamp 1999, Khan & Walters 2000; but see Cockburn 1998). To be adaptive, the inclusive fitness benefit of delaying dispersal and helping must exceed the alternative strategy of dispersal and independent breeding. The current utility of helping in the White-browed Treecreeper, in terms of the indirect component of a helper’s inclusive fitness, can be estimated (following Mumme 1992). I assume that the costs of helping for White-browed Treecreepers are negligible (Crick 1992, Mumme 1992 but see Heinsohn & Legge 1999) and that the increased reproductive success in groups was entirely due to the alloparental care of helpers. Although this probably over-estimates the benefits of helping, the costs of dispersal and the probability of finding a territory and a mate are ignored, which overstates the fitness benefits of independent breeding (Brown 1978).

Pooled across both seasons, groups produced an average of 0.987 more fledglings per breeding unit per season than pairs. If the additional fledglings are partitioned by the mean number of helpers per group (11 helpers / 9 group-years = 1.222 helpers
per group), the average increase in productivity attributable to each helper was 
\((0.987 / 1.222) = 0.808\) fledglings per helper per season. The relatedness of helpers to 
the recipient brood was not known at all nests. Therefore, a range in the mean 
coefficient of relatedness between helpers and their recipient brood \((r_{HR})\) was 
calculated. If helpers of unknown origin were assumed to be half-sibs of the brood 
they assisted \((r_{HR} = 0.25)\), the minimum mean co-efficient of relatedness among the 
11 helpers was 0.33. In contrast, the maximum mean co-efficient of relatedness \((r_{HR} = 0.46)\) assumed helpers of unknown origin were full-sibs of the recipient brood \((r_{HR} = 0.50)\). This is compared with a coefficient of relatedness of 0.50 between parents 
and offspring \((r_{HO})\).

The increase in a helper’s inclusive fitness that is attributable to allopasternal care (i.e. 
the indirect component of inclusive fitness) was calculated as the product of \(r_{HR}\) and 
the mean increase in fledgling productivity in groups (0.808). This ranged from 0.27 
to 0.37 fledgling equivalents per helper per season compared with the direct fitness 
benefits from independent breeding of 0.62 fledgling equivalents per season. Thus, 
breeding is more productive than helping if a breeding position can be obtained. 
Nonetheless, although crude, these figures indicate that allopasternal behaviour can 
substantially increase the inclusive fitness of individuals unable to obtain an 
independent breeding position. In addition, if helpers increase the survival of 
breeders or the probability that breeders will have helpers in subsequent years, 
helpers will further enhance their inclusive fitness by virtue of the future, or deferred, 
component of indirect fitness (Mumme et al. 1989, Creel 1990, Crick 1992, 
Cockburn 1998).

Importantly, when calculated separately for each season, the indirect fitness gained 
from helping in 1998 was only 0.044 – 0.063 fledgling equivalents per helper 
compared with 0.563 fledgling equivalents per independent breeder. Thus, 
independent breeding returned substantially greater fitness benefits than helping in 
1998, assuming a territory could be obtained. However, in 1999, helping was much 
more profitable, with indirect fitness gains of 0.417 – 0.556 fledgling equivalents per 
helper. However, breeding was still more productive with 0.667 fledgling equivalents 
per independent breeder. This demonstrates the seasonal variability in the adaptive 
advantage of allopasternal behaviour from the helper’s perspective. This variability 
underpins the heterogeneity in breeding strategies present in the White-browed
Cooperative breeding

Treecreeper population at Yarrara. Thus, given a low probability of gaining an independent breeding territory, the option to help provides a profitable alternative means for young White-browed Treecreepers to maximize their inclusive fitness, supporting the hypothesis that kin selection is a key mechanism by which cooperative breeding is maintained in the White-browed Treecreeper population.

Alternative explanations for helping

Cockburn (1998) contends that the evidence for inclusive fitness gains from helping is more compelling for females, and that males usually help to enhance their direct fitness. Therefore, alternative explanations for helping in the White-browed Treecreeper ought to be canvassed. It is likely that helping provides fitness benefits to non-breeders from several quarters concurrently and that a single, generalized explanation will be neither universally satisfactory nor specifically applicable in many cases (Emlen et al. 1991, Ligon & Stacey 1991, Clarke 1995). Cockburn (1998) grouped the many hypotheses for helping into six adaptive explanations. The first of these, increased production of non-descendent kin, was considered above.

Second, helpers may obtain direct fitness benefits from living in a group or inheriting the natal territory, as discussed in relation to philopatry. However, the presence of helpers may impose costs upon the breeders in terms of shared resources, and helping behaviour may have evolved as ‘payment’, in response to parental coercion, for remaining in the group or on the territory (Gaston 1978b, Dunn et al. 1995). Contrary to the predictions of the payment hypothesis (Clarke 1995), semi-resident non-helping female White-browed Treecreepers were occasionally tolerated by breeders. This is difficult to reconcile with the payment hypothesis other than to suggest that breeders may have viewed the non-helping females as potential mates for the resident helpers, thereby facilitating breeding opportunities for their offspring (i.e. the helper). In support of this, the helper regularly escorted the non-helping female and was observed to provision her with items of food.

The third adaptive explanation for helping relates to access to mating opportunities, either within the group (e.g. Macgrath & Whittingham 1997), outside the group (e.g. Brooker et al. 1990, Mulder et al. 1994) or in the future (e.g. Reyer 1990, Sherley 1990, Luck 2000). In the absence of molecular data, it is difficult to assess the
importance of extra-pair fertilizations for helpers either within or outside their group. However, within-group reproductive sharing would be limited to those atypical groups in which the helper and the breeding female are unrelated, and I have argued against the likelihood of extra-pair fertilizations outside the group in Chapter 6. Access to mating opportunities in the future also largely pertains to ‘step-families’ although a different perspective is given by one unusual case. In territory 13, the male disappeared near the end of the incubation period (Fig. 6.4). He was immediately replaced by a putatively unrelated male, who had not been observed assisting in that territory previously. The replacement male continued to care for the female and the ensuing brood, fulfilling the definition of a helper, without the inclusive fitness benefits. However, by demonstrating his parenting abilities, the male became ensconced in the territory and gained paternity for the second brood (which failed) and presumably for subsequent breeding seasons.

The fourth of Cockburn’s (1998) categories is ‘enhancement of local conditions’ through expansion of the territory (e.g. Woolfenden & Fitzpatrick 1990) or reciprocity, in which helpers benefit because the young they assist may later help them in breeding (Trivers 1971). For White-browed Treecreepers, there was no evidence that an increase in group size enhanced territory size and because juveniles tended to disperse when helpers were already present, the opportunity for reciprocity was minimal. Even in species in which contact between helpers and the recipient brood is maintained, reciprocity has not been substantiated (Clarke 1995, Cockburn 1998, Khan & Walters 2000).

Fifth, strategic alliances between helpers or between helpers and the young they assist may enhance the success of helpers in obtaining a breeding territory in the future (Emlen & Demong 1980, Zahavi 1990, Heinsohn 1991a). This has been reported for the Brown Treecreeper (Higgins et al. 2001) but does not appear relevant to White-browed Treecreepers because the small number of helpers in most cooperative groups limits the establishment of coalitions between helpers, group dispersal was not detected and juveniles dispersed in the presence of older helpers. Finally, helping may provide valuable experience that increases productivity when helpers eventually breed independently (Cockburn 1998). Evidence in support of this hypothesis is mounting (e.g. Komdeur 1996, Hatchwell et al. 1999, Van Bael &
Cooperative breeding

Pruett-Jones 2000) but experience was not a good explanatory variable of productivity for White-browed Treecreepers.

Thus, kin selection provides the most persuasive argument for helping in the White-browed Treecreeper given the demonstrable gains in the indirect component of inclusive fitness. Males may also derive some direct fitness benefits from helping as a form of payment for the privilege to remain in the natal territory or to gain access to future mating opportunities. However, the male-bias in helping can not be explained by specific benefits of helping available only to males. It is more likely to be an artifact of the female-bias in dispersal. That is, if females delayed dispersal, they would be expected to help as well, as occurs in other treecreeper species (Noske 1991, Luck 2000). However, as discussed previously, the female-bias in dispersal may be due to benefits of philopatry that are exclusive to males.

10.6 Evolution of the White-browed Treecreeper breeding strategy

The relative importance of life-history and ecological factors in the evolution of cooperative breeding has occupied researchers for several decades (e.g. Ricklefs 1974, Dow 1980a, Ford et al. 1988, Arnold & Owens 1998, 1999). The low reproductive rate and low annual adult mortality of White-browed Treecreepers are demographic attributes typical of cooperatively breeding species (Brown 1987, Hatchwell 1999; but see Poiani & Jermiin 1994). Following the proposition of Arnold and Owens (1998, 1999), low mortality is the key factor that predisposed the White-browed Treecreeper to cooperative breeding, although ecological factors were probably crucial in the adoption of cooperative breeding. The absence of severe winters may have enabled permanent occupation of territories, leading to habitat saturation and delayed dispersal (Ford et al. 1988, Arnold & Owens 1999). However, the circularity of this argument precludes a definitive assessment of the sequence of events (Hatchwell & Komdeur 2000). That is, did an aseasonal and warm climate result in low mortality or was low mortality a phylogenetic trait common to the treecreeper lineage before radiation into the arid woodlands of the Australian interior? It was likely that several factors were operating simultaneously to slow the rate of turnover of breeding opportunities, facilitating selection for delayed dispersal in this species.
Cooperative breeding

The role of phylogeny in the current expression of cooperative breeding casts a different light on the evolutionary pathway. Cooperative breeding is a highly conserved trait in avian evolution (Cockburn 1996). Therefore, the predominance of cooperatively breeding species in lineages such as the Climacteridae and Maluridae probably reflects phylogenetic inertia rather than independent evolution in each species (Russell 1989, Ligon 1993, Cockburn 1996). This has two important implications. First, cooperative breeding may persist in contemporary species as a relic of their phylogenetic history but may be selectively neutral or be eroding out of the population under current ecological or demographic conditions. This may explain the occurrence of cooperative breeding in a minority of breeding unit-years in the White-browed Treecreeper. However, evidence from this study indicates there was current utility of cooperative breeding for both breeders and helpers. This points to the second implication: that neither life-history nor ecological factors peculiar to the White-browed Treecreeper may satisfactorily explain the evolutionary origin of cooperative breeding in this species, although they may account for the current utility and persistence of the strategy (Ligon 1993). These possibilities could be explored via data collected over a longer period and under contrasting ecological conditions to assess the adaptive flexibility of White-browed Treecreepers with respect to their breeding strategy. I emphasize the need for further research to determine whether my hypotheses about the breeding strategy of the White-browed Treecreeper are typical of the species or peculiar to specific conditions of the study or the population at Yarrara.

Comparisons with other species of treecreeper may provide insights into the evolutionary history of cooperative breeding in this species. Helpers were present in a lower proportion of White-browed Treecreeper breeding units (36%) than in other Climacteris species, in which the fraction was closer to two-thirds (Noske 1991, Luck 2000). In contrast, the White-throated Treecreeper breeds exclusively in pairs (Noske 1991). How might these differences have evolved within the same family?

Ford et al. (1988) suggest that group living (and ultimately cooperative breeding) would be favoured in species vulnerable to predation, such as birds of open woodlands that forage predominantly on the ground. The White-throated Treecreeper is exclusively arboreal (Noske 1979), which conforms with expectations. Both the Brown Treecreeper (Noske 1979, Walters et al. 1999) and the Rufous Treecreeper
Cooperative breeding

(Luck et al. 2001) spend more time foraging on the ground than the White-browed Treecreeper (personal observation) and therefore may gain greater benefit from group living. Hence, selection for philopatry and cooperative breeding may be stronger in the Brown Treecreeper and Rufous Treecreeper than in the White-browed Treecreeper on this basis alone.

Further, the larger group size and propensity for cooperative breeding in the Brown Treecreeper and Rufous Treecreeper may be related to body size, and specifically larger nestlings (but see Poiani and Jermiin 1994). More helpers may be necessary to satisfy the energy requirements of larger nestlings, compared to smaller treecreeper species. In support of this, the overall rate of nestling provisioning is higher in larger treecreepers. An autecological study of the Black-tailed Treecreeper has not been conducted, although cooperative breeding has been confirmed (Noske 1980). Based on its large size, preference for open Eucalyptus woodland and its terrestrial foraging habits (Higgins et al. 2001), I expect that a majority of Black-tailed Treecreeper breeding units would contain helpers.

Cooperative breeding may be more prevalent in those species that are habitat specialists, unable to exploit marginal habitat, than habitat generalists because the constraints on independent breeding are intensified (Zack & Ligon 1985a, Koenig et al. 1992). Noske (1991) ventured that the specialized foraging, roosting and nesting requirements of the Red-browed Treecreeper were the principal reasons for the evolution of cooperative breeding in this species. White-browed Treecreepers appear to be able to exploit other foraging substrates more than Red-browed Treecreepers (e.g. ground, shrubs) and were not severely limited by nest sites (Chapter 7). Thus, there may be more opportunity for young White-browed Treecreepers to breed independently.

The scale and landscape context of the respective study areas may have ramifications on breeding behaviour, particularly as the species have similar area requirements per territory. The Red-browed Treecreeper was studied in a 50 ha study area at Wollomombi Falls that was surrounded by unsuitable habitat (Noske 1979, 1991). In contrast, this study focused on a 100 ha study plot within a much larger remnant (2200 ha) of predominantly suitable habitat. Therefore, the probability of successful short-distance dispersal to establish an independent breeding territory may have been greater at Yarrara than Wollomombi Falls, resulting in a lower incidence of
cooperative breeding. Moreover, both studies were limited in their spatial extent, whereas the incidence of cooperative breeding may vary considerably across a species range (e.g. Austad & Rabenold 1986, Rowley & Russell 1993, Luck 2000).

10.7 Conclusions

Given the landscape modifications that have occurred in north-west Victoria over the last century (LCC 1987), it is possible that the selection pressures currently experienced by White-browed Treecreepers differ markedly from those in operation during the evolution of cooperative breeding in this species. Nonetheless, cooperative breeding and helping behaviour appear to have current selective utility from the perspective of both breeder and helper, particularly in populations with limited independent breeding opportunities and under favourable climatic conditions for breeding. Elements of both the ‘ecological constraints’ (Emlen 1982a) and ‘benefits of philopatry’ (Stacey and Ligon 1987) hypotheses are invoked to explain philopatry in the White-browed Treecreeper, suggesting a more generalist framework is warranted, such as the ‘delayed-dispersal threshold’ model (Koenig et al. 1992). The role of breeders in facilitating philopatry as a means for ensuring their offspring obtain a breeding position is probably greater than is generally appreciated. Helping behaviour appears to increase the inclusive fitness of philopatric individuals.

However, the persistence, and indeed numerical dominance, of unassisted breeders in the population suggests that selection does not always favour cooperative breeding. Pairs may be selectively favoured under conditions of environmental stress, particularly if food resources become limiting for adult survival. Under such conditions, breeders may evict helpers from their territories, regardless of kinship. Longer-term data from multiple sites is required to fully understand the intricacies of those environmental and demographic factors operating on dispersal decisions and therefore influencing the relative frequency and success of the two strategies.
Chapter 11

Conclusions
11.1 Conservation status of the White-browed Treecreeper

This thesis presents empirical data documenting key ecological and life-history traits of the White-browed Treecreeper. In many areas of investigation, this represents the first empirical data collected for this species. I have outlined the distribution of the species in north-west Victoria, providing a sound basis for future comparisons, and identified biophysical and habitat features that influence its distribution across several spatial scales. New information is presented on the species’ habitat requirements for foraging and nesting. I conducted an intensive study of the social organization and breeding biology of the White-browed Treecreeper, which provided novel data on the breeding strategy, survival, territoriality, nesting biology, reproductive success and parental care of the species.

This research supports the listing of the White-browed Treecreeper as threatened under the Victorian Government’s Flora and Fauna Guarantee Act (1988). The species is restricted to remnant Belah and Pine-Buloke woodland, with the majority of the Victorian population located in Yarrara FFR, Mallanbool FFR and the Pine Plains district of Wyperfeld NP. Significant populations also persist in Meringur FFR, Timberoo FFR and pockets of Belah woodland in the Murray-Sunset NP (Mopoke Hut area and northern boundary). Populations of less than five pairs can be found in woodland fragments in the Yarrara district and near the townships of Walpeup and Patchewollock. Thus, the species is rare in terms of distribution.

Population density could not be reliably estimated during the regional surveys (Chapter 2). Moreover, the effective population size is likely to be smaller than the observed density, due to surplus male helpers in cooperative groups. A more precise estimate of population density can be obtained from the breeding study at Yarrara FFR, where 15 breeding pairs (with or without helpers) were detected in approximately 130 ha. However, this is unlikely to be representative of other populations because density was patently higher at Yarrara FFR and Mallanbool FFR than any of the other occupied patches. At Wyperfeld, an estimate of only 2.5 pairs per 100 ha was derived from many hours of observation of colour-banded individuals during the habitat selection study. White-browed Treecreepers were not detected on any of the 10 surveys at Timberoo FFR but are known to occur there. Presumably, they persist at lower densities at Timberoo than patches where they were detected. If these crude estimates are extrapolated to all habitat known to be occupied by the
White-browed Treecreeper, an upper estimate of the effective population size in Victoria is 480 breeding pairs. The worst case scenario is around 380 pairs. Clearly, the species is also rare in terms of abundance, although locally common in a small number of reserves.

Comparison of the current distribution of the White-browed Treecreeper with historical records indicates its range is contracting. There is rarely a single factor, or combination of factors, demonstrably responsible for the decline of a species (Harris 1988, Date et al. 2000). In this instance, range contraction originates from habitat loss and the subsequent insularization of remnant habitat. The White-browed Treecreeper is a habitat specialist. Therefore, destruction of its habitat will result in population decreases because it is unable to survive in alternative habitat. Furthermore, I have demonstrated that it is unlikely to occupy very small or isolated patches: that is, it is sensitive to habitat fragmentation. Thus, the extent of population decline is likely to be proportionally greater than expected from habitat loss alone (Andrén 1994, With & Crist 1995). Accordingly, configuration of remnant habitat will affect the probability of persistence of local populations.

Other factors have contributed to the decline of the White-browed Treecreeper. Grazing by stock suppresses regeneration of woodland trees and reduces the diversity and abundance of the shrub community. This reduces the quality of the woodland as habitat for the White-browed Treecreeper. Population density is likely to be lower in woodlands with fewer and smaller trees, and in woodlands without a healthy shrub community. Further, sustainability of treecreeper populations is compromised in woodlands with limited recruitment of hollow-bearing nest-trees. Several woodlands that currently support White-browed Treecreepers are senescing and rapidly losing hollow-bearing trees through wind and fire damage. The impact of feral predators on fledgling survival may also be contributing to the decline of the species. A reduction in habitat quality (due to grazing or feral predators) may not be sufficient to cause range contraction on its own but is likely to increase the susceptibility of small populations to stochastic extinction by reducing population density (Shaffer 1981, Gilpin & Soulé 1986). Thus, the decline of the White-browed Treecreeper has arisen from the cumulative and synergistic effects of habitat loss, habitat fragmentation and habitat degradation (i.e. impacts of grazing and feral predators).
What is the current level of threat to the White-browed Treecreeper population from these factors? Although Belah and Pine-Buloke woodlands in north-west Victoria are now protected under vegetation clearance controls, illegal clearing on private land remains a threat. Even if the size of the illegally cleared patches is too small to support White-browed Treecreepers, the cumulative effect of incremental losses will continue to harm the species by reducing the functional connectivity of the landscape. However, the residual effect of historical habitat loss on the current population is of greater concern. Given the susceptibility of the species to habitat fragmentation, it is feasible that the consequences of habitat loss for the White-browed Treecreeper population have yet to be fully realized. Grazing by stock continues to limit regeneration of native vegetation in many remnants on private land. Kangaroos, goats and rabbits pose a similar threat in public reserves and parks. The restricted distribution of the treecreeper in north-west Victoria means that localized catastrophic events, such as fire, wind-storms and disease, will affect a larger proportion of the regional population than when its distribution was more widespread. Thus, the White-browed Treecreeper is prone to future threats and liable to continued decline from past practices.

11.2 Implications for management

What needs to be done to firstly, arrest the decline and secondly, ensure the sustainability of the White-browed Treecreeper in north-west Victoria? Survival of the species is not assured simply by creating conservation reserves, although this was the critical first step (LCC 1987). Active management of the reserves and ecosystem restoration within agricultural landscapes is now critical (Goldney et al. 1995, Hobbs & Saunders 2000). The goal must be to create, restore or preserve landscapes that contain sufficient habitat of adequate quality to support a viable and interactive local population, with connections to other local populations that allow for genetic exchange over generations. This presents many challenges for land managers, which must be met at several spatial scales (see Chapter 5).

Management agencies cannot resource autecological studies on all species of conservation concern, let alone all inhabitants, within the semi-arid woodlands of north-west Victoria. However, many of the overarching principles involved in the
development of these recommendations hold true for other species. Therefore, the recommendations that follow may benefit other woodland species, and, in the absence of more informed data, provide a useful template for the management of a range of species. In particular, management actions that focus on landscape restoration and increasing structural connectivity are likely to have multiple benefits. Factors identified as important determinants of habitat use for the White-browed Treecreeper are also likely to be relevant for ecologically-similar species. While this may provide useful guidance for streamlining research on other species, specific recommendations for individual species should be based on empirical data. In addition, some of the recommendations that follow may not benefit all species that inhabit semi-arid woodlands, particularly prescriptions for vegetation management. For example, management of the shrub layer for the White-browed Treecreeper may not be ideal for some shrub-dependent species (e.g. Spiny-cheeked Honeyeater *Acanthagenys rufogularis*).

**Regional vision**

Currently, there are two populations of the White-browed Treecreeper in north-west Victoria that are probably self-sustaining, Yarrara and Pine Plains, with possibly a third at Timberoo / Walpeup. The first objective must be to increase the size and expand the spatial extent of these populations. However, the long-term vision must be to increase the number of self-sustaining populations in the region. There is potential for populations to be established or re-introduced in each of the regional districts I surveyed (Chapter 2). In addition, Belah or Pine-Buloke woodland occurs in several other locations in north-west Victoria, which could potentially increase the area of occupancy of the White-browed Treecreeper in the region.

The regional vision (*sensu* Hobbs & Saunders 2000) for the White-browed Treecreeper should aim to increase the overall area of Belah or Pine-Buloke woodland in the region. Plainly, soil and hydrological conditions are not appropriate for Belah or Pine-Buloke throughout the study area, but a target of 20% woodland cover in suitable areas could provide up to 80% probability of occupancy in patches that meet minimum area requirements (from Fig. 2.11a). Most districts are currently well below this target and are therefore unlikely to be able to support viable
populations. Re-introductions cannot be contemplated until the primary threatening process responsible for the recent decline of the species, habitat loss, is redressed. Clearly, ecosystem restoration will need to occur in many areas before this can happen.

**Landscape strategy**

To fulfil the regional vision, a strategy or blueprint for ecosystem restoration must be followed in each landscape. Large expanses of natural habitat are essential for biodiversity conservation, and where possible, should form the backbone of any landscape strategy for the White-browed Treecreeper. Large patches are important for the amount of habitat they provide *per se*, but may also be critical for maintaining social cohesion and population dynamics (see below). Unfortunately, it is not possible to recreate expanses of continuous woodland. Thus, strategic restoration should be focused on the largest existing patch of Belah or Pine-Buloke woodland in the landscape.

In production landscapes, a network of smaller patches that functions like continuous habitat is the most pragmatic solution for providing habitat for wildlife (e.g. Lamberson *et al.* 1994, Soulé 1995, Beyer *et al.* 1996, Freudenberger 1999). For the White-browed Treecreeper, configuration of habitat should ensure that minimum area requirements are met (i.e. patches of at least 20 ha) and functional connectivity is maintained. The most effective way to meet area requirements is to expand existing patches, where possible. The demographic isolation threshold of 8.3 km in natural vegetation or 3 km in agricultural landscapes (Fig. 2.9) provides a quantitative objective for the maximum distance between *populations* when establishing or restoring substantial habitat patches.

However, additional habitat may be required to maintain functional connectivity in the landscape. This is because the demographic isolation threshold relates only to patches capable of supporting several breeding pairs (i.e. greater than 50 ha). It does not account for small patches that may support one or two pairs but nevertheless are an important link between the larger patches across generations (Mills & Allendorf 1996, Bennett 1999). Further, the demographic threshold is greater than the ‘gap-distance’ (Desrochers & Hannon 1997, Brooker *et al.* 1999) over cleared land that
individuals are prepared to cross, estimated to be 450 m for the White-browed Treecreeper.

Functional connectivity may be provided by habitat elements and vegetation communities that may not be suitable for permanent residence but are conduits for movement, such as linear vegetation along roads, waterways and fences or clusters of small patches within the threshold gap-distance (‘stepping stones’). For example, the persistence of the White-browed Treecreeper in the Yarrara district is undoubtedly facilitated by the existence of a network of linear vegetation and many small ‘stepping-stone’ remnants that are close together. The role of scattered paddock trees in facilitating movement of treecreepers deserves further attention (McIntyre & Barrett 1992). Agricultural practices that are sympathetic to animal movements [e.g. alley farming (Knight et al. 1998)] could also be trialed. The key is an integrated landscape approach that minimizes the impact of agricultural practices on wildlife, reconstructs landscapes capable of supporting viable populations and recognizes the needs of the farming community (e.g. Lambeck et al. 2000).

The models of patch occupancy developed in this thesis may be used to prioritize actions for ecosystem restoration. They could be used in preliminary cost - benefit analyses of the addition or removal of vegetation in particular spatial configurations (e.g. Bell et al. 1997) or the feasibility of translocations or reintroductions (e.g. Friend 1987) of the White-browed Treecreeper. Although the models in this thesis must be interpreted judiciously, I am confident that they are sufficiently robust to instigate management actions. However, because they represent a landscape-scale assessment of habitat suitability, neglect of factors operating within patches may counteract remedial work at the regional or landscape scale. Therefore, continuous monitoring and review is required at all scales, within a framework of adaptive management (Holling 1978, Hobbs & Saunders 2000).

**Vegetation management**

The importance of understanding the relationship between habitat selection and the distribution and abundance of species for effective wildlife management is universally recognized (Verner et al. 1986, Hopkins & Saunders 1987, Morris 1987). The management of threatened species in particular, is predicated on the provision of
suitable habitat, which is grounded in studies of habitat use and assessment of threatening processes (Block & Brennan 1993). This thesis describes several aspects of habitat selection by the White-browed Treecreeper that can be used to direct management actions.

Much of the difference in the density of White-browed Treecreepers between Yarrara and Wyperfeld was explained by the vegetation parameters identified in the regional syndrome, which reflect the contrasting management histories of the sites. A long history of pastoralism at Wyperfeld has resulted in an aging, low-density woodland, with a depleted shrub community. The relatively undisturbed habitat at Yarrara FFR and Mallanbool FFR supports a higher population density of White-browed Treecreepers than at Wyperfeld. Thus, a priority for habitat management in woodlands that have been subject to stock grazing should be to restore the shrub community and encourage regeneration of canopy tree species. The application of this priority will vary among remnants but, in general, should embrace strategies to ease grazing pressure, restore soil structure and improve nutrient and water retention to encourage natural regeneration of woodlands (Chesterfield & Parsons 1985, Yates et al. 2000).

At many locations, removal of stock will be insufficient because feral herbivores such as rabbits and goats, and native animals continue to suppress natural plant regeneration. Therefore, an integrated management strategy that includes stock removal, fencing, exclusion plots to facilitate regeneration in sensitive areas, rabbit and goat control, management of kangaroo density, and revegetation strategies is required. Progress in implementing such restoration programs has been made in some areas [e.g. kangaroo management (Sluiter et al. 1997), rabbit control (NRE 1998), direct seeding trials (Walters 2001)] and the Mallee Native Vegetation Plan (MCMA 2000) is a welcome framework for co-ordinating and overseeing further improvements in native vegetation management.

Alterations to historical fire regimes can have significant effects on bird populations (Woinarski & Recher 1997). Garnett & Crowley (1995) suggest that the decline of the Black Treecreeper *C. picumnus melanota* in northern Queensland has been due to a decrease in the availability of suitable foraging habitat because of changes in the fire regime to more intensive and extensive late-season fires that burn larger tracts of woodland. The impact of fire on the White-browed Treecreeper is not clear.
Although Belah and Pine-Buloke woodlands have low flammability, they have high fire mortality rates and low regeneration following fire (Chesterfield & Parsons 1985, LCC 1987, Parsons 1989). Therefore, I expect populations would suffer a severe decline in food abundance and foraging habitat if large parts of their current habitat were burnt. The availability of nesting hollows would also decrease with the death and collapse of mature trees. An opportunity to examine the effect of fire on White-browed Treecreepers exists at Wyperfeld. Large tracts of Pine-Buloke woodland to the north of the main study area at Pine Plains were burnt in 1987. A comparative study of habitat use in the burnt and unburnt areas would increase our understanding of the impact of fire on White-browed Treecreeper habitat use and population density. Meanwhile, it would be prudent to implement strategies to prevent fire in existing and potential treecreeper habitat.

A number of other non-natural disturbances have implications for the habitat management of the White-browed Treecreeper. Extensive harvesting of Slender Cypress-pine has resulted in an almost monospecific canopy tree layer of Belah at Yarrara FFR, Mallanbool FFR and other remnants of Pine-Belah woodland in the north of the study area. Although logging has been prohibited for several decades, the impact on faunal communities of the alterations to the floristic composition of these woodlands is not known. At Wyperfeld, White-browed Treecreepers probably benefit from having two major foraging resources (i.e. Buloke and Slender Cypress-pine trees) (unpublished data). Therefore, actions that promote the re-establishment of Slender Cypress-pine in remnants of Belah woodland should be encouraged. Furthermore, the smaller mean diameter of trees in the habitat plots at Yarrara compared with Wyperfeld, and the rarity of very large trees, may be linked to forestry practices. While this does not appear to have had detrimental consequences for the foraging or nesting success of the White-browed Treecreeper, the impact on other species, particularly birds dependent on larger hollows (e.g. owls, cockatoos, parrots) may be considerable.

Habitat management for the White-browed Treecreeper must also limit disturbances associated directly with human use, such as firewood collection, motorized recreational activities (e.g. trail-bikes, four-wheel drives, dune buggies), and rubbish dumping. These activities reduce habitat complexity, particularly of the ground layer, stifle plant regeneration and reduce the amount of dead wood (fallen and standing) in
the woodland. Each of these effects reduces the diversity and abundance of foraging substrates for White-browed Treecreepers. Moreover, exotic weeds, which may out-compete native shrubs, and feral predators often gain their first foothold in native vegetation communities via these types of disturbances.

**Recommendations for habitat restoration**

The following recommendations are intended as guidelines for habitat restoration and ongoing management of Belah and Pine-Buloke woodland for the conservation of the White-browed Treecreeper. They relate to habitat management within a woodland patch, and complement the landscape design principles outlined in the preceding sections. While some of these recommendations are quite specific, they are intended as average values rather than a uniform prescription. Spatial heterogeneity is encouraged at all scales (Freudenberger 2000, Tongway & Ludwig 1990, 1994).

1. Increase representation of Belah, Buloke and Slender Cypress-pine in woodland patches.

2. Increase tree density to a minimum of 170 stems per ha (from Fig 4.10), with a minimum basal area of 9 m$^2$/ha (from Fig. 4.12). This equates to 170 trees with a mean DBH of 26 cm per ha.

3. Ensure a minimum of 5 hollow-bearing trees per ha.

4. Retain dead standing trees where possible.

5. Rehabilitate the shrub layer, particularly in woodlands that have been grazed. Aim for 15% cover in both the 0-1 m and 1-3 m height classes.

6. Minimize disturbance of the ground layer to restore complexity, especially in relation to lichen cover, fallen log density and development of a shrubby understorey.

7. Manage excessive growth of tall shrubs (3-5 m); i.e. prevent a ‘closed’ sub-canopy from developing. Aim for 5% cover in clumps, rather than evenly spread throughout the woodland.
Whilst these recommendations were developed specifically for the White-browed Treecreeper, many other species are likely to benefit from the protection and restoration of Pine-Buloke and Belah woodlands. These include several bird species that are also closely associated with Pine-Buloke or Belah woodlands, such as the Striped Honeyeater *Plectorhyncha lanceolata*, Gilbert’s Whistler *Pachycephala inornata*, Chestnut-crowned Babbler *Pomatostomus ruficeps*, Pink Cockatoo *Cacatua leadbeateri*, and possibly Bush Stone-curlew *Burhinus grallarius*, as well as reptiles such as the Carpet Python *Morelia spilota variegata*, Beaked Gecko *Rhynchoedura ornata* and Bandy-bandy *Vermicella annulata* (LCC 1987, Reid 1999, Major *et al.* 2001, MCMA 2000). In addition, habitat rehabilitation may benefit a number of insectivorous woodland residents that were observed during this study and which are considered to be declining across south-east Australia (e.g. Australian Owlet-nightjar *Aegotheles cristatus*, Red-capped Robin *Petroica goodenovii*, Hooded Robin *Melanodryas cucullata*, Varied Sittella *Daphoenositta chrysoptera*, White-browed Babbler *Pomatostomus superciliosus*, Apostlebird *Struthidea cinerea*, Chestnut-rumped Thornbill *Acanthiza uryopygialis*, Inland Thornbill *Acanthiza apicalis*, Crested Bellbird *Oreoica gutturalis*) (Robinson 1991, Bennett & Ford 1997, Freudenberger 1999, Reid 2000). Finally, rehabilitation of the shrub community may particularly benefit nomadic honeyeaters that track flowering shrubs and trees (Ford & Paton 1985, Oliver 2000), several of which were observed feeding on shrubs within Belah and Pine-Buloke woodland (e.g. Pied Honeyeater *Certhionyx variegatus*, Black Honeyeater *Certhionyx niger*, White-fronted Honeyeater *Phylidonyris albigrons*).

### 11.3 Survival in fragmented landscapes – future directions for research

In this thesis, I first considered the ways in which the amount, spatial configuration and quality of habitat affect the distribution patterns of the White-browed Treecreeper in fragmented landscapes. Then, in a separate study, I examined the social structure and reproductive success of a population in continuous woodland. The next step is to link these research paradigms – the most urgent research priority to evolve from this thesis is to identify the mechanisms by which habitat fragmentation threatens the survival of the White-browed Treecreeper.
Initially, this should involve an assessment of reproductive success in fragmented landscapes and whether fledglings produced in fragments are recruited into the adult population. That is, are fragments source habitat that contribute recruits to the local population, or are they demographic sinks maintained by immigrants from more productive source populations (sensu Pulliam 1988)? Although there is ample evidence that breeding success is depressed in fragmented landscapes (e.g. Robinson et al. 1995, Hinsley et al. 1999, Major et al. 1999b, Morse & Robinson 1999), large patches are not inevitably source populations, nor are small fragments necessarily sinks (Nour et al. 1998, Tewksbury et al. 1998, Trine 1998). For example, Zanette (2000) compared reproductive success and adult survival of the Eastern Yellow Robin *Eopsaltria australis* in two small (55 ha) and two large (> 500 ha) patches in north-east NSW and found one source and one sink population in each size class.

The nest success of White-browed Treecreepers in continuous habitat was 56%, with predation the most common cause of nest failure. Schmidt and Whelan (1999) suggest that predation rates greater than 65% severely compromise the sustainability of bird populations. Thus, a 20% reduction in nesting success may jeopardize the viability of populations in fragmented landscapes. There are many reasons why breeding success may decline in fragmented landscapes. An increase in the rate of nest predation associated with edge effects is frequently suggested (Andrén & Angelstam 1988, Robinson et al. 1995, Gardiner 1998, Luck et al. 1999). I have argued that edge effects are not likely to be responsible for the increased area requirements of White-browed Treecreepers in fragments (Chapter 3), and foraging behaviour was not affected by proximity to the edge (Chapter 4). However, the impact of predators (especially exotic species) from the matrix (Janzen 1983, 1986, McCollin 1998) on nest success and adult survival of the White-browed Treecreeper deserves further evaluation.

The synergistic effects of habitat fragmentation, livestock grazing and biotic invasions (Hobbs 2001) may impinge on reproductive success through reduced habitat quality. Luck (2000) suggested that the lower reproductive success of the Rufous Treecreeper in a fragmented landscape might be related to lower food availability and habitat quality. Patterns of patch occupancy of the White-browed Treecreeper in the Yarrara district point to an interaction between grazing and patch size (Chapter 3). This suggests that grazing reduces the viability of marginal (in
Cooperatively breeding birds often have complex social dynamics that are readily disrupted in fragmented habitat with dire consequences for the species persistence in the landscape. The Brown Treecreeper (Cooper & Walters 2002), Rufous Treecreeper (Luck 2000) and Grey-crowned Babbler (Doug Robinson, personal communication) are pertinent examples. The social structure of the White-browed Treecreeper has several traits that suggest it may also be adversely affected in fragmented landscapes, such as abutting territories and their propensity to seek breeding positions in adjacent territories.

The key process that links reproductive success and habitat fragmentation is dispersal. More particularly, it is the impact habitat isolation may have on the ability of individuals to disperse successfully that may threaten the viability of populations (Villard et al. 1993, Cooper & Walters 2002). Empirical data on dispersal is critical, although resource-intensive to collect, for the management of woodland-dependent species in fragmented landscapes (Walters 2000). Dispersal data is also essential to test the validity of metapopulation theory in sub-divided populations (Rolstad 1991, Hansson 1991).

In cooperatively breeding species, philopatric males may acquire breeding positions through inheritance of the natal territory or short-distance dispersal to adjacent territories (Stacey & Koenig 1990; Chapter 10). The alternative strategy is to disperse and search for breeding vacancies in more remote habitat. The probability that dispersing individuals will successfully secure a breeding position increases with the number of territories that they encounter. Conversely, the probability that an unpaired bird in an established territory will gain a mate increases with the number of prospecting birds that visit. Cooperatively breeding species usually disperse over short distances (Zack 1990, Koenig et al. 2000 but see Koenig et al. 1996) and Australian treecreepers do not appear to depart from this generality. I did not collect data on dispersal but the mean dispersal distance recorded for male Brown Treecreepers was $0.06 \pm 0.19$ (s.d.) km ($n = 23$) and $1.14 \pm 1.25$ (s.d.) km ($n = 17$)
for female Brown Treecreepers (Cooper & Walters 2002) and 2.2 ± 0.8 (s.e.) km for the Rufous Treecreeper (Luck 2000).

Thus, for a given territory, the area from which dispersing birds may be drawn, or to which they may emigrate, is relatively small. Fragmentation of the habitat surrounding that territory, therefore, may disrupt dispersal by increasing the distance between potential territories, creating barriers to movement and reducing the number of territories within the dispersal range of individuals (Doak et al. 1992, Cooper & Walters 2002). Territory contiguity facilitates informed dispersal (Reed et al. 1999) but this is severely disrupted with increasing fragmentation. Put simply, habitat fragmentation reduces the number of territories that a dispersing individual will encounter and reduces the number of potential mates visiting unpaired birds. Under this hypothesis, it is predicted that the proportion of territories with an unpaired bird will be higher in fragmented landscapes than continuous habitat, but nesting success in territories with bonded pairs will not differ. This has been demonstrated for the Brown Treecreeper (Walters et al. 1999, Cooper & Walters 2002), and could readily be tested for the White-browed Treecreeper.

The majority of the White-browed Treecreeper’s habitat in north-west Victoria is in conservation reserves. Many of these reserves are relatively small remnants embedded in agricultural landscapes. Remnants on private land also have the potential to contribute significantly to the conservation of the species. Therefore, an understanding of population dynamics and stability in fragmented landscapes will greatly increase the probability that restoration actions will achieve the desired conservation benefits. This thesis provides the first steps to understanding the response of the White-browed Treecreeper to habitat fragmentation but further research on mechanisms and processes is required for an adequate and comprehensive understanding. I have highlighted research on reproductive success, resource availability, predation rates and dispersal success in fragmented landscapes as the crucial next step.
11.4 Prospects for the White-browed Treecreeper

A battery of conservation strategies has been designed to tackle ecosystem restoration. Focal species, umbrella species, flagship species, habitat corridors and biolinks, multi-use landscapes, landscape mosaics, minimum cover thresholds and the greater ecosystem concept are examples of strategies, each with their foibles and strengths, that have been proposed to counter biodiversity loss stemming from human-induced changes to the environment (Noss 1983, 1990, Grumbine 1990, Launer & Murphy 1994, Forman 1995b, Lambeck 1997, Simberloff 1998, Bennett 1999, Nickoll & Horwitz 2000, Rosoman & Lucas 2000, Lindemayer et al. 2002). The White-browed Treecreeper could play a significant role in these strategies. It has strong credentials as a focal species (sensu Lambeck 1997). In the agricultural landscape of the Yarrara district, the White-browed Treecreeper was considerably more sensitive to patch area and isolation than the Hooded Robin (JQR, unpublished data), which is widely heralded as a potential focal species (Freudenberger 1999). This may reflect the higher abundance of the Hooded Robin in Casuarina or Callitris woodland than in eucalypt woodland (M. Antos, personal communication) but also illustrates that focal species from one landscape cannot be uncritically applied to other landscapes.

In addition, it scores reasonably well against the checklist for potential flagship species (Nickoll & Horwitz 2000). The White-browed Treecreeper may not be considered as charismatic as brightly-coloured parrots or cockatoos, but a ‘Friends of the White-browed Treecreeper’ group has been established (Wilson & McCulloch 1998) and its profile in the region is increasing. Over 150 people attended an information night in June 2001 that focused on the plight of the White-browed Treecreeper and its affinity with Belah woodland (Anon. 2001). Community-based projects, such as the Yarrara Ridge project, which aims to re-establish a landscape corridor (‘biolink’) of Belah woodland along the Yarrara sandstone ridge, will greatly benefit the White-browed Treecreeper. In turn, the White-browed Treecreeper would be an appropriate emblem for the project. Projects such as this are vital to restoration efforts because they combine community education with action, and critically, are led by the local community.
We should not be mistaken that the White-browed Treecreeper, like many other woodland-dependent species in production landscapes (Recher 1999, Ford et al. 2001), is in danger of disappearing from north-west Victoria. It will not happen this year, probably not this decade but possibly by the middle of this century. It currently persists in relatively small populations that are vulnerable to local extinction, and re-colonization is hindered by the fragmented distribution of its habitat and its limited capacity to move through the landscape. It has declined in range and abundance, and the reality is that smaller and isolated populations will probably continue to disappear, even if remedial action commences today. Certainly, the prospects for long-term survival of the species in Victoria are grave in the absence of substantial landscape restoration and habitat management. However, the situation is not irredeemable. Strategic land-use planning and ecosystem restoration, combined with enlightened vegetation management practices could see a reversal of fortunes for the White-browed Treecreeper, and a host of woodland species in the same predicament, in the latter part of this century.

I have devoted a significant part of this thesis to recommendations for landscape restoration and vegetation management to enhance habitat for the White-browed Treecreeper. This thesis is a scientific document: it is concerned with applying scientific method and rigour to a matter of conservation concern in order to produce defendable principles for sustainable management. It concentrates on two of the three requirements identified by Freudenberger (2000) for the integration of conservation and production, namely knowledge and the capacity to act. However, the most important ingredient for conservation is beyond the realm of scientific research – motivation to act. Without the political, social and cultural will to change, scientific knowledge and capacity is impotent. David Yencken and Debra Wilkinson (2000) describe the ‘four pillars of wisdom’ as ecological, economic, social and cultural sustainability, and illustrate how they are interwoven to form the fabric of our society. Their message is that sustainability in one ‘pillar’ cannot be achieved without sustainability in the other three, and that we have significant progress to make on all fronts. For the sake of the White-browed Treecreeper, I hope we heed their advice.


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