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Landscape differences in the ecology of the Rufous Treecreeper *Climacteris Rufa*

Gary W. Luck
Edith Cowan University

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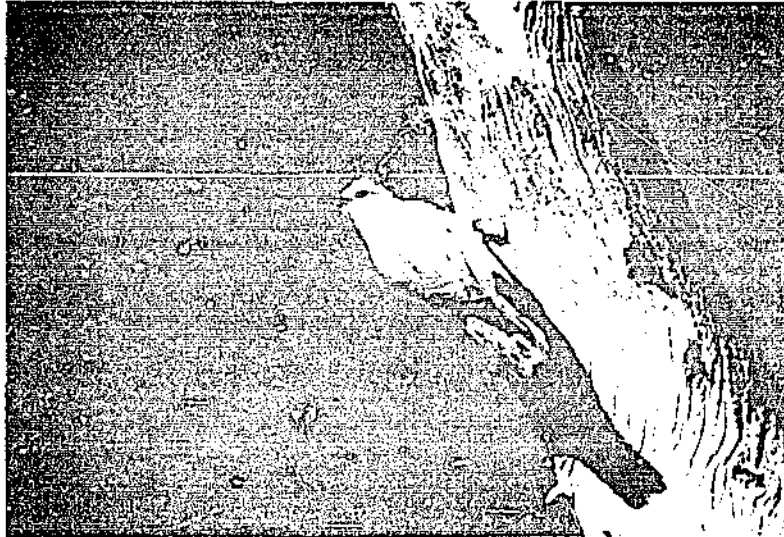
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**Landscape Differences in the Ecology
of the Rufous Treecreeper *Climacteris rufa***



Gary W. Luck

B.App.Sc. *University of South Australia*

(Hons) *University of Adelaide*

October 2000

A thesis submitted for the degree of Doctor of Philosophy
of Edith Cowan University

Faculty: Communication, Health and Science, Joondalup Campus

ABSTRACT

Anthropogenic habitat modification is a significant threat to the conservation of global biodiversity. The fragmentation and alteration of woodland habitat has resulted in the substantial decline of many woodland bird species in the agricultural regions of southern Australia. The Rufous Treecreeper *Climacteris rufa*, a once common woodland resident, has declined in abundance in the wheatbelt of Western Australia and appears to be sensitive to habitat fragmentation. The reasons for this are unclear because our knowledge of the species and the threats posed by fragmentation are limited.

In this study, I compared the social organisation, habitat selection, reproductive success, dispersal and population dynamics of two Rufous Treecreeper populations living in the Western Australian wheatbelt. The first population occupied a large (8,500 ha), relatively undisturbed and unfragmented landscape. The second occurred in an equivalent sized area that had been substantially modified by agriculture. I hypothesised that habitat fragmentation and alteration would adversely affect the viability of the population living in the agricultural landscape.

In the unfragmented landscape, treecreepers lived in cooperatively breeding, territorial groups. A group usually comprised a primary (assumed to be breeding) male and female, and philopatric offspring (helpers) from previous breeding seasons. Helpers assisted in the feeding and caring of nestlings and there was a positive relationship between group size and reproductive output. Breeding groups often formed interactive neighbourhoods whereby resident individuals from one territory would feed nestlings in adjacent territories. A total of 77.7% of 148 nesting attempts produced at least one fledgling. Annual productivity per breeding group ($n = 90$ group years) was 2.1 ± 0.18 fledglings. Fledgling and juvenile survival rates (0.76 ± 0.04 and 0.46 ± 0.03 respectively) were comparatively high, as was the annual survival rate of primary males (0.77 ± 0.06) and females (0.75 ± 0.05).

A multi-scaled analysis of habitat use in the unfragmented landscape identified preferential habitat selection by the species at three spatial scales. At the landscape scale, treecreepers used Wandoo *Eucalyptus wandoo* woodland at a significantly higher rate than predicted by the availability of this woodland type. Territory selection was positively correlated with the density of hollow bearing logs

and nest sites, and tree age. These structural characteristics were also positively correlated with reproductive success and survival in treecreepers, indicating that habitat structure may be a useful measure of territory quality. Nest sites (hollows) were preferentially used if they had a spout angle of $\geq 50^\circ$ and an entrance size of 5 – 10 cm, but nest-site selection was not related to nest success.

The ecological traits of the treecreeper population living in the agricultural landscape differed from the population in the unfragmented area in a number of ways. Habitat fragmentation in the agricultural landscape disrupted territory contiguity with adverse consequences for social interaction. Nest success and annual productivity were significantly lower in the agricultural landscape, although they varied between different categories of habitat remnants. Reproductive success was lowest in grazed remnants supporting comparatively high population densities. Landscape differences in success did not appear to be a result of a disparity in nest predation levels, but may be related to variation in food availability and habitat quality.

The spatial structure and dynamics of the subdivided population in the agricultural landscape were consistent with certain aspects of metapopulation theory. Treecreepers lived in spatially discrete local populations that were unlikely to persist without immigration owing to low reproductive and survival rates. However, movement between habitat remnants appeared to be sufficient to rescue these local populations from extinction. Although declining in numbers during the study, the subdivided population in the agricultural landscape appeared to be fluctuating around equilibrium owing to immigration from outside the study area.

The consequences of habitat fragmentation for the Rufous Treecreeper are complex and interactive. A reduction in habitat area and an increase in remnant isolation disrupts the social organisation of the species and results in small, localised populations that are susceptible to extinction. Modification of the remaining vegetation may reduce habitat quality leading to poor reproductive success. In addition to increasing habitat area and maintaining landscape connectivity, future management of fragmented landscapes must focus on improving the quality of remnant vegetation by removing degrading processes and ensuring the recruitment of endemic plant species.

DECLARATION

I certify that this thesis does not, to the best of my knowledge and belief:

- (i) incorporate without acknowledgement any material previously submitted for a degree or diploma in any institution of higher education;
- (ii) contain any material previously published or written by another person except where due reference is made in the text; or
- (iii) contain any defamatory material.

Signed

✓ Gary Lück

ACKNOWLEDGEMENTS

The process of a PhD can be a challenging, frustrating, and rewarding task. Fleeting glimpses of progress are often shrouded in the mists of anxiety. However, the light at the end of the tunnel always beckoned. It is my pleasure to thank those who helped me reach the light. My principal supervisor, Professor Harry Recher, always offered encouragement and pushed me to perform above my own expectations. He was ever willing to offer advice and I even heeded some of it. My other principal supervisor, Dr Robert Lambeck, also offered encouragement and constructive criticism. His good humour and relaxed attitude were a welcome relief during the times of mini-crisis. Harry and Robert were mentors and friends, and their professional and personal support were greatly appreciated.

Technical and administrative staff at Edith Cowan University always helped when I needed it and I would particularly like to thank Mairead O'Shea and Jon Luff. Lynn Barton deserves a special mention for her help with all those annoying bits of red tape. Similarly, the administrative and technical staff at CSIRO Sustainable Ecosystems (formerly Wildlife and Ecology) were a great help. I would especially like to thank John Ingram, Jean Rae and Joe Leone for assistance with a variety of problems.

The staff at CALM Narrogin provided maps, background information on Dryandra and listened to me when I begged them not to burn my study sites. I would particularly like to thank Anthony Desmond, Clare Anthony and Steve Gorton. Access to private land at Yilliminning was granted by the McDougall, Mead, Brown and Short families, for which I am immensely grateful. Perry de Rebeira gave freely of his expertise on banding, Alan Rose discussed treecreepers with me at the beginning of the study, and Allan Burbidge and Eleanor Russell commented on my proposal. I thank the volunteers who assisted in the field, although I can't remember all your names. Special thanks to Anne Charmantier and Pauline Ezanno for working harder than I expected on a monotonous and repetitive project.

A number of people provided comments on drafts of chapters or manuscripts. Thank you to Michael and Lesley Brooker, Nick Nicholls, Chris Norwood, Eleanor Russell, Ian Rowley and Alex Watson. Elaine Pascoe, Nick Nicholls and Mike Claver provided much needed advice on statistics. Brett Melbourne and Kendi Davies helped immensely during the write-up stage by

answering my annoying questions and commenting on drafts of manuscripts and chapters. My colleagues in the "Treecreeper Mafia", Jim Radford and Erik and Veronica Doerr, were always willing to discuss the most fascinating bird family on earth, and offered advice and support throughout the project. I would especially like to thank Peter Cale for commenting on drafts of chapters, stimulating and challenging discussions about cooperative breeding and fragmentation, and continued support over the past three and a half years.

In an extensive field-based study such as this, one of the greatest hurdles is obtaining enough funding to cover the burgeoning project costs. This project would not have proceeded without the generous support of CSIRO Sustainable Ecosystems, which provided the majority of funding. I am also grateful to CSIRO for providing a quiet and comfortable work environment during the write-up of the thesis. The Centre for Ecosystem Management (Edith Cowan University) also provided a significant amount of funding for conference attendance, fieldwork and equipment. The postgraduate funding opportunities offered by the Centre were a progressive and welcome initiative. The Australian Bird Study Association, Stuart Leslie Bird Research Fund (Birds Australia) and Ecological Society of Australia also provided funding support. My living expenses were supported by an Australian Postgraduate Award Scholarship.

My personal thanks go to Judy Recher for her unfailing support in improving my public speaking skills, and to Graham and Maureen Henderson for making Dryandra Village a friendly and relaxing place to stay. In no small way, they made Dryandra my home away from home. To my colleagues and friends at CSIRO Sustainable Ecosystems and Edith Cowan University, thanks for your help, support and good humour.

The most important acknowledgements always come last. Thank you to my family for their encouragement and belief. To my soul mate Gayle, your love and understanding knows no bounds. I can't thank you enough for all your support; this thesis is as much yours, as it is mine. Finally, to a little rufous bird that shared its life with me for a brief moment. I miss you already, but I promise to visit whenever I can. This thesis is dedicated to my mum for her enduring strength and constant inspiration, and to all those who believed in themselves, took a chance, and changed their life.

PREFACE

Publications

The following sections of this research were published, accepted for publication or submitted prior to completion of the thesis.

Appendix 2.1: Plumage and size variation in adult and juvenile Rufous Treecreepers. *Corella* **23**: 71-76.

Appendix 3.1: Variability in provisioning rates to nestlings in the cooperatively breeding Rufous Treecreeper. *Emu* **in press**.

Appendix 4.1: Seasonal and landscape differences in the foraging behaviour of the Rufous Treecreeper. *Pacific Conservation Biology* **in press** (with co-authors A. Charmantier and P. Ezanno).

Chapter 7: Differences in the reproductive success and survival of the Rufous Treecreeper *Climacteris rufa* between a fragmented and unfragmented landscape. *Conservation Biology* **submitted**.

In the co-authored paper, A. Charmantier and P. Ezanno collected the foraging data, but I wrote the paper and conducted most of the data analysis. Appendices 2.1, 3.1 and 4.1 are in the form of the manuscript submitted to each journal. Therefore, repetition of certain sections (e.g., description of study sites) occurs. The manuscript originating from Chapter 7 was an abridged version of the text presented here.

Scientific names

Scientific names for all species are used the first time they are mentioned *in each chapter or appendix*, except for the Rufous Treecreeper whose scientific name is used the first time it is mentioned in the thesis. Thereafter, common names are used.

Photographs and poems

I took all the photographs used in this thesis and wrote the poems appearing on the section dividers unless indicated otherwise.

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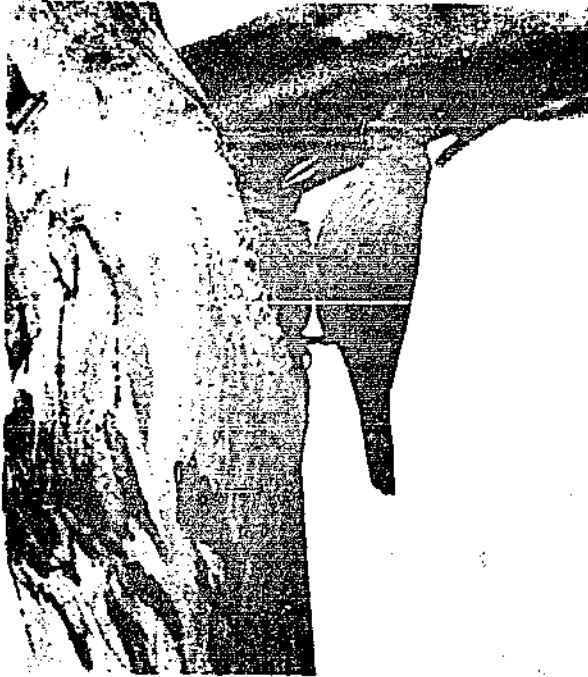
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Part I
BACKGROUND TO STUDY



Vultures

*Life is born of cultures
Picked clean by bloodied vultures
Which feed on dreams decaying
Of corpses that lie praying
For hope to end the slaughter
Of Mother's favourite daughter*

CHAPTER 1 *INTRODUCTION*

1.1 GENERAL INTRODUCTION AND THESIS OVERVIEW

1.1.1 Anthropogenic modification of landscapes

Human population growth and high per capita resource consumption results in the loss, fragmentation and alteration of indigenous habitat. Habitat modification by human activity is a global phenomenon and understanding its effects on the functioning of ecological systems is a significant problem in ecology. There is little hope for the conservation of native species and the maintenance of biological diversity unless we develop a detailed knowledge of the influence of habitat change on the persistence of species (Hobbs 1994).

The term habitat fragmentation is generally used to describe three processes: a reduction in the total amount of indigenous habitat, a decrease in the size of habitat remnants (indigenous habitat remaining after clearance), and an increase in the distance between remnants (Burgess and Sharpe 1981). These processes can have a significant negative impact on population viability and biological diversity (Wilcox 1980; Wilcox and Murphy 1985). Consequently, the effects of habitat fragmentation on native biota have been a major focus in ecological research (Wilcove et al. 1986; Haila et al. 1993; Hobbs and Saunders 1993; Andr n 1994; Collinge 1996).

Habitat fragmentation is often the result of agriculture, forestry or urban development. These activities lead to quantitative changes in the spatial characteristics of habitat, but they may also alter ecological function within habitat remnants. Native vegetation surrounded by agricultural land experiences abiotic (e.g., microclimate) and biotic (e.g., predator density) changes associated with the predominant land use (Saunders et al. 1991). These external influences may modify the ecological processes occurring in remnants to the detriment of species that rely on native vegetation. It is important to recognise that the consequences of habitat fragmentation encompass more than just spatial changes to indigenous habitat.

The effects of habitat fragmentation have been of particular interest to Australian researchers (Hobbs and Saunders 1993; Saunders et al. 1993; Bennett and Ford 1997; Catterall et al. 1998). Australian ecosystems have been substantially

modified since European settlement leading to the decline or extinction of many native species (Commonwealth of Australia 1996). In particular, extensive areas of native vegetation have been cleared or altered in regions now used for agricultural production. These regions serve as useful “natural experiments” on the consequences of habitat fragmentation for native species and have been the focus of comprehensive research (Saunders et al. 1993; Barrett et al. 1994).

1.1.2 The theory of habitat fragmentation

The theoretical frameworks of island biogeography (MacArthur and Wilson 1967) and metapopulation dynamics (Levins 1969) have had a significant influence on empirical investigations of the effects of habitat fragmentation on species diversity and persistence. The theory of island biogeography, originally applied to oceanic islands, has driven many community-level studies of species assemblages occupying habitat “islands” (remnants) in fragmented terrestrial systems (Howe 1984; Hino 1985; Opdam et al. 1985; Blake and Karr 1987; Haila et al. 1987; Soulé et al. 1988; Arnold and Weeldenburg 1990; Hinsley et al. 1996; Berg 1997). The main tenets of the theory are that species assemblages are a consequence of an equilibrium between immigration and local extinction, and a reduction in island area and an increase in isolation (e.g., distance from a large source patch of immigrants) will result in lower species richness. Application of the theory to fragmented terrestrial systems has been questioned by a number of authors (Gilbert 1980; Margules et al. 1982; Simberloff and Abele 1982; Mader 1984) and its strengths and weaknesses have been extensively reviewed elsewhere (Diamond 1975, 1976; Simberloff and Abele 1976, 1982; Connor and McCoy 1979; Murphy and Wilcox 1986).

Despite any limitations, community-level studies of species-area/isolation relationships have been valuable in identifying species that are consistently absent from small, isolated habitat remnants, and may be vulnerable to the negative effects of habitat fragmentation. Subsequent, intensive research on selected species from within this vulnerable group may be a useful approach to identifying fragmentation-related mechanisms that could be responsible for population decline.

Metapopulation theory arose out of the recognition that populations may be spatially subdivided rather than uniformly distributed across a landscape. A

metapopulation is a spatially structured assemblage of local populations with a level of interaction (e.g., dispersal) between them that has some effect on local population dynamics (Hanski and Simberloff 1997). The theory is similar to island biogeography in that habitat area and isolation are thought to play an important role in the extinction-colonisation dynamics of local populations (Drechsler and Wissel 1998; Hanski 1998; Moilanen and Hanski 1998).

The metapopulation model stresses the importance of within and between local population dynamics on the persistence of a species over time. Its concepts are intuitively appealing to researchers studying the dynamics of organisms living in anthropogenically fragmented landscapes because the distribution of many species is spatially subdivided. In these situations, it is important to determine the level of demographic interaction occurring between spatially discrete local populations and the likelihood that populations will persist without immigration. If the persistence of a species is the result of a balance between the extinction of local populations and re-colonisation of empty habitat from extant neighbouring populations, then metapopulation dynamics may be the most appropriate theoretical framework. However, there is scant evidence in nature to support classic metapopulation theory and further empirical studies are required to assess its generality (Harrison 1991, 1994; Harrison and Taylor 1997). This is an extremely important issue in relation to how species persist in fragmented landscapes and is discussed further in Chapter 8.

One of the limitations of island biogeography and metapopulation theory is the often strong dichotomy between remnant and matrix (the predominant vegetation/land-use type surrounding a remnant). This dichotomy does not recognise that the matrix may be useable habitat to some species and processes occurring in the matrix may influence population dynamics in remnants. Landscape ecology attempts to address this issue by providing a more holistic approach to the study of species persistence in fragmented systems (Hansson and Angelstam 1991; Hobbs 1994; Lidicker 1995). It recognises that ecological processes are not confined by anthropogenically created boundaries and the persistence of species may rely on the sympathetic management of the entire landscape. However, landscape ecology lacks the strong theoretical framework of metapopulation dynamics and Wiens (1997) suggests a synthesis of the two approaches would prove beneficial to future empirical investigations.

Most definitions of “landscape” emphasise spatial heterogeneity among a collection of interacting systems (see Wiens 1997 p. 45). A landscape may be considered a level of organisation (Gosz 1993; Lidicker 1995) or a scale of investigation (Forman and Gordon 1986; Hansen et al. 1993). The latter is restrictive if considered from a purely anthropogenic perspective. The ecological traits of a species and the questions being asked should dictate the scale of inquiry (Wiens 1989a). My study was framed within a landscape context and the scale of investigation was largely defined by current knowledge of the life-history characteristics and space-use requirements of the Rufous Treecreeper *Climacteris rufa*. However, I focussed mostly on the structural and ecological differences between a fragmented and unfragmented landscape rather than the influence of within-landscape spatial heterogeneity on species dynamics.

1.1.3 Avifaunal decline associated with habitat fragmentation

Habitat fragmentation has led to a decline in the abundance and species richness of birds in many regions of the world (McLellan et al. 1986; Newmark 1990; Andr n 1994; Simberloff 1994; Recher 1999). In Australia, widespread decline in the abundance of many woodland birds has occurred in landscapes altered by agriculture and pastoralism (Howe 1984; Saunders 1989; Saunders and Curry 1990; Barrett et al. 1994; Recher 1999; Reid 1999; Ford et al. 2001). Open woodlands and grasslands are often associated with the more productive soils and were preferentially cleared in agricultural regions (Ford and Barrett 1995; Yates and Hobbs 1997). This preferential clearing has resulted in the decline of bird (and other) species associated with these vegetation types (Saunders and Ingram 1995; Robinson and Traill 1996).

In the wheatbelt of Western Australia, woodlands on lower slopes and valley floors (e.g., Salmon Gum *Eucalyptus salmonophloia* and Wandoo *E. wandoo*) were preferentially cleared and are now poorly represented in the region (Beard and Sprenger 1984; Hobbs and Mooney 1998). Much of the remaining vegetation occurs in small, isolated remnants subject to external influences emanating from the surrounding landscape. A number of bird species that use these woodland types have become rare or locally extinct in certain agricultural districts (Saunders and Ingram 1995).

Recent studies of the effects of habitat alteration on birds highlight a number of characteristic ecological traits that may increase the probability that a species will decline in fragmented systems. These include specialised habitat requirements (Tellería and Santos 1995), poor dispersal ability (Haas 1995; Brooker et al. 1999), ground or low shrub nesting (Wilcove and Robinson 1990; Luck et al. 1999a) and ground foraging (Reid 1999). Examining the mechanisms of decline requires detailed, autecological studies of selected species (Gilpin and Soulé 1986; Zimmerman and Bierregaard 1986; Brussard 1991; Simberloff and Martin 1991). In an agricultural context, these investigations are not only useful for assessing fragmentation theory, but can contribute to the development of appropriate management strategies that will assist in maintaining a balance between conservation and agricultural production.

1.1.4 The Rufous Treecreeper: a case study

Autecological studies designed to examine the consequences of habitat fragmentation on population viability should focus on species that have previously been identified as sensitive to habitat change and attempt to determine the reasons behind this. The Rufous Treecreeper is a bird species that has become rare or locally extinct in certain regions subject to agricultural and urban development, and appears to be sensitive to habitat alteration (Kitchener et al. 1982; Saunders 1989; Storr 1991). The specific factors leading to its decline are unclear and our knowledge of the Rufous Treecreeper is very limited with only one published study on its territorial and breeding behaviour (Rose 1996). Therefore, a case study on this species is not only useful as an empirical evaluation of the consequences of habitat fragmentation, but provides valuable information on a vulnerable species that is poorly known.

1.1.5 Aim and structure of thesis

In this study, I used the Rufous Treecreeper to explore the effects of habitat fragmentation on ecological processes in the Western Australian wheatbelt. The processes that I considered were social and spatial organisation, habitat selection, reproductive behaviour and success, dispersal and population dynamics. The general aim of my study was to compare landscape differences in these processes between a

large (8,500 ha), unfragmented study area, and an equivalent sized area that has been modified by agriculture. The underlying thesis of my research was that landscape alteration by agriculture results in changes to ecological processes, adversely affecting the ability of the Rufous Treecreeper to persist in the agricultural landscape.

The thesis is divided into four parts and nine chapters (Figure 1.1). In the following chapter, I describe my study areas and general methods, and provide brief background information on the biology of the Rufous Treecreeper. In Part II (Chapters 3 – 5), I examine the ecology of the treecreeper in the unfragmented landscape. This includes its cooperative breeding behaviour (Chapter 3), a multi-scaled analysis of habitat use (Chapter 4) and the relationship between habitat quality and reproductive output (Chapter 5). The purpose of these chapters is to develop a sound knowledge of the life-history characteristics of the species in a relatively undisturbed area. This is fundamental to understanding the potential consequences of habitat alteration on population viability.

In Part III (Chapters 6 – 8), I examine the ecology of the treecreeper in the fragmented agricultural landscape and compare this with the findings from the unfragmented area. Specifically, these chapters assess differences in habitat use, population density and cooperative behaviour (Chapter 6), reproductive success (Chapter 7) and population dynamics (Chapter 8). In Part IV (Chapter 9), I synthesise the information from the preceding six chapters to present a general discussion of the consequences of habitat fragmentation for the Rufous Treecreeper. In the introduction to Chapters 3 – 8, I provide a brief review of the literature relevant to the topic discussed. Each chapter is formatted in the style of a scientific paper, but provides a more in depth description of methods and discussion of results than would be presented in a standard scientific publication.

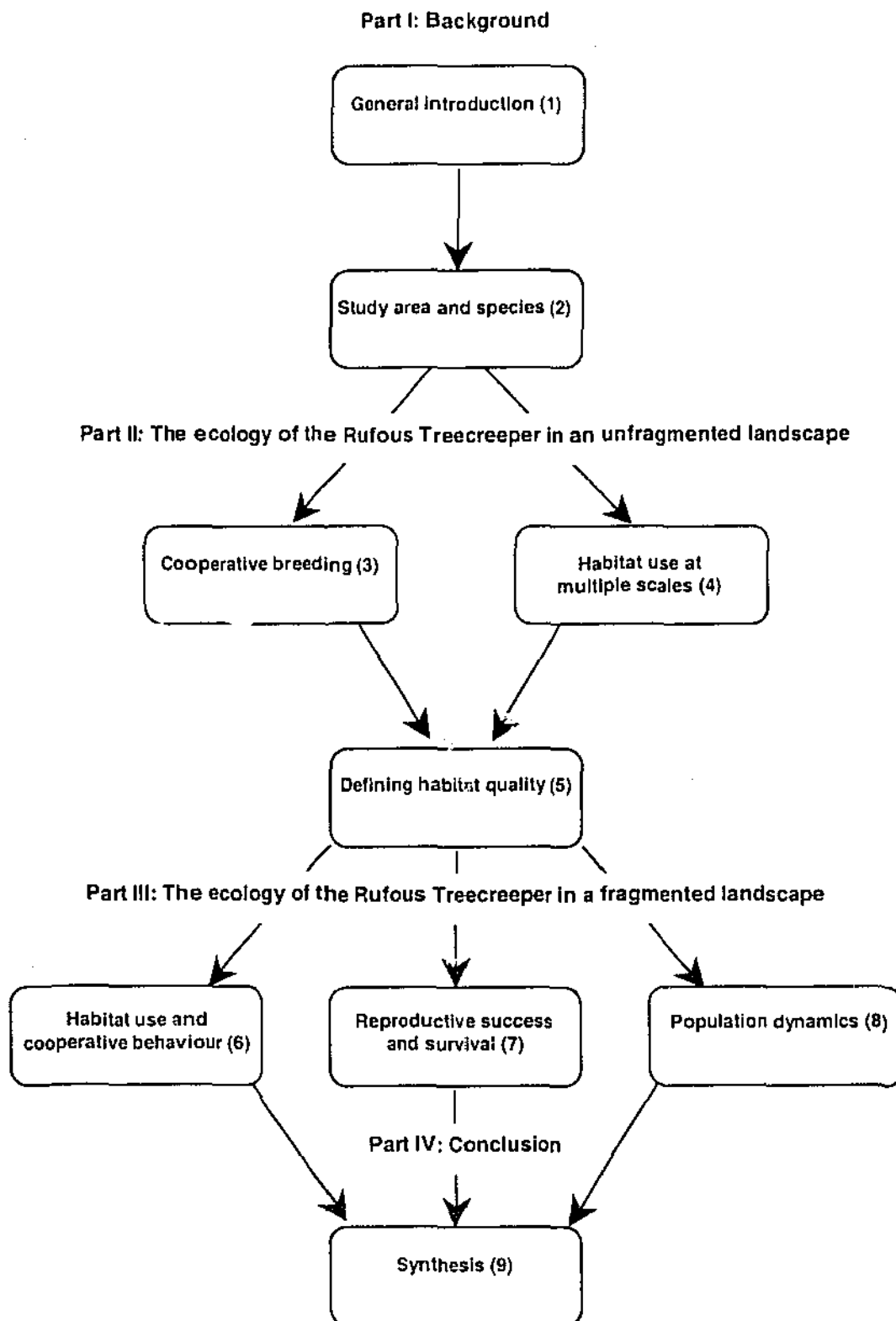


Figure 1.1 Thesis structure. The numbers in brackets indicate relevant chapters.

CHAPTER 2
STUDY AREAS, RUFIOUS TREECREEPER BIOLOGY,
AND GENERAL METHODS

2.1 STUDY AREAS

2.1.1 Introduction

I studied the Rufous Treecreeper in two areas in the central west wheatbelt of Western Australia; Dryandra Woodland (centred on 32°45'S, 116°55'E) and the Yilliminning agricultural district (centred on 32°54'S, 117°24'E). Dryandra is located approximately 160 km southeast of Perth, and Yilliminning is approximately 35 km southeast of Dryandra (Figure 2.1). In this chapter, I provide a general description of the climate, topography, vegetation associations and clearance history of the central west wheatbelt. I also include a description of the two study areas, my criteria for site selection and the location of study sites and territories. Comparisons are made for rainfall, temperature and vegetation cover between Dryandra and Yilliminning. Finally, I present background information on the Rufous Treecreeper and describe the general methods I used to mark and monitor my populations.

2.1.2 The central west wheatbelt

The central west wheatbelt experiences a Mediterranean climate with hot, dry summers and mild, wet winters (McArthur et al. 1977). Average annual rainfall is 504 mm with most falling in the winter months (June – August). The landscape is gently undulating with occasional breakaway slopes and granite outcrops. Landforms in the region can be broadly classified into four main types supporting characteristic vegetation communities:

- a) lateritic uplands – supporting dense shrubland of *Dryandra* spp. and *Petrophile* spp., occasionally with a sparse overstorey of Jarrah *Eucalyptus marginata* and Powderbark Wandoo *E. accedens*;
- b) upper valley slopes – supporting Brown Mallet *E. astringens* and Powderbark Wandoo woodlands;
- c) mid to lower valley slopes – supporting Wandoo *E. wandoo*, Marri *E. calophylla* and Rock Sheoak *Allocasuarina huegeliana* woodlands; and

- d) valley floors – supporting York Gum *E. loxophleba* and Jam Wattle *Acacia acuminata* woodlands (McArthur et al. 1977; Coates 1993; Department of Conservation and Land Management 1995).

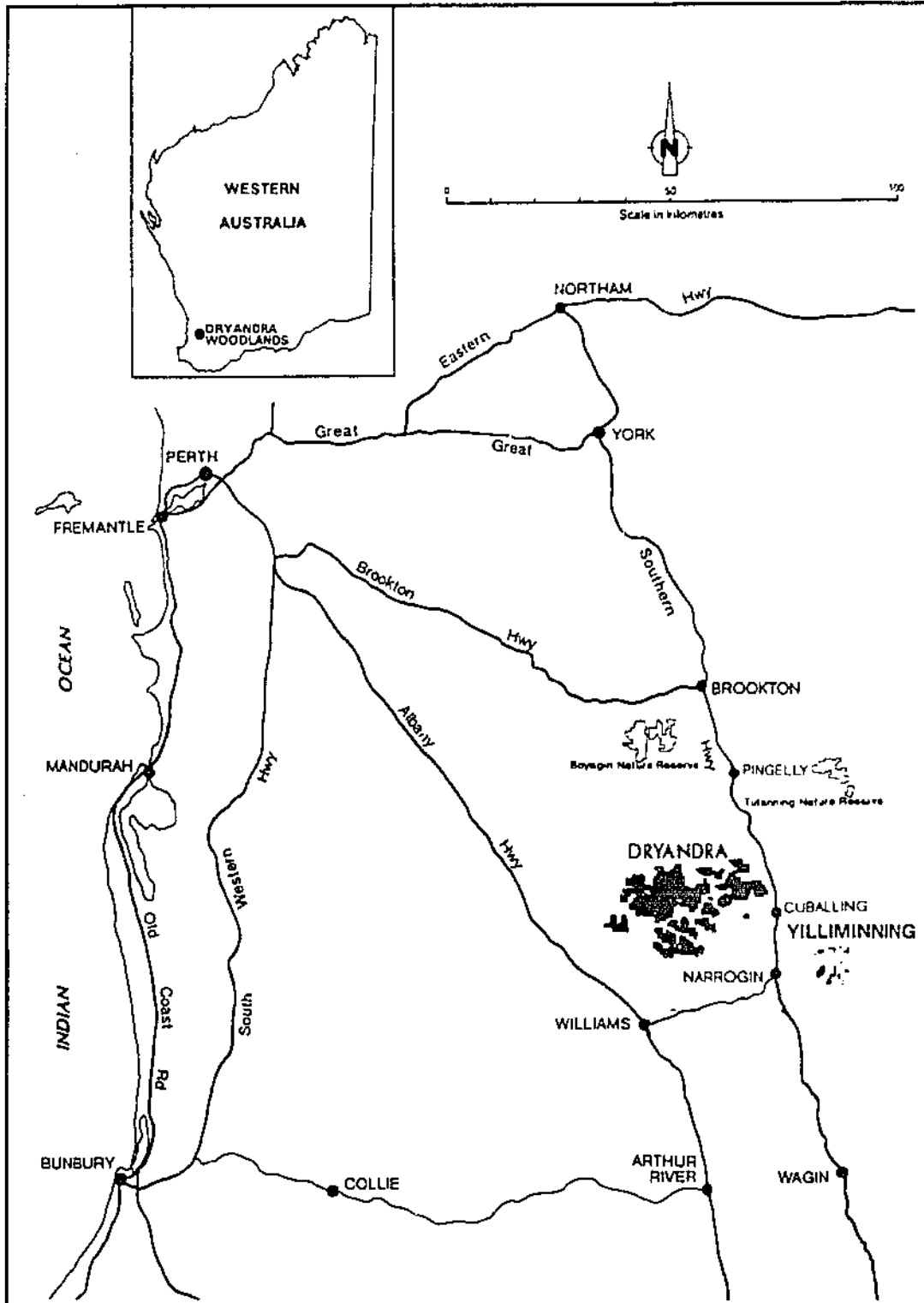


Figure 2.1 Location of Dryandra and Yilliminning (modified from the Department of Conservation and Land Management 1995).

Woodland communities in the region are characterised by a tall (canopy height ≈ 25 m) and generally open ($< 30\%$ projected foliage cover) overstorey. The understorey varies from dense in Marri woodlands to very sparse in Wandoo and Powderbark Wandoo woodlands. Most shrub species are < 2 m in height and common genera include *Dryandra*, *Banksia*, *Grevillea*, *Hakea* and *Gastrolobium*. As with most other regions in the wheatbelt, native vegetation has been extensively cleared for agriculture over the last 50 – 100 years. In the Shire of Narrogin, it is estimated that only 15% of the original native vegetation remains (Figure 2.2; Grein 1994).

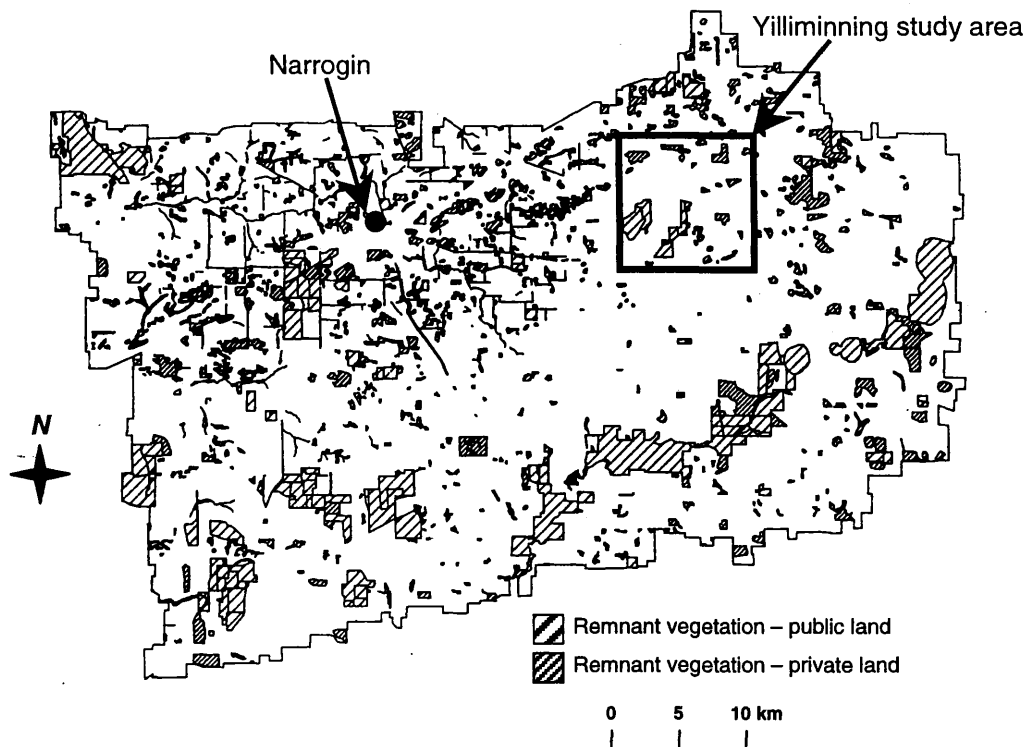


Figure 2.2 Native vegetation cover in the Shire of Narrogin and the location of the Yilliminning study area (modified from Grein 1994).

Most of the agricultural land in the region is used for cropping (wheat and canola) or sheep grazing. This land use can have significant consequences for the remaining native vegetation. Threats to remnant vegetation embedded in this agricultural matrix include over-grazing by introduced and native herbivores, weed invasion, spray drift, altered water and nutrient status, microclimate changes and salinity. These threats, along with habitat clearance and fragmentation, have significant implications for the persistence of many native species reliant on remnant vegetation.

2.1.3 Description of study areas

Dryandra

Dryandra Woodland is fragmented into 10 discrete habitat blocks with much of the surrounding land cleared for agriculture (Figure 2.3). The largest block is 12,283 ha (Department of Conservation and Land Management 1995). Dryandra is ecologically important for many reasons. It is the largest and most floristically diverse conservation reserve in the region and harbours a number of rare species including the Numbat *Myrmecobius fasciatus*, Woylie *Bettongia penicillata* and Red-tailed Phascogale *Phascogale calura* (Department of Conservation and Land Management 1995).

The vegetation communities in Dryandra are characteristic of the western wheatbelt. The main woodland types are Brown Mallet and Powderbark Wandoo on upper slopes and Wandoo on the mid – lower slopes (see Coates 1993 for a detailed description of the vegetation of Dryandra). Large areas within the main habitat blocks support Brown Mallet plantations that were established from 1925 – 1962 to service the tannin industry (Department of Conservation and Land Management 1995). These plantations are currently subjected to small-scale selective logging, which represents one of the few significant disturbances occurring in the reserve.

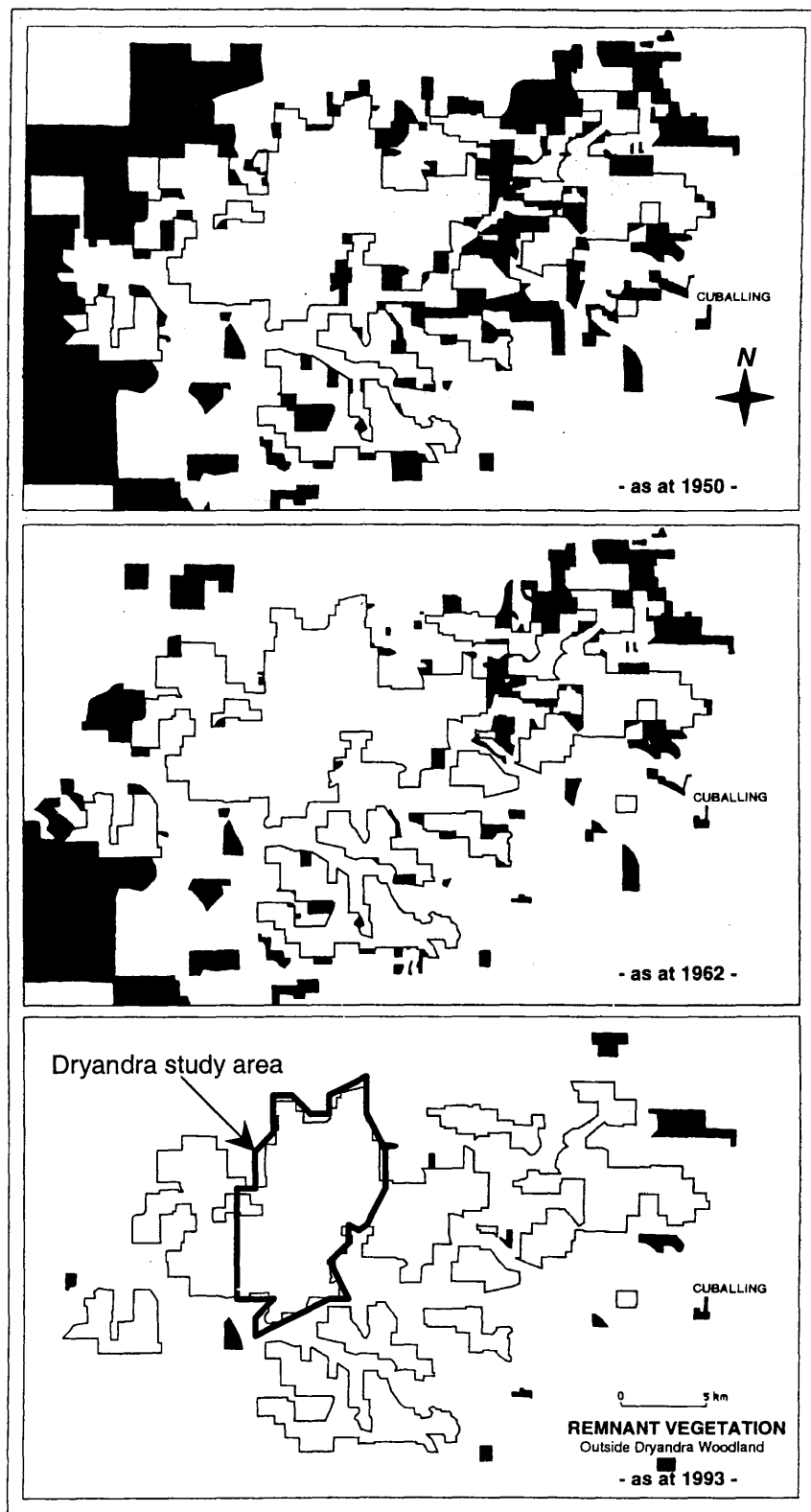


Figure 2.3 The main remnant vegetation blocks at Dryandra Woodland (light grey), and the clearance of native vegetation outside Dryandra (black) from 1950 to 1993. The final panel shows the location of the Dryandra study area (modified from the Department of Conservation and Land Management 1995).

Yilliminning

Most of the native vegetation in the Yilliminning agricultural district was cleared prior to 1960 (Shire of Narrogin, pers. comm., August 1998). The remainder occurs in remnants of between 1 – 250 ha in size, surrounded by agricultural land used primarily for cropping and sheep grazing. These remnants have been, and continue to be, subjected to a range of disturbances characteristic of remnant vegetation in the wheatbelt (e.g., grazing, weed invasion and the removal of timber for fuel).

The main vegetation types in the region are similar to those found in Dryandra. Wandoo, Brown Mallet and Rock Sheoak woodlands, and *Dryandra*, *Hakea* and *Banksia* shrublands are common. The district also supports small patches of Morrel *E. longicornis* and Salmon Gum *E. salmonophloia* open woodland, which generally have a sparse understorey. The Salmon Gum is mostly interspersed within the more predominant Wandoo woodlands and was not considered a distinct woodland type for the purposes of my study.

Selection of study areas

A study area was selected in Dryandra and Yilliminning based on the following criteria:

- a) large enough to be considered a landscape in an organisational and spatial sense with reference to the characteristic scales of Rufous Treecreeper activity (see Section 1.1.2);
- b) logistically manageable;
- c) containing sufficient numbers of treecreepers for statistical analysis;
- d) in Dryandra, native vegetation should be continuous and relatively undisturbed; and
- e) in Yilliminning, vegetation remnants should vary in size and disturbance level (e.g., grazed or ungrazed).

The Dryandra study area (landscape) covered approximately 8,500 ha of native vegetation occurring in the centre of the largest vegetation block (see Figure 2.3). At Yilliminning, the study landscape covered 10,000 ha encompassing a number of vegetation remnants ranging in size from 1 – 250 ha (see Figure 2.2).

I considered 30 treecreeper territories per landscape as a suitable sample size for comparative analysis. In Dryandra, these were located in three spatially discrete sites approximately 1.5 – 3 km apart (Figure 2.4). These sites were selected because they occurred in the same vegetation type (open Wandoo woodland) and each contained at least 10 contiguous territories (the number of potential territories was determined by preliminary survey work). This design allowed me to examine within landscape differences in ecological traits, and territory contiguity was considered important to study the social behaviour of the species. For the duration of the study (1997 – 1999), these sites also appeared to be demographically discrete, as no interchange of marked individuals occurred between sites.

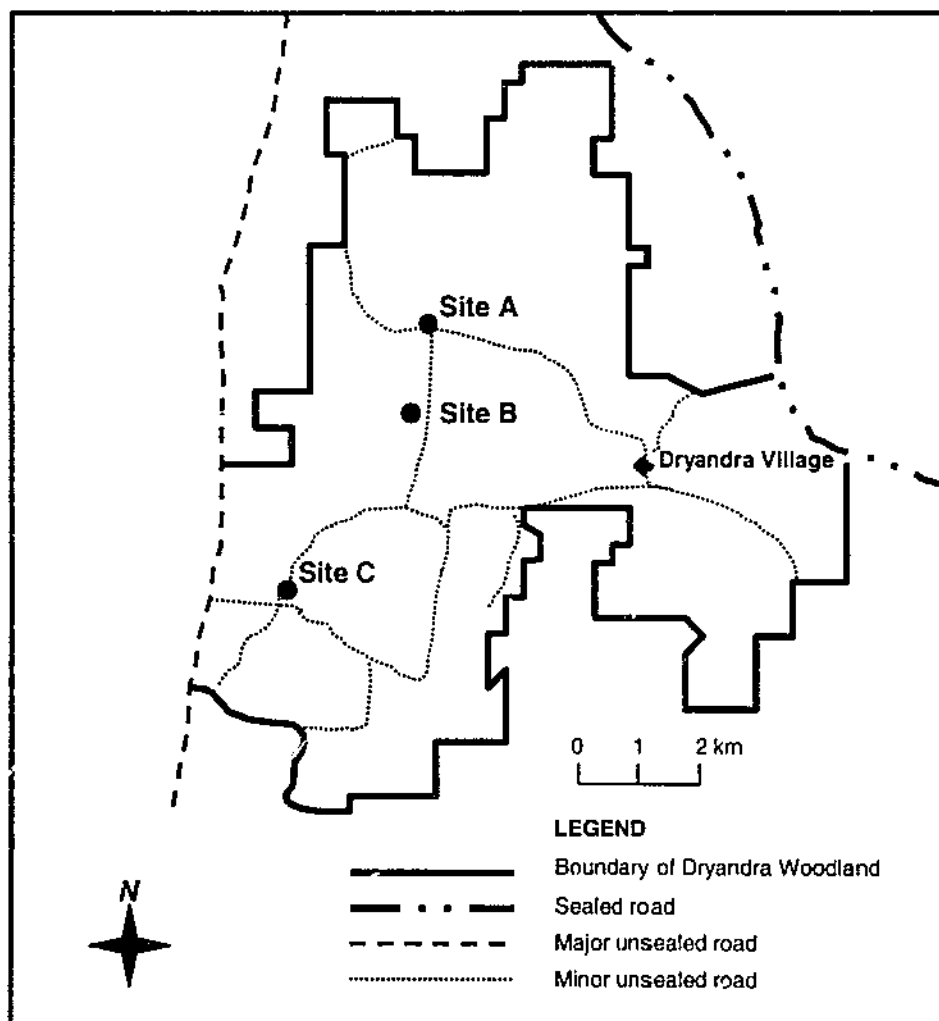


Figure 2.4 The location of the three study sites in Dryandra.

In Yilliminning, the 30 territories were distributed among 10 vegetation remnants out of a total of 12 containing treecreepers (Figure 2.5). A remnant was considered spatially discrete if it was separated from other remnants by at least 50 m or if it was attached to an adjacent remnant by a narrow (< 20 m wide) strip of vegetation. This classification is arbitrary, but was used to account for the potentially detrimental influence of edge effects.

The 10 study remnants ranged in size from 5 – 250 ha. Each remnant was arbitrarily classified as small (≤ 30 ha), large (≥ 60 ha), grazed (subject to annual or biannual grazing by sheep) or ungrazed (free from stock grazing for at least 15 years). The number of remnants (and territories) in each class were: large ungrazed, two (nine); large grazed, one (eight); small ungrazed, four (six); and small grazed, three (seven) (Figure 2.5). This design allowed me to examine differences in the ecological traits of the treecreeper between remnants that varied in size and grazing intensity.

2.1.4 Differences in climate and vegetation cover between landscapes

Rainfall and temperature

Total monthly rainfall figures were obtained in each landscape for the duration of the study (Figure 2.6). For the years when comparative data were collected on the treecreeper populations (1998 and 1999), total annual rainfall at Yilliminning was 502 mm and 532 mm compared to 445 mm and 481 mm at Dryandra. Fluctuations in total monthly rainfall were reasonably consistent between the landscapes, although at Dryandra, slightly more rain fell in August (the beginning of the breeding season) each year (Figure 2.6).

I also obtained average minimum and maximum temperatures for each month of the main breeding season in 1998 and 1999 (Figure 2.7). Average minimum temperatures were almost identical in each landscape, whereas average maximum temperatures were always slightly higher at Dryandra.

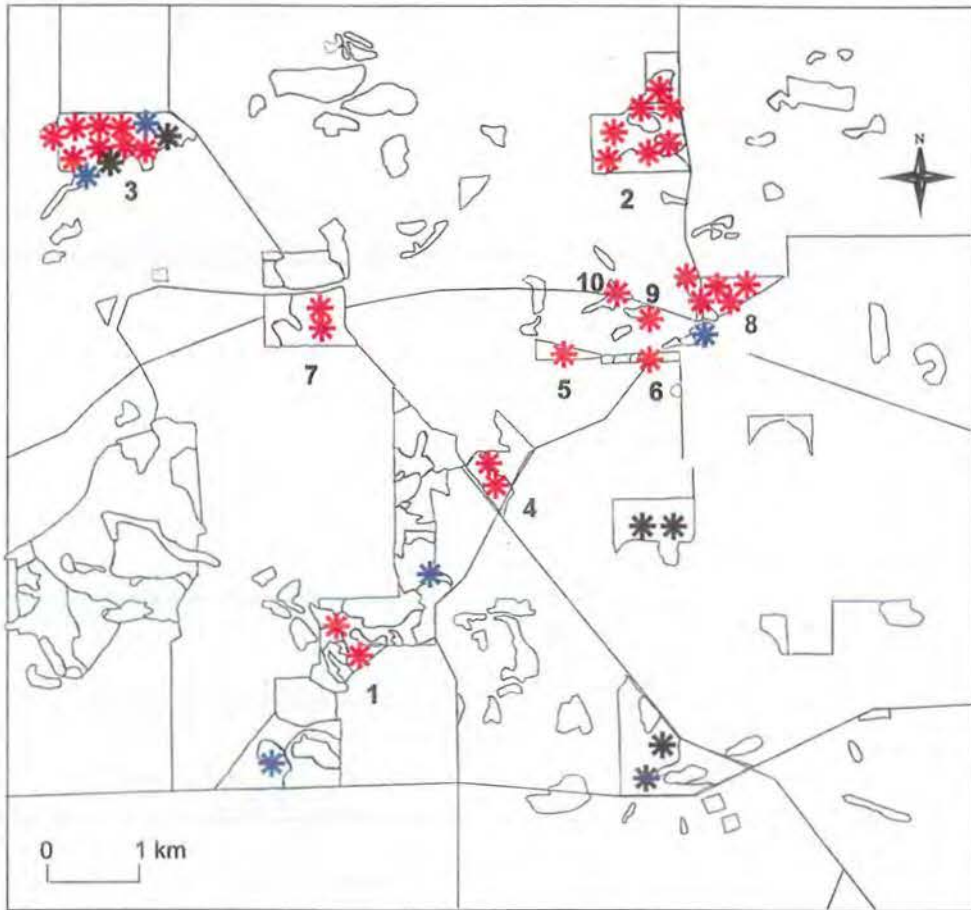


Figure 2.5 The location of tree creeper territories in Yilliminning. Red asterisks = the 30 closely monitored territories, blue asterisks = irregularly monitored territories with banded birds, and black asterisks = irregularly monitored territories with unbanded birds. Dark grey shading is remnant native vegetation. Single lines between remnants are linear strips of vegetation. Numbers refer to size and disturbance category of remnant: 1-2 large ungrazed; 3 large grazed; 4-7 small ungrazed; 8-10 small grazed.

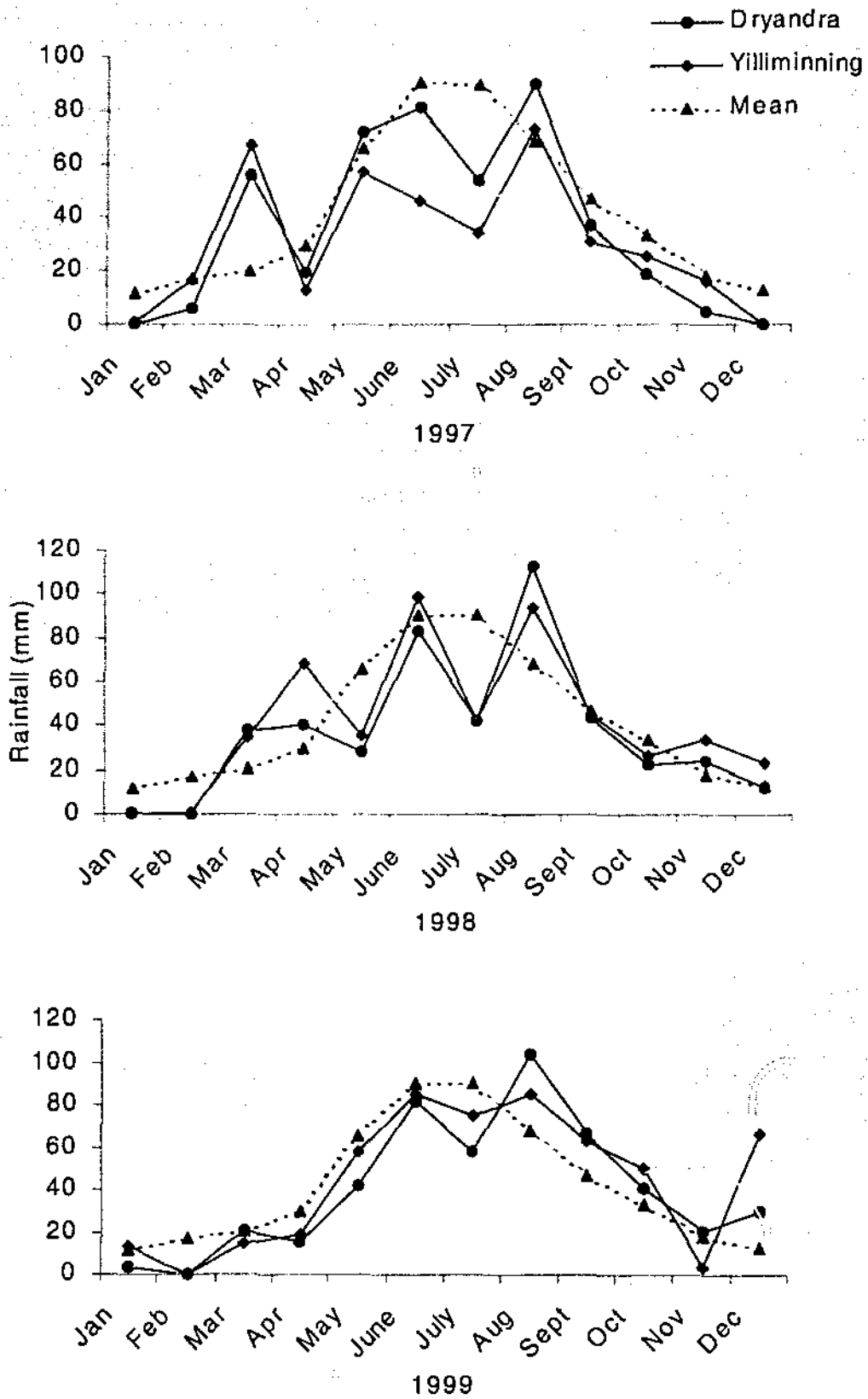


Figure 2.6 Total monthly rainfall at Dryandra and Yilliminning (1997 – 1999) and long-term mean monthly rainfall (recorded at Narrogin).

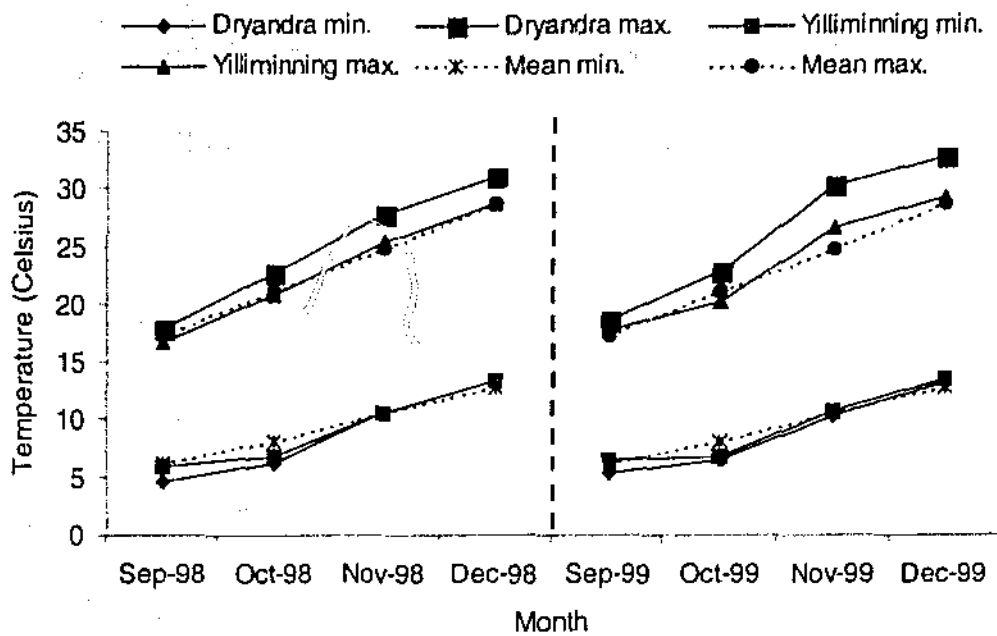


Figure 2.7 Mean minimum and maximum temperatures at Dryandra and Yilliminning, and long-term mean minimum and maximum temperatures (recorded at Narrogin) for each month of the main breeding season in the two comparative years of the study.

Vegetation cover

Coates (1993) mapped the vegetation of Dryandra using aerial photographs and ground truthing and produced 1:27,000 scale sheet maps. Each map delineated boundaries between the predominant vegetation associations. I used these maps as a basis for developing a digitised version of the vegetation associations in my study landscape (Figure 2.8). The digitised map was captured using the Geographical Information System (GIS) ARC/VIEW Version 3.1. For Yilliminning, I used aerial photographs and extensive ground truthing to produce a sheet map (1:25,000), which was also digitised (Figure 2.9).

Using ARC/VIEW, I calculated the percent cover of each vegetation/land-use type in the two landscapes (Table 2.1). The most common vegetation association in Dryandra was Wandoo woodland (28.1% of the total area), although Brown Mallet and Powderbark Wandoo occurred in similar proportions. In Yilliminning, the most common native vegetation association was also Wandoo (5.7%), but the most common land-use type was agricultural (cleared) land, which comprised 85.2% of the study landscape. This is in contrast to Dryandra with only 1.6% of cleared land (Table 2.1).

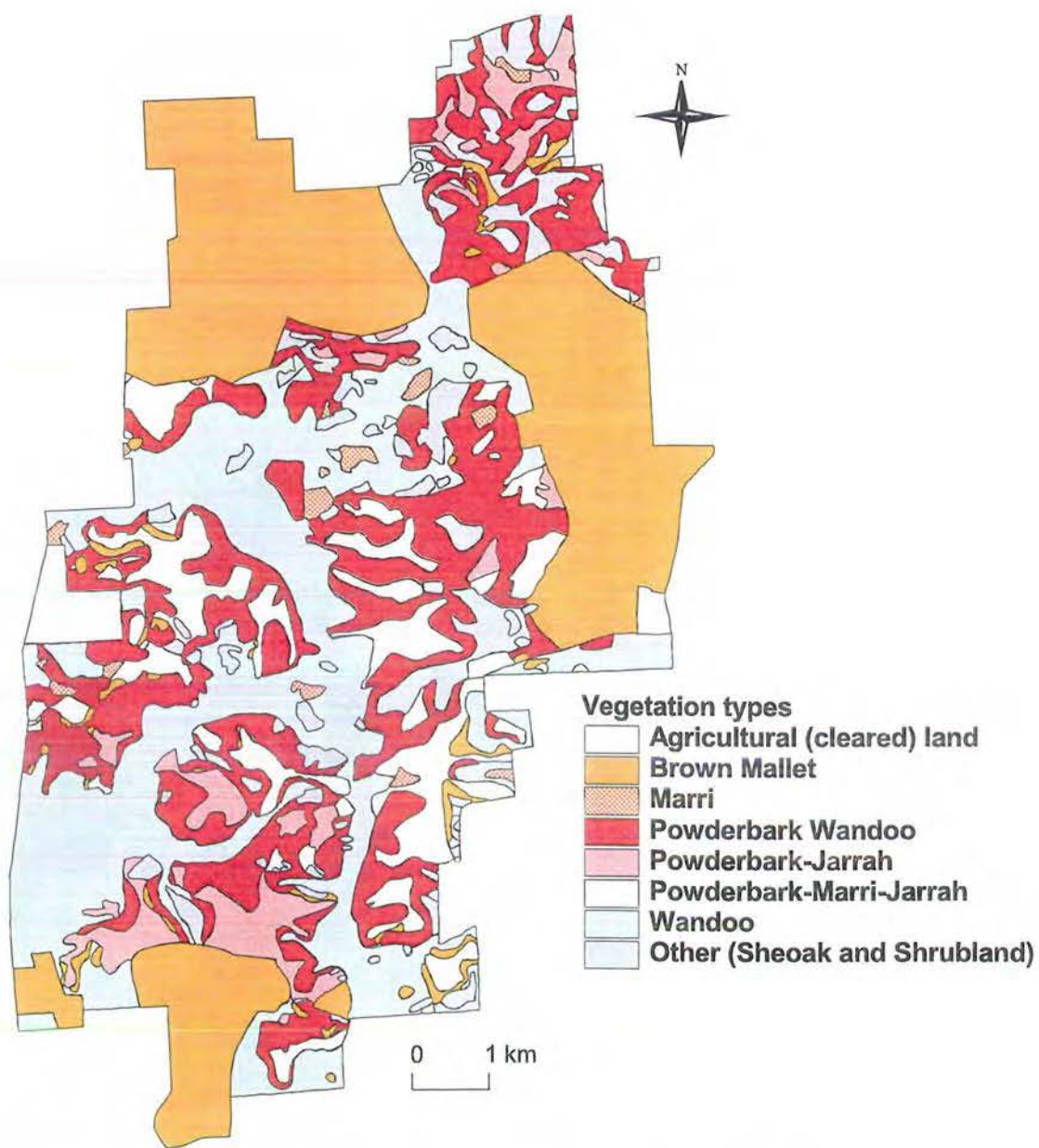


Figure 2.8 Vegetation types in the Dryandra study landscape (mapped from Coates 1993).

Vegetation types

- Agricultural (cleared) land
- Brown Mallet
- Morrel
- Sheoak
- Shrubland
- Wandoo
- Wandoo-Morrel-Salmon Gum
- Other (Granite, Saltmarsh, Revegetation)

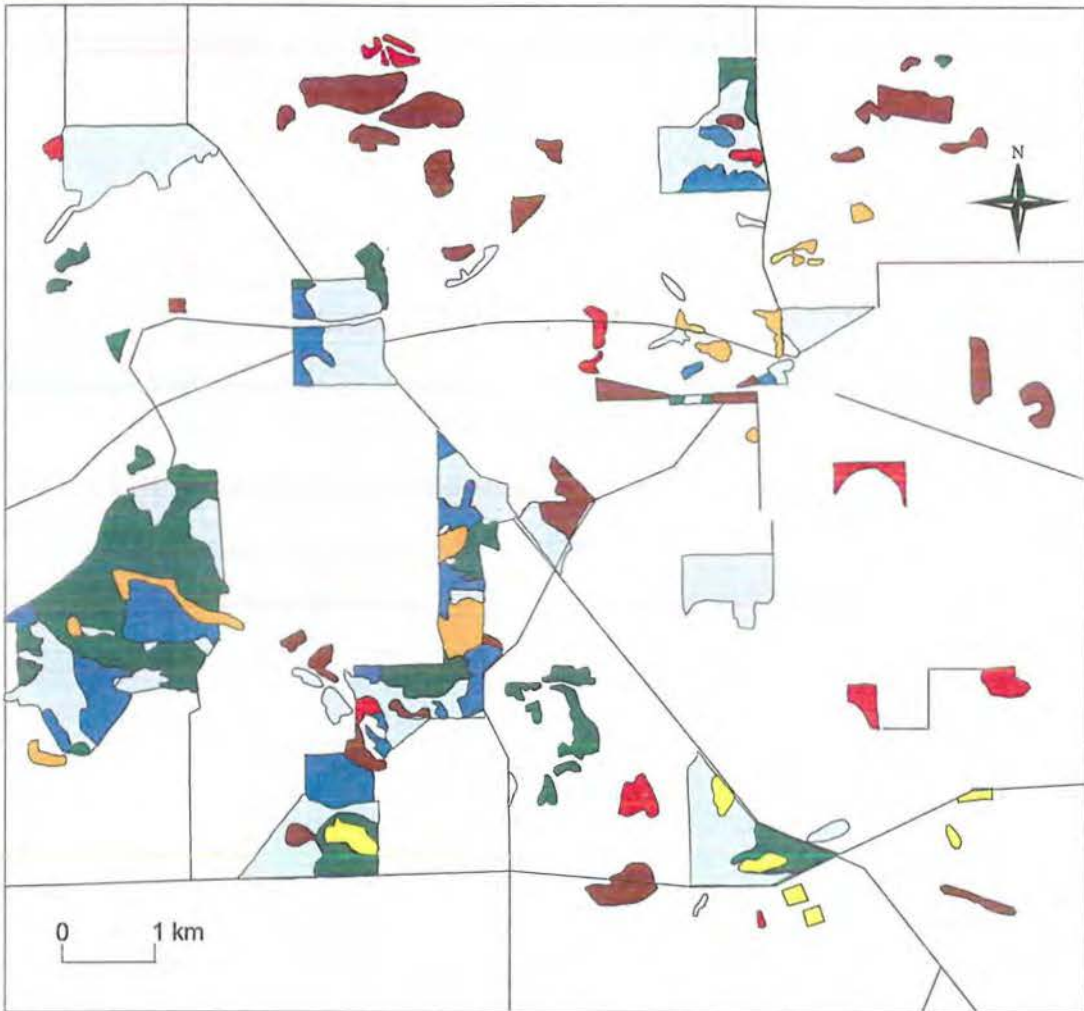


Figure 2.9 Vegetation types in the Yilliminning study landscape. Single lines are vegetation corridors occurring along roads, railway tracks or other linear features.

Table 2.1 The percent cover of each vegetation/land-use type occurring in the Dryandra and Yilliminning study areas.

Vegetation/land-use type	% cover of total area	
	Dryandra	Yilliminning
Agricultural (cleared) land	1.6	85.2
Brown Mallet	26.7	0.7
Marri	1.0	-
Morrel	-	0.6
Powderbark Wandoo	23.7	-
Powderbark Wandoo-Jarrah	4.9	-
Powderbark Wandoo-Marri-Jarrah	8.8	-
Sheoak	(see Other 1)	3.4
Shrubland	(see Other 1)	1.9
Wandoo	28.1	5.7
Wandoo-Morrel-Salmon Gum	-	2.2
Other 1 (Sheoak and Shrubland)	5.2	-
Other 2 (Saltmarsh and Agroforestry)	-	0.3

2.2 THE BIOLOGY OF THE RUFOUS TREECREEPER

2.2.1 Taxonomy, plumage and distribution

There are currently seven recognised species in the family Climacteridae (treecreepers), which is endemic to Australia and Papua New Guinea. Six of these occur in Australia, five in the genus *Climacteris* and one in the genus *Cormobates* (Sibley et al. 1984). Climacteridae is considered one of the "old endemic" families (parvorder Corvi), which originated in Australia and Papua New Guinea (Sibley et al. 1984; Sibley and Ahlquist 1985). The Rufous Treecreeper is closely related to the Brown Treecreeper *Climacteris picumnus*, which occurs in similar woodland associations in eastern Australia (Sibley et al. 1984).

I collected detailed information on plumage and size characteristics of adult and juvenile Rufous Treecreepers of both sexes. This information is presented in Appendix 2.1 and summarised here. The plumage of adult treecreepers is sexually dichromatic; males have buff white streaking with black margins on their upper breast and females have finer buff white streaking with rufous margins (Figure 2.10). The remainder of the plumage is practically identical, characterised by light brown-cinnamon upperparts, salmon-rufous underparts, and a rufous wing bar visible during flight. The differences in upper breast plumage are distinctive enough for birds to be sexed at a distance.



Figure 2.10 The distinctive upper breast plumage of the: a) adult male, b) adult female, c) juvenile male, and d) juvenile female.

The plumage of juvenile (< 2 months fledged) treecreepers differs between sexes and from adults. The upper breast pattern in juvenile males is more diffuse than adult males, with cinnamon rufous streaking down the rachis rather than buff white. Juvenile females have no discernible upper breast streaking, which begins to develop at 2 – 3 months post-fledging. Overall, juvenile plumage is slightly darker than adult, particularly in the face, crown, forehead and nape (Figure 2.10). Significant size dimorphism also occurs between the sexes in both adults and juveniles. Males are generally larger than females with significant variation in weight, head-bill, wing and tail measurements (Appendix 2.1).

The Rufous Treecreeper is endemic to southern Australia and has a continuous distribution, confined to temperate forests and woodlands, stretching from southwest Western Australia to western South Australia (Figure 2.11). At the western edge of its range it occurs in Jarrah and Karri *E. diversicolor* forest, but is considered to have closer distributional affinities to open temperate and semi-arid woodlands (Ford 1971; Blakers et al. 1984).



Figure 2.11 The distribution of the Rufous Treecreeper (from Schodde and Tidemann 1997).

2.2.2 Basic biology

The Rufous Treecreeper is generally considered a bark forager, but may spend a significant amount of time foraging on the ground in particular seasons (Recher and Davis 1998). Apart from the ground, common foraging locations include logs (fallen timber) and the trunks and branches of primarily eucalypt trees (Harrison 1969; Abbott 1981; Recher and Davis 1998). It feeds mostly on invertebrates (Barker and Vestjens 1990).

Based on current information, the species appears to be sedentary and territorial, living in pairs or groups of up to four individuals (Rose 1996). It is a cooperative breeder, with individuals in addition to the breeding pair recorded provisioning nestlings (Noske 1980; Rose 1996). It nests primarily in tree hollows (Whitlock 1911; Howe 1921; Rose 1996), but has been recorded nesting in hollow stumps or hollow logs on the ground (Carnaby 1933; Serventy 1958). The nest hollow may be “built-up” with strips of bark on which is placed the nest cup lined with dry grass, feathers, fur or other soft material (Harrison 1969; Serventy and Whittell 1976; Rose 1996; see Chapter 3).

The species breeds between August and January, although early breeding has been recorded in June and July after unseasonally heavy summer and autumn rains (Serventy and Marshall 1957). Clutch size can range from one to three, but is usually two (White 1913; Serventy and Whittell 1976; Rose 1996). Incubation and nestling periods are approximately 17 and 28 days respectively (Rose 1996).

2.3 GENERAL METHODS

2.3.1 Field work

The majority of fieldwork was undertaken between May 1997 and January 2000. A minimum of 12 days was spent in the field each month. During the breeding season, I spent an average of 20 days in the field per month. I began studying the *Dryandra* population in May 1997 and the Yilliminning population in April 1998.

2.3.2 Trapping and colour banding

I attempted to trap (mist-net) and colour-band all resident treecreepers in the 60 study territories and any new birds immigrating into the study sites. This

objective was overly optimistic owing to the level of turnover occurring in territories. However, at any given point in time, approximately 95% of the study populations were banded. I tried to ensure that only one unbanded bird occurred per territory. If a territory occupant remained unbanded for any length of time, I assumed it was the same individual for data collection purposes.

Banding was conducted between June 1997 and January 2000. A metal band supplied by the Australian Bird and Bat Banding Scheme (ABBBS) was placed on the left leg with a colour band (the master colour) placed above the metal band. Two colour bands were placed on the right leg so that each individual had a unique identity.

2.3.3 Monitoring

Monitoring of birds was conducted by re-trapping, or repeated re-sighting of banded individuals using 8 × 40 binoculars or a 22× wide-angle-lens telescope. From July 1997 – January 2000 (Dryandra) and July 1998 – January 2000 (Yilliminning), every territory was visited at least once a month (more frequently during the breeding season, see Chapter 3). Two seasonal visits were also conducted in April (autumn) and July (winter) 2000. The primary purpose of the monthly visits was to re-locate banded individuals. However, as the number of banded individuals grew, it became increasingly difficult to monitor the progress of all birds. Therefore, I allocated a maximum time period of 1 hour per territory per month to specifically re-locate banded birds. Birds seen outside this period were also recorded.

Appendix 2.1 PLUMAGE AND SIZE VARIATION IN ADULT AND JUVENILE RUFIOUS TREECREEPERS

Published in Corella, 1999, 23(4): 71-76

Summary

Plumage descriptions and morphometric measurements were obtained from adult and juvenile Rufous Treecreepers of both sexes. Plumage characteristics differed between sexes in adults and juveniles, and between adults and juveniles of the same sex. The main plumage differences between adults and juveniles were the overall darker colouration of the juvenile plumage and the variation in upper breast pattern. Males and females and adults and juveniles (of the same sex) also exhibited significant size dimorphism in a number of morphometric characters.

Introduction

Differences in plumage and size are widely used to sex and age birds. In Rufous Treecreepers, the plumage of adult birds is sexually dichromatic (Keast 1957). Males have buff white streaking with black margins on their upper breast and females have finer buff white streaking with rufous margins. Females are also described as being slightly smaller than males (MacDonald 1973; Simpson and Day 1996; Schodde and Tidemann 1997), but a significant size difference between the sexes has not been determined. Simpson and Day (1996) also note that the plumage of juvenile Rufous Treecreepers has not been adequately described. Documenting the plumage and morphometric characteristics of juveniles can assist in sexing and aging individuals.

Previous descriptions of the Rufous Treecreeper have recorded some variation in colour and size throughout its distribution. Male specimens from the Eyre Peninsula, South Australia were described as having more prominent black and white upper breast streaking (Howe 1921; Condon 1951; Keast 1957) and being generally paler in colour (Matthews cited in Ford 1971) than those from the southwest of Western Australia. However, Ford (1971) suggested that chest markings are more prominent in recently moulted birds and that descriptions of geographic differences in plumage have not considered fading, wear and stage of moult. Keast (1957) provided measurements of wing and tail length showing that

birds from the Eyre Peninsula are larger than those from the southwest of Western Australia.

In the above studies, descriptions of plumage colour were not based on a standard measure (e.g., a colour guide) and morphometric measurements were generally collected on very few individuals from any given area. Therefore, comparisons between geographic regions are tenuous. The aims of my study were to: a) provide a detailed description of the plumage of adults and juveniles using a standard measure; b) determine the extent of size differences between sexes in adults and juveniles; and c) determine the extent of size differences between adults and juveniles of the same sex.

Methods

Study area and sample population

As part of a detailed study on the ecology of the Rufous Treecreeper, I colour-banded 222 adults and 139 juveniles between June 1997 and January 1999 at Dryandra Woodland (centred on 32°45'S, 116°55'E) and the nearby Yilliminning agricultural district (centred on 32°54'S, 117°24'E) in the wheatbelt of Western Australia. All data collected on individuals classified as juveniles were from known age birds that had recently fledged from monitored nests. Most of these individuals (95%) were < 2 months old (i.e., < 1 month fledged). Birds of unknown age (i.e., those banded prior to the first breeding season and dispersers moving into the study area) were classified as adults.

Plumage

The primary criterion for sexing adult Rufous Treecreepers is the difference in upper breast plumage. This is widely accepted as truly representing the sex of an individual (Keast 1957; Noske 1980; Rose 1996) and is supported by dissected specimens (Ford 1971). I have included a description of adult plumage to allow for comparison with juveniles rather than to re-ascribe plumage differences between adult males and females. The sexing of juveniles based on plumage is more problematic because juvenile plumage has previously not been described in detail. However, every juvenile classified as male or female based on the differences I

describe, that remained in the study area for > 3 months, developed adult plumage characteristics consistent with their ascribed sex.

A detailed description of adult and juvenile plumage of both sexes was recorded using the plumage and soft parts description sheet issued by the Australian Bird and Bat Banding Scheme (ABBBS). Plumage colour was described using the Naturalist's Color Guide (Smithe 1975). As this is a time consuming process, these descriptions were obtained from single individuals to reduce extended handling of birds. Notes on important plumage characteristics (e.g., upper breast plumage and face markings) were recorded from approximately 20 individuals in each sex and age class.

Measurements

Head-bill, tail and maximum chord wing length measurements were taken on each bird following the procedures described in Lowe (1989). Birds were weighed in a weighing cone (see de Rebeira 1997) placed on an electronic balance.

Data analysis

Morphometric data were examined for departures from normality using normal probability plots and the Kolmogorov-Smirnov test. Tail measurements did not meet the assumptions of normality and were subsequently log (base 10) transformed. I used a two-sample *t* test to determine the significance of size differences between sexes in the same age class, and between ages of the same sex. These data are not independent, so an α level of 0.01 is considered statistically significant.

Results

Plumage

A detailed description of the plumage of adult and juvenile Rufous Treecreepers is included in Attachment A. Table 1 summarises the main plumage differences between sexes and adults and juveniles. In the following results, I focus primarily on plumage differences between adults and juveniles.

Table 1 Main plumage differences between adults and juveniles.

Character	Adult male	Adult female	Juvenile male	Juvenile female
Bill	Bill, cere and gape flange blackish neutral grey.	As male	Blackish neutral grey to light neutral grey. Paler at edges and lower base, pearl grey to pale horn. Bill becomes darker with age. Gape flange enlarged, cream colour.	As male
Head and shoulders	Forehead and crown dark neutral grey. Cinnamon rufous eyebrow from bill to behind eye. Nape, mantle and scapulars ground cinnamon with robin rufous tinge.	As male	Forehead blackish neutral grey, crown slightly lighter. No cinnamon rufous eyebrow. Ear coverts robin rufous with dark neutral grey tinge. Nape medium neutral grey, mantle ground cinnamon, both tinged robin rufous. Scapulars Vandyke brown with edge of feathers robin rufous.	As male
Other face markings			Face and crown/forehead/nape complex darker than adult.	As male
Underparts	Upper breast streaked with individual feathers comprising a buff white centre with blackish neutral grey bands and a light cinnamon rufous fringe on either side. Lower breast cinnamon rufous with faint buff white streaks down centre of feathers.	Upper breast streaked with individual feathers comprising a buff white centre and rich cinnamon rufous fringe on either side. Lower breast light cinnamon rufous with ground cinnamon tinge extending around to top of shoulders giving bird a greyish 'collar'.	Throat and breast heavily streaked with individual feathers comprising a light cinnamon rufous centre with blackish neutral grey bands and a light cinnamon rufous fringe on either side. Lower breast light cinnamon rufous with dark neutral grey spots near end of feathers.	Throat light cinnamon rufous with a medium neutral grey tinge. Upper breast as throat with no discernible streaking of rufous and buff white feathers. Lower breast light cinnamon rufous.

Generally, juveniles have darker plumage than adults do. The face and crown/forehead/neck complex is very dark and this is easily identifiable when observing birds in the field. Juveniles do not have a cinnamon rufous eyebrow (characteristic of older birds), but this develops quite rapidly (occurring in birds of 3 – 4 months of age). Very young birds (1 – 2 weeks post-fledging) may have wispy blackish neutral grey feathers protruding approximately 5 mm from the crown. These feathers fall out easily when the birds are handled and do not occur on older fledglings. This is a useful characteristic for identifying birds that have recently left the nest.

The bill of recently fledged birds, although primarily blackish neutral grey, is often paler at the edges and lower base with a pearl grey to pale horn colour. The gape flange is enlarged and cream coloured, and the palate is orange yellow (Table 1). The bill and gape flange become darker with age and the gape flange reduces in size.

The throat and upper breast of juvenile males is streaked with individual feathers consisting of a light cinnamon rufous stripe running down the rachis (rather than the buff white found in adults) and blackish neutral grey bands with a cinnamon rufous fringe on either side. The streaking can vary between individuals, but is usually more extensive and diffuse than in adults. In juvenile females, there is almost no sign of streaking, the throat and upper breast being a uniform light cinnamon rufous (or salmon colour) with a medium neutral grey tinge.

At approximately 2 – 3 months after fledging, juvenile plumage begins to develop distinct adult characteristics. A cinnamon rufous eyebrow is usually present and the plumage of the face and crown is much lighter than younger birds. Buff white streaking begins to show on the upper breast of females and the breast streaking on males is less extensive and more characteristic of adult males. Within 6 months of fledging, juvenile plumage closely resembles that of an adult and there does not appear to be an immature plumage stage.

Measurements

There were clear size differences between males and females and adults and juveniles for almost all of the measurements taken (Table 2). In adults, males had significantly higher mean weight, head-bill, wing and tail measurements (Table 3).

illustrating that sexual dimorphism is not confined to plumage. These measures were generally useful in discriminating between the sexes, but they were not mutually exclusive. For example, 89.5% of males had a head-bill measure > 39 mm, whereas 85% of females were \leq to 39 mm; 85.5% of males weighed > 32.5 grams, 87% of females weighed ≤ 32.5 grams. These two measures provided the clearest separation between the sexes (Figure 1).

Table 2 Summary of morphometric measurements (Mn = mean, Sd = standard deviation, Rng = range).

	No.	Weight (grams)			Head-bill (mm)			Wing (mm)			Tail (mm)		
		Mn	Sd	Rng	Mn	Sd	Rng	Mn	Sd	Rng	Mn	Sd	Rng
Adults													
Male	123	34.6	1.95	29.5-39.5	39.9	0.79	37.7-41.8	88.8	1.97	83-93	68.8	2.54	60-74
Female	99	30.8	2.04	25.7-38.3	38.4	0.75	36.7-40.9	85.8	2.32	80-90	66.5	2.33	61-72
Juveniles													
Male	72	30.5	2.23	24.9-36.0	36.9	1.09	34.4-39.8	80.3	5.60	68-90	60.1	7.52	41-71
Female	67	27.7	1.85	23.5-31.7	35.8	0.87	34.1-38.3	78.5	5.48	64-87	59.1	6.90	39-66

Table 3 Results of the *t* tests comparing differences in the morphometric measurements taken on adults and juveniles. The comparisons made were adult male - adult female (degrees of freedom (df) 220); adult male - juvenile male (df 193); adult female - juvenile female (df 164) and juvenile male - juvenile female (df 137). The table shows *t* values and levels of significance (**P* < 0.001; n.s. not significant).

	Adult male				Juvenile female			
	Weight	Head-bill	Wing	Tail	Weight	Head-bill	Wing	Tail
Adult female	13.6	13.9	10.0	6.6	9.9	21.1	11.8	9.4
Juvenile male	13.2	22.5	15.2	11.3	8.1	6.8	2.0 n.s.	0.7 n.s.

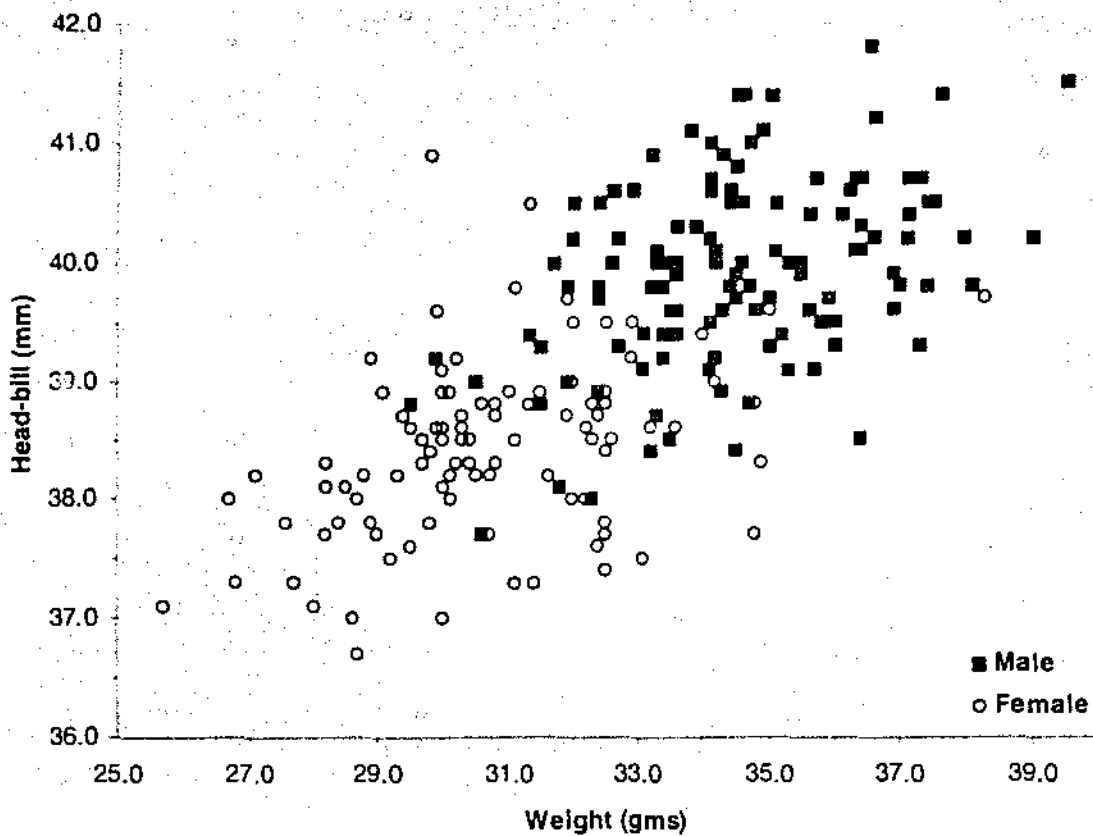


Figure 1 Distribution of weight and head-bill measurements for adult male and female Rufous Treecreepers.

There were significant size differences between sexes in juveniles for weight and head-bill measurements (Table 3), but these differences were not as discrete as they were in adults (Figure 2). Weight had the clearest separation, 79% of males weighed > 29 grams, whereas 76% of females weighed ≤ 29 grams. The less clear separation in juveniles is probably a result of the rapid growth of young birds. Although the majority of individuals were measured within a month of fledging, there may be considerable size differences between recently fledged and 1-month fledged individuals.

There were significant size differences between adults and juveniles of the same sex (Table 3) and morphometric measurements are useful in the aging of Rufous Treecreepers. Head-bill is probably the best measure to use, as wing and tail measurements for juveniles had high standard deviations (Table 2). For example, 94.5% of adult males had a head-bill > 38.5 mm, whereas 91.5% of juvenile males

were ≤ 38.5 mm; 97% of adult females had a head-bill > 37 mm, 95.5% of juvenile females were ≤ 37 mm.

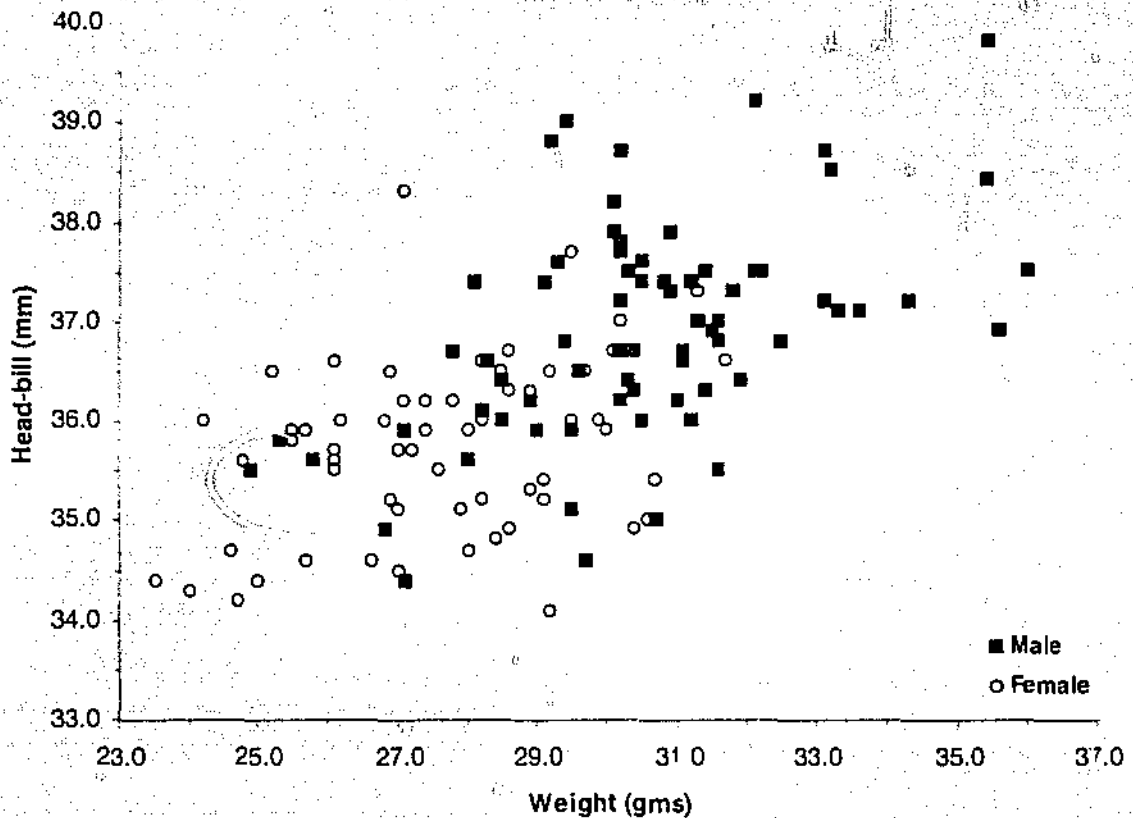


Figure 2 Distribution of weight and head-bill measurements for juvenile male and female Rufous Treecreepers.

Discussion

Plumage

The main plumage differences between juvenile (< 2 months old) and adult Rufous Treecreepers in my study area are the generally darker colouration of the juvenile plumage and the variations in upper breast pattern and colour (Table 1). The darker colouration is particularly strong in the face, crown, forehead and nape. The streaking on the upper breast plumage of juvenile males is generally more extensive than the adult and is slightly different in colour. Juvenile females have almost no discernible upper breast streaking.

Bill and gape flange colour are also useful in identifying young birds, although the corner of the gape flange may retain a hint of cream for up to 18

months in some individuals and should be used with caution as an aging characteristic. Recently fledged birds may be recognised by the presence of small, wispy feathers protruding from the crown. Any attempts to age Rufous Treecreepers should use a combination of the above characteristics for confident identification.

I recorded differences in the upper breast plumage of approximately 20-day-old nestling males ($n = 6$) and females ($n = 3$) and this may be a useful characteristic for sexing birds in the nest. Noske (1982) noted that nestling Brown Treecreepers *Climacteris picumnus* show plumage differences at approximately 14–16 days.

Ford (1971) suggested that immediate post-moult plumage of Rufous Treecreepers is quite bold (particularly the upper breast of males) and this may explain differences in plumage descriptions. In my study, plumage descriptions were taken during the early to mid breeding season (September – November). Primary moult for adults occurs between November and May (unpubl. data) and plumage colour in autumn and early winter may be slightly different than described here. Also, as I only recorded detailed plumage descriptions from single specimens, I have no data on individual variation for most of the plumage characteristics described.

Measurements

Male Rufous Treecreepers are significantly larger than females and this trend is common in a number of avian species (Amadon 1977). Sexual dimorphism develops at an early age. Juvenile birds exhibit clear size and plumage differences. In the closely related Brown Treecreeper, there is also strong sexual dimorphism based on morphometric measurements and plumage (Noske 1982).

The most significant size differences between males and females, in both age classes, occurred in head-bill and body weight (Table 3). Head-bill was generally a reliable measure with relatively small standard deviations (Table 2), but in some species (e.g., Eastern Spinebill *Acanthorhynchus tenuirostris*) head-bill length may vary seasonally probably owing to different foraging behaviours (e.g., moving from nectar to insect feeding; Jordan 1987). This is unlikely to occur in Rufous Treecreepers because the bill is quite sturdy and foraging behaviour does not differ markedly between seasons (Appendix 4.1).

Although body weight differed between the sexes, this result should be interpreted with caution as weight can fluctuate widely over short time periods.

Clark (1979) noted that body weight is influenced by factors such as time of day, season, stage of reproductive cycle and year to year variation in food availability. I made no attempt to control for these factors when weighing birds. The relatively small standard deviations recorded for weight measurements suggests that Rufous Treecreepers may not show marked fluctuations and this may be characteristic of non-migratory temperate woodland and forest species (Clark 1979).

Body weight may fluctuate within a particular range for a particular sex, thereby still exhibiting overall differences between males and females. In Rufous Treecreepers, weight may fluctuate more widely for breeding females owing to egg production, incubation (only females incubate; Chapter 3) and care of young. The weight range for adult females was 12.6 grams, which was slightly higher than males at 10.0 grams (Table 2). However, I found no difference in the body weight of adult females measured at the beginning of the breeding season (August/September: mean weight 31.14 grams) compared to the end of the season (December/January: mean weight 30.38 grams; $t = 1.28_{49}$, $P = 0.21$).

Plumage differences between adult male and female Rufous Treecreepers have long been recognised (e.g., Keast 1957). In my study, I have shown that plumage also differs between juvenile males and females and these differences are not the same as those recorded for adults. In addition to the sexually dichromatic plumage, males and females exhibit significant size dimorphism in a number of morphometric characters. As I have used a standard, repeatable measure for recording plumage and size characteristics, this should allow valid comparisons between the results from my study and future studies conducted in different regions, on live birds, using the same methods. This will contribute to our knowledge of geographic variation in the plumage and size of Rufous Treecreepers.

Attachment A to Appendix 2.1

Full plumage descriptions of adult and juvenile Rufous Treecreepers. Numbers in brackets are colour codes from Smithe (1975).

Juvenile female (< 2 months old)

Bill

Upper mandible blackish neutral grey (82) grading to light neutral grey (85), paler at edges and base, pearl grey (81) to almost white/pale horn colour (92). Lower mandible as above, pinkish flesh colour (5) where base of bill meets chin. Bill becomes darker with age. Cere dark neutral grey (83). Gape flange enlarged, cream colour (54). Palate orange yellow (18).

Eye

Inner iris jet black (89), outer iris dark brownish olive (129). Ring skin blackish neutral grey. Ring feathers robin rufous (340), darker than adults.

Head and shoulders

Lores robin rufous with a dark neutral grey tinge. Forehead blackish neutral grey, crown slightly lighter. No cinnamon rufous (40) eyebrow. Ear coverts robin rufous with a dark neutral grey tinge. Nape medium neutral grey (84), mantle ground cinnamon (239), both tinged robin rufous. Scapulars Vandyke brown (221) with edge of feathers robin rufous.

Other face markings

Face is darker than adult. has blackish neutral grey striations prominent when observing birds in the field. Crown/forehead/nape complex darker than adult. In certain individuals (mostly less than one week old fledglings), wispy feathers of blackish neutral grey protrude about 5 mm from the crown. These are very fine, but are visible in the field. They fall out easily when birds are handled and do not occur on older individuals.

Back

Upper and lower back ground cinnamon with a robin rufous tinge. Rump and uppertail coverts robin rufous. Uppertail ground cinnamon with a blackish neutral grey band (not on outer feathers), lighter at tips.

Legs and feet

Tibia skin flesh colour with cinnamon rufous feathers. Tarsus, toes and claws medium neutral grey becoming darker with age. Soles pale neutral grey (86).

Underparts

Chin light cinnamon rufous/salmon colour (106), bristles around base of bill blackish neutral grey. Throat light cinnamon rufous/salmon with a medium neutral grey tinge. Upper breast as throat with no rufous and buff white (124) feathers as found in adult females. Lower breast light cinnamon rufous/salmon, flanks rich cinnamon rufous. Belly light cinnamon rufous/salmon with dark neutral grey spots occurring near the end of some feathers, usually in pairs on opposite sides of the rachis. Undertail coverts cinnamon rufous with dark neutral grey spots as described above. Undertail ground cinnamon with same band as uppertail, but much paler.

Upperwing

Primaries and secondaries Vandyke brown with a cinnamon rufous centre band and leading edge. Tertiaries natal brown (219a) with a cinnamon rufous edge, but no band. Primary, secondary, median and lesser coverts, and alula, Vandyke brown with a robin rufous edge.

Underwing

Primaries and secondaries ground cinnamon, lighter at tips and much lighter than upperwing. Centre band true cinnamon (139) rather than cinnamon rufous. Axillaries light ground cinnamon with cinnamon rufous edge, underwing coverts light cinnamon rufous/salmon.

Juvenile male

As female except:

Underparts

Throat and breast heavily streaked (streaking much more extensive than adult male, although variable), individual feathers consist of a centre shaft of light cinnamon rufous/salmon (rather than the buff white in adult males) with a blackish neutral grey band and light cinnamon rufous fringe on either side. Lower breast light cinnamon rufous/salmon with dark neutral grey spots as described above.

Attachment A (continued)**Adult female (1+)***Bill*

Upper and lower mandible, cere and gape flange a blackish neutral grey. Palate cream colour.

Eye

Inner iris jet black, outer iris Prout's brown (121a), ring skin blackish neutral grey, ring feathers cinnamon rufous.

Head and shoulders

Lores and ear coverts robin rufous with a dark neutral grey tinge. Forehead and crown dark neutral grey. Nape, mantle and scapulars ground cinnamon with a robin rufous tinge. Cinnamon rufous eyebrow from bill to behind eye. In the field, face appears lighter than males.

Back

Upper and lower back ground cinnamon with a robin rufous tinge. Uppertail coverts robin rufous, uppertail ground cinnamon at base grading to robin rufous and lighter at tips with a blackish neutral grey band.

Legs and feet

Tibia, tarsus, toes and claws blackish neutral grey (cinnamon rufous feathers around tibia), soles pale neutral grey.

Underparts

Chin and throat light cinnamon rufous/salmon. Upper breast streaked with individual feathers comprising buff white centre and a rich cinnamon rufous fringe on either side. Lower breast light cinnamon rufous with a ground cinnamon tinge extending around to the top of the shoulders giving the bird a greyish 'collar'. Flanks rich cinnamon rufous with white/pale horn colour streaks down centre of feathers. Belly light cinnamon rufous/salmon with pale streaks down centre of feathers (as above). Undertail coverts light cinnamon rufous, paler at tips, medium neutral grey spots (in pairs) on either side of feather shaft near ends of feathers. Undertail as uppertail, but paler.

Upperwing

Primaries and secondaries Vandyke brown with a cinnamon rufous centre band. Tertiaries Vandyke brown. Primary, secondary, median and lesser coverts, and alula, Vandyke brown with robin rufous edge.

Underwing

Primaries, secondaries and axillaries as upperwing, but paler. Underwing coverts light cinnamon rufous.

Adult Male

As female except:

Underparts

Upper breast streaked with individual feathers comprising buff white centre with blackish neutral grey bands and a light cinnamon rufous/salmon fringe on either side. Lower breast cinnamon rufous with buff white streaks down centre of feathers.

Part II
THE ECOLOGY OF THE RUFOUS TREECREEPER
IN AN UNFRAGMENTED LANDSCAPE



My Woodland Home: Part I

*On a frozen September morning
Warm sun on thawing ground
Gives rise to misty clouds
That shroud my woodland home*

*Amid the tall wandoo
Sunlight rays shine through
Feathers rufous in flight
Then alighting on the ground*

*I brush my fingers on powder
Where dryandra flower
Nectar bathers gather
To shower in pollen rain*

*Termites dodge the striped marauder
Deep inside their rotting larder
But escaping the myopic splines
Gets harder every day*

*That evening, on their dusky stage
Underneath a luminous gaze
The curlews dance and sing
For a million diamond eyes*

*I lie awake and wonder
Of this woodland beauty plundered
And hope the chance to share
Will save it from demise*

CHAPTER 3
COOPERATIVE BREEDING IN AN UNFRAGMENTED LANDSCAPE

SUMMARY

A detailed analysis of the social organisation, breeding behaviour, demography and dispersal of the Rufous Treecreeper was undertaken in Dryandra to gain a sound knowledge of the ecological traits of the species in a relatively undisturbed landscape. I measured the nest success and annual productivity of breeding groups, and ascertained survival rates for fledglings, juveniles and adults. This involved extensive monitoring of colour-banded individuals over 3 years at three spatially discrete study sites.

The Rufous Treecreeper occupied territories year-round, which were used for foraging and nesting. Each territory contained a breeding group of between two to seven individuals. Most groups comprised a primary (probably breeding) male and female and offspring from previous breeding seasons. Territoriality was apparent, but variable, particularly during the breeding season when individuals would feed nestlings in adjacent territories. The social organisation of the species was based on neighbourhoods of interacting territories.

All group members provisioned nestlings. There was no correlation between the number of helpers at the nest and total provisioning rate to nestlings because the primary male and female significantly reduced their provisioning effort as the number of helpers increased. Total nest success for the 3 years was high (77.7%). Multibroodedness was relatively common, but was significantly greater for larger groups. Annual productivity differed significantly between sites and was highest for larger groups. Helpers appeared to have a positive effect on productivity by reducing the workload of breeders, which allowed a greater number of nest attempts in a season and subsequently increased reproductive output.

Fledgling and juvenile survival rates were relatively high (0.76 and 0.46 respectively) compared to other cooperative and non-cooperative species, but adult survival rate (0.76) was comparable to other southern temperate passerines. Dispersal of juveniles appeared to be female biased. Recorded dispersal distances were short (one to two territories), but this undoubtedly under-estimates the actual

distribution of dispersal distances. Short-distance dispersal appeared to be influenced by territory quality, as did visits to neighbouring territories that involved the provisioning of nestlings. This "cross-territorial" provisioning may be a vehicle for non-breeding birds to assess the quality of adjacent territories and the potential for obtaining a breeding position.

The demography of the Rufous Treecreeper was consistent with other old endemic Australian passerines, characterised by small clutch size, low annual productivity, and high survival. High adult survival means that there are few breeding vacancies for non-breeders and this is probably an important influential factor in the evolution of cooperative breeding in the species. Cooperative breeding may also be influenced by ecological constraints (e.g., habitat saturation) and a cost-benefit trade-off between remaining philopatric in high quality territories and dispersing to poorer quality territories where reproductive success may be low.

3.1 INTRODUCTION

3.1.1 Overview

The purpose of the following three chapters is to examine in detail the ecological characteristics of the Rufous Treecreeper in the unfragmented landscape of Dryandra. This establishes a reference point to which results from the agricultural landscape at Yilliminning can be compared, and is fundamental to understanding the potential effects of habitat fragmentation on population viability. In this chapter, I examine the demography, and social and spatial organisation of the treecreeper. I also explore the evolution of cooperative breeding in the species in some depth because the consequences of habitat alteration for cooperative behaviour have rarely been addressed. Finally, I briefly describe the dispersal behaviour of the species. The aims of this chapter are to determine:

- a) territory size and territorial behaviour;
- b) population sex ratio, and group size and composition;
- c) breeding behaviour;
- d) differences in reproductive success and survival between years, sites and group sizes; and
- e) dispersal behaviour.

3.1.2 Demography of Australian passerines

In general, Australian passerines are characterised by greater longevity and smaller clutch sizes compared to their Northern Hemisphere counterparts (Woinarski 1985; Yom-Tov 1987; Rowley and Russell 1991). This appears to occur primarily in the old endemic species rather than species that are comparatively recent invaders to Australia (Yom-Tov 1987). In comparing leaf-gleaning birds between Australia and the Northern Hemisphere, Woinarski (1985) found that Australian species generally had a longer breeding season. Small clutch size and an extended breeding season may be characteristic of species that produce multiple broods (Woinarski 1985; Yom-Tov 1987). Multibroodedness occurs when a female lays a second clutch in the same season after successfully raising the first clutch to fledging. Further data are required, but Australian passerines also appear to be characterised by longer fledgling dependence periods, lower annual productivity and higher adult survival

than Northern Hemisphere species (Rowley and Russell 1991). These data can only be obtained from comprehensive population studies where individually marked birds are monitored over a number of years.

3.1.3 Cooperative breeding

Why remain philopatric?

Cooperative breeding occurs when individuals in addition to the breeding pair assist in rearing young (Brown 1978, 1987). This situation has fascinated behavioural ecologists since the pioneering work of Skutch (1935, 1961) and Rowley (1965). The following is a brief introduction to the subject of cooperative breeding. For more detailed accounts, see the reviews of Brown (1987), Clarke (1995) and Cockburn (1998).

Investigations into cooperative breeding in birds have generally been driven by two questions: a) why do some individuals remain on their natal territory (philopatry) as members of a family group, or join a group in another territory, rather than breeding independently; and b) why do these individuals often assist in rearing young that are not their own? Explanations for extended natal philopatry have invoked the "ecological constraints" (Emlen 1982), "benefits-of-philopatry" (Stacey and Ligon 1987, 1991), and "life history" hypotheses (Arnold and Owens 1998; Hatchwell and Komdeur 2000). These hypotheses have divergent predictions (see below), but may act in combination to influence extended philopatry in particular species (Hatchwell and Komdeur 2000).

The ecological constraints hypothesis predicts that some individuals are unable to establish territories and breed independently owing to the restricted availability of particular resources (e.g., mates, food or nesting sites). Habitat saturation is a specific version of the ecological constraints hypothesis and suggests that when all suitable habitat is occupied, potential dispersers are more likely to remain philopatric (Brown 1974; Gaston 1978; Stacey 1979; Koenig 1981; Walters et al. 1988).

The benefits-of-philopatry hypothesis predicts that non-breeding individuals will remain on their natal territory when the fitness benefit of doing so outweighs the option of dispersing and breeding independently. This will generally occur when

there is significant variation in territory quality or if individual fitness is greater in larger groups (Stacey and Ligon 1991). This hypothesis has been interpreted as another version of the ecological constraints model (i.e., the “benefit” of a cost-benefit equation; Emlen 1991; Clarke 1995) and has generally been accommodated within this theoretical framework (Emlen 1994; Hatchwell and Komdeur 2000). However, Stacey and Ligon (1991) stated that the two hypotheses yield different predictions and point out that all species face ecological constraints and this is not a robust explanation for cooperative breeding *per se*.

The life history hypothesis emphasises specific life history characteristics as important influences on the evolution of cooperative breeding. These characteristics include delayed maturity, high adult survival, low reproductive rates (e.g., small clutch size) and increased sedentariness (Arnold and Owens 1998; Hatchwell and Komdeur 2000). Low annual mortality appears to be a key characteristic influencing cooperative breeding in certain avian lineages (Arnold and Owens 1998). This may lead to low population turnover in relatively stable environments where species are sedentary and natality is greater than mortality (Hatchwell and Komdeur 2000). In short, when survival rates are high and ecological conditions allow year-round territory occupation, population turnover will be low and the habitat may become saturated predisposing a species to cooperative breeding.

The key distinction between the life history and ecological constraints models is that the life history hypothesis predicts that cooperative breeding will evolve only in those avian lineages with the appropriate life history characteristics, whereas the ecological constraints hypothesis predicts that any species may cooperatively breed if faced with resource restrictions (Hatchwell and Komdeur 2000). Hatchwell and Komdeur (2000) conclude that this distinction is artificial and propose a broader constraints hypothesis, incorporating characteristics of the ecological and life history models, to assess the evolution of cooperative breeding.

Why help?

Many hypotheses have been generated to explain helping behaviour and Cockburn (1998) provides an excellent discussion on why helpers help. He summarises the adaptive explanations for help (there are also non-adaptive

explanations, for example, Jamieson 1986, 1991) into six main classes (p. 145): a) enhanced production of non-descendant kin (kin selection theory); b) payment of rent (allowing access to group or territory derived benefits); c) direct access to parentage (e.g., inheriting the natal territory); d) enhancement of territory or group size leading to improvements in subsequent direct reproduction opportunities; e) enhancement of social circumstances via formation of alliances that improve reproductive prospects; and f) acquisition of skills required for future, successful reproduction.

Helping behaviour as a function of kin selection is one of the better supported theories in the cooperative breeding literature. Kin selection theory predicts that non-breeding helpers should preferentially assist in rearing closely related young compared to unrelated individuals (Hamilton 1964; Brown 1978). By helping close relatives, non-breeders gain indirect fitness benefits by increasing their own genetic representation in subsequent generations via copies of genes shared by the relatives they help (Komdeur and Hatchwell 1999). Preferential help of closely related kin (when helping more distantly related kin was also an option) has been demonstrated in many studies of cooperatively breeding birds (Curry 1988; Emlen and Wrege 1988; Conrad et al. 1998). However, a number of studies show that helpers assist non-related breeders (Ligon and Ligon 1990a; Reyer 1990), or that related, philopatric individuals do not always help (Magrath and Yezerinac 1997). These findings question the broad generality of kin selection theory and encourage support for the range of alternative hypotheses proposed to explain helping behaviour (see Clarke 1995 and Cockburn 1998).

The evolution of helping as an adaptive behaviour relies on helpers gaining indirect or direct fitness benefits. Improvements in indirect fitness may be achieved if helpers increase the reproductive output of the breeding pair, thereby increasing their own genetic representation in future generations. It is relatively easy to document the kinds of activities helpers engage in, which could potentially improve breeder productivity. These include assisting in territorial defence, predator surveillance and mobbing, nest building, incubation, feeding nestlings and feeding and caring for fledglings (Brown 1978; Stacey and Koenig 1990). It is much more difficult to demonstrate increased productivity directly attributable to the presence of

helpers owing to the confounding effects of territory and breeder quality. Results from manipulative (e.g., experimental removal of helpers) and comparative (comparing the productivity of the same breeding pair with and without help) studies on the effect of helpers on reproductive success have been equivocal (see Table 2 in Cockburn 1998).

Direct fitness benefits to helpers, as a consequence of helping behaviour (e.g., subsequently increasing the number of their own offspring as a result of helping) are also difficult to demonstrate, particularly in short-term studies. In their 17-year study of the Splendid Fairy-wren *Malurus splendens*, Russell and Rowley (1993) showed that philopatric individuals had a high probability of inheriting the natal territory, demonstrating the value of the stay-at-home strategy. Komdeur (1996) found that in the Seychelles Warbler *Acrocephalus sechellensis*, first-time breeders with some helping experience had higher reproductive success than those with no experience.

Helpers are predominantly male in a number of species (Noske 1982; Walters et al. 1988; Marzluff and Balda 1990; Davies 1992; Dickinson et al. 1996). This is often a consequence of female-biased dispersal in many passerines (Greenwood 1980; Greenwood and Harvey 1982). In species where females remain philopatric at least until the next breeding season (e.g., Splendid and Red-Winged Fairy-wren *M. elegans*), helping behaviour may be just as prevalent in females as it is in males (Russell and Rowley 1988, 2000). In some species (e.g., Seychelles Warbler), helpers are predominantly females (Komdeur 1994).

3.1.4 Cooperative breeding in Australian birds

On a global scale, cooperative breeding in birds is rare with approximately 3.2% of 9,672 species known to breed cooperatively (Sibley and Monroe 1990; Arnold and Owens 1998). In Australia, cooperative breeding is much more common with 12% of 667 species being recorded as cooperative breeders (Clarke 1995). This figure is likely to increase as more species are studied in detail. Russell (1989) was the first to point out that cooperative breeding is more prevalent in the old endemic passerine families with a long evolutionary history in Australia compared to relatively recent invaders. Climacteridae is included in the old endemics.

Ford et al. (1988) documented patterns in the distribution and behavioural characteristics of Australian cooperative breeders. They found that cooperative breeding was more prevalent in eucalypt and semi-arid woodlands, among insectivores that pursued their prey, and among ground-foragers. Ford et al. (1988) suggested that the evolution of cooperative breeding in Australia was influenced by the aseasonality of the habitats that cooperative breeders tend to occupy. However, as Russell (1989) and Cockburn (1996) point out, evolutionary interpretations of cooperative breeding must consider the environmental influences that occurred during the early evolution of cooperative breeding (possibly > 15 – 20 million years ago; Russell 1989).

In a recent review of cooperative breeding in Australian birds, Cockburn (1996) outlined important evolutionary and ecological characteristics of cooperative breeders. He suggested that phylogenetic history is an important determinant in cooperative breeding by highlighting the prevalence of cooperation in the passerine group known as the Corvida. Within the Corvida, Cockburn (1996) found that cooperative breeding was more likely to evolve in open habitats (facilitating group cohesion) and that longevity is a precursor to the retention of young in the natal territory. Cooperative Australian species commonly occur in open habitats (Dow 1980; Ford et al. 1988), but few data have been collected in closed vegetation associations (e.g., rainforests) to adequately test this hypothesis (E. Russell, pers. comm., July 2000).

3.1.5 Dispersal

There are two main types of dispersal involving the inter-territory movement of birds. Natal dispersal is generally defined as the movement of an individual from its place of birth to the place where it breeds or may potentially breed (Greenwood and Harvey 1982; Johnson and Gaines 1990). Breeding dispersal is the movement of an individual from a site where it reproduces or attempts to reproduce to another site where it also attempts reproduction (Greenwood and Harvey 1982; Johnson and Gaines 1990). Particularly well documented in cooperatively breeding birds is the movement of individuals between territories that involves “visits” to neighbouring groups where an individual may eventually return to its territory of origin (Clarke

and Heathcote 1990; Russell and Rowley 1993; Cale 1999). In this thesis, I use the terms natal and breeding dispersal as defined above. I also use the term visit (*sensu* Cale 1999) to describe movements that do not involve dispersal.

Dispersal in birds is generally female-biased, but exceptions do occur (Clarke et al. 1997). Hypotheses invoked to explain this bias involve resource or intrasexual mate competition, or inbreeding avoidance, but these are not mutually exclusive and may interact to influence dispersal (Dobson and Jones 1986). Greenwood (1980) suggested that female-biased dispersal in birds was a consequence of a predominantly monogamous mating system where males would gain most by remaining philopatric and defending sufficient resources to attract females. However, some species with promiscuous mating systems also have female-biased dispersal (e.g., Splendid Fairy-wren, Russell and Rowley 1993). Wolff and Plisner (1998) proposed the “first-choice” hypothesis, which predicts that the sex that has first choice of mating sites will be philopatric while the other will disperse. Their hypothesis is well supported in migratory passerines where males typically arrive at breeding sites before females and have first choice of breeding location (and natal dispersal is female biased). The evidence from resident, sedentary passerines is equivocal based in some part on the lack of data and the difficulty of determining who actually “chooses” a breeding site.

It is generally assumed that cooperatively breeding birds are characterised by short-distance dispersal (Zack 1990). Measuring true dispersal distance for highly mobile species like birds is difficult owing to the limited size of study areas and the low probability of locating long distance dispersers (Baker et al. 1995). Recent evidence suggests that dispersal distances derived from capture-recapture (re-sighting) data may be severely underestimated (Koenig et al. 1996, 2000). In this chapter, I report on dispersals observed within the study sites, but make no attempt to calculate the actual distribution of dispersal distances for Rufous Treecreepers. This issue is discussed further in Chapter 8.

3.2 METHODS

3.2.1 Study sites

Most of the data presented in this chapter are from the three study sites in Dryandra. In certain cases, I also include data from Yilliminning to increase sample size. Study site description and general methods are presented in Chapter 2. Throughout this thesis I use the term group year (pairs are also referred to as groups). One group year is equivalent to one group studied for 1 year. In Dryandra, I studied 30 groups for 3 years, which totals 90 group years.

3.2.2 Territoriality and territory size

Allocation of individuals to territories and groups was initially determined during the period of extensive colour-banding at the beginning of the study (Chapter 2) and subsequently by detailed observations of behavioural interactions. Treecreepers formed relatively cohesive groups that would communicate via contact calls and often foraged together. The openness of the habitat also facilitated observation of inter- and intra-group interactions. To determine the extent of territoriality in treecreepers, I recorded behavioural interactions between neighbouring birds (over 12 months) and followed individuals for extended periods (up to 1 hour) to ascertain if they readily crossed supposed territorial boundaries.

I recorded the location of territory occupants in each of the 30 study territories in Dryandra on at least a monthly basis for the duration of the study. These locations were initially marked in the field with flagging tape and later identified using a Global Positioning System (GPS). The level of accuracy of the GPS could vary from 20 – 100 m depending on the number of satellites within range of the receiver and their relative position. Owing to this, I took three readings at each flagged location during different times of the day and used the mean of these as the actual location.

I recorded a minimum of 40 locational “fixes” per territory (except territories A3 = 24 and A9 = 30). Only one fix per visit was taken to ensure independence of observations (i.e., if the territory had three occupants, I only recorded the location of one of them). The time period between fixes (i.e., a minimum of 1 week) should not result in spatial autocorrelation problems (Hansteen et al. 1997).

GPS coordinates were entered into the software package CALHOME (Kie et al. 1994) and the minimum convex polygon (MCP) method (Mohr 1947) was used to calculate territory size. This method has been criticised for over-estimating territory sizes (Anderson 1982). Therefore, I calculated 100%, 95% (considered a close approximation to actual territory area; Jaremovic and Croft 1987; Mazur et al. 1998), and 50% (approximating the "core area"; Jaremovic and Croft 1987) values for each territory. The number of fixes was plotted against territory area to determine the appropriateness of the sample size. For eight of the 30 territories, an asymptote did not appear to be reached within the 40 locational fixes and the size of some territories (e.g., A3 and A9) may be underestimated.

3.2.3 Sex ratio and group size

Banded individuals were monitored by the methods described in Chapter 2 (Section 2.3.3). At the beginning of each breeding season (mid – late August), an extensive annual census was conducted to collect data on population size, sex ratio, and group size and composition. I collected the data at a fixed point in time because these variables may change throughout the year. An individual was allocated to a group based on site fidelity, behavioural observations and knowledge of group history (e.g., if an individual was a fledgling from a previous season).

3.2.4 Nesting and provisioning behaviour

Determining contributions to nesting and nestling provisioning required an allocation of status to group members. I use the terms primary male, primary female and helper throughout this thesis. I avoid use of the terms breeder and non-breeder, as I have no data on genetic parentage of young, but if social parentage is equivalent to genetic parentage then behavioural observations indicated that the primary male and female were the breeding birds. The status of individuals within a group was defined according to the following criteria.

- a) Primary male (PM) – for pairs or groups that had only one male, the designation of primary male was straightforward. During the second and third years of the study, most helper males were young from the previous breeding season(s) so the oldest male was designated the primary male. If

a male was resident in a territory for all three breeding seasons, it was designated primary male in each season. If a male disappeared and was replaced by a new male immigrating into the territory, the disappearing male was considered the primary male for the breeding season(s) it was present and the new male was considered the primary male for subsequent seasons (it was unlikely that helper males were replaced – see Results). The main limitation with these methods is that during the first year of the study, some primary males that disappeared may have been replaced by their sons (i.e., inheriting the natal territory). Where doubt existed, groups were not used in analyses involving identification of primary birds and helpers ($n = 7$ of 90 group years).

- b) Primary female (PF) – most of the above pertains to the designation of primary females. These individuals could also be identified by their nesting behaviour. Only one female was observed incubating the eggs or brooding the young and she was designated the primary female.
- c) Helper – birds other than the primary male or female that were resident on the territory (mostly young from previous breeding seasons) and assisted in feeding nestlings were designated as helpers.

In some cases, members of a group would feed nestlings in territories adjacent to their own (these were temporary visits and are referred to as cross-territorial provisioning from here on). Therefore, I classified helpers into four categories: resident male (RM), resident female (RF), non-resident male (NRM), and non-resident female (NRF). I also differentiate between group size (which includes only resident individuals) and total number of nest attendants (which can include resident and non-resident individuals). At a few nests, offspring from the first brood of the season were recorded feeding nestlings in the second brood. These contributions were considered in the calculations of resident helper provisioning rate.

During the breeding season (August – January), territories were visited mostly on a weekly basis. Fieldwork was constrained to 2 weeks per month at the beginning (early August) and end (late December) of the breeding season and territories were only visited fortnightly during these periods. I attempted to locate

nects in all territories by following birds that were carrying nesting material and/or food, and observing female behaviour.

Nests were watched throughout the day (0600 – 1600 hrs) for 60 minutes per session during the various nesting stages (all nests were in tree hollows). I used a 22x telescope located approximately 15 – 20 m from the nest. I observed 121 of 148 recorded nesting attempts at some stage of the nesting cycle (a number of nests were watched more than once). In 1997, 10 nests were observed during the building stage to determine the division of labour between males and females. For all years combined, 12 nests were watched during the incubation stage to determine if birds other than the primary female incubated. Of these, five nests had more than one female in the group. A total of 112 nests were watched when adults were feeding nestlings.

As treecreepers are hollow-nesters and average nest height was 8.5 m (Chapter 4), accessibility to nests was limited and nesting stages had to be determined by behavioural observations of birds. The building stage was defined as the period when birds were seen repeatedly carrying nesting material to the nest, but the primary female did not spend extended periods of time inside the hollow suggesting that eggs had not been laid. The incubation stage was defined as the period when the female consistently returned to the hollow, without nesting material or food, and remained inside for periods of up to 35 minutes. The nestling stage was defined as the period when nestlings could be heard calling or adult birds repeatedly brought food to the hollow (for methods on designation of nesting stage when nestlings were present see Appendix 3.1).

The primary aim of the nest watches was to record the provisioning rate per hour to nestlings and the proportional contribution made by each nest attendant. Environmental and demographic factors correlated with overall provisioning rate are analysed in Appendix 3.1. The proportional contribution made by group members and those from adjacent territories was determined by recording the identity (colour-band combination) of each bird when it visited the nest with food. Non-feeding visits were not considered. When banded birds could not be identified (< 10% of all provisioning visits), an "unknown" visit was recorded and at the end of the nest watch these were allocated to identified individuals in proportion to the provisioning

rate of those birds (Clarke 1984). If a known group member was unbanded, it was considered the same individual during nest watches. If all group members were banded and an unbanded bird(s) was recorded provisioning nestlings (7% of all nest watches), it was considered the same individual (i.e., not multiple individuals) unless unbanded birds of the opposite sex were recorded, and was classified as a non-resident helper.

When nests were watched on multiple occasions, a single nest watch per nesting attempt per territory (chosen randomly) was used in the analyses of provisioning contribution. I treated data from watches of the first and second nesting attempts from the same group in the same year as independent because the number and composition of nest attendants often differed between attempts.

3.2.5 Reproductive success

Owing to the difficulty of accessing nests directly, reproductive success was measured in two ways:

- a) nest success – a nest was considered successful if it produced at least one fledgling; and
- b) group productivity – the total number of fledglings produced per breeding group per season.

Opportunistic observations of clutch size for accessible nests were also made. During the latter stages of nesting, nests were visited at least once every 2 – 3 days, except for some late nests in December and January of each year, to determine reproductive success. A nestling was considered to have fledged if it had left the nest hollow. Identifying the presence of fledglings was relatively easy owing to their constant begging and visits by adult birds. Fledglings were banded during this period, which also assisted in determining if more than one fledgling was present.

The measure of nest success may be overestimated because some groups may have begun nests that failed before I was able to locate them. Conversely, nest success and group productivity may be underestimated because some nestlings may have fledged, yet died before I was able to re-visit the territory (in which case the nest would be categorised as unsuccessful). I was unable to use the Mayfield (1961) estimate of nest success because inaccessibility of nests precluded unequivocal

determination of nest stage. For successful nests, behavioural categorisation of nest stage (see above) could be cross-validated by back-dating from fledging date (Appendix 3.1), but this was not possible for failed nests. As I had a specified number of groups in which I expected to find nests and spent an extensive amount of time with each group, I estimate that only a small percentage of nests were not found.

When examining relationships between helpers and reproductive success, I used group size values rather than the total number of nest attendants. Only using data on the number of nest attendants is biased because not all nests were watched and these tended to be the ones that failed early in the nesting cycle. The substitution of total nest attendants with group size does not alter the general relationships in the data, as both were positively correlated with reproductive success.

3.2.6 Juvenile and adult survival

During the first year of the study, fledglings were monitored at least weekly in 10 territories to determine the level of dependence (i.e., still receiving regular feeds) on adult birds. Based on these and other opportunistic observations, fledglings remained relatively dependent on adults for at least 30 days post-fledging. Any disappearances that occurred within this period were more likely to be a result of death rather than dispersal and this was the most appropriate time period to calculate fledgling survival. All territories with fledglings were visited at 30 days post-fledging (or as close to this period as practical) with the aim of re-locating offspring to determine survival rate. Post-breeding season, territories were visited at least monthly to monitor the progress of juveniles (individuals that had reached independence, but were < 1 year old).

The following survival measures were calculated:

- a) fledgling survival rate – the probability of a fledgling surviving to independence (at least 30 days post-fledging);
- b) juvenile survival rate – the probability of a juvenile surviving from fledging to the beginning of the next breeding season;

- c) juvenile survival rate post-independence – the probability of a juvenile surviving from independence to the beginning of the next breeding season; and
- d) adult survival rate – the probability of an adult surviving from the beginning of one breeding season to the beginning of the following season.

Adult survival rate was calculated for primary males and females only because the disappearance of these birds was more likely to be a result of death rather than dispersal (breeding dispersal was rarely recorded during the study, see Section 3.3.7). For the two measures of juvenile survival, values were calculated for males and females combined and for males only. Survival rates for males provided a more accurate measure of survival because dispersal appeared to be female biased and there was a higher probability that the disappearance of male juveniles represented death rather than dispersal. The measures of juvenile survival are conservative because it is likely that a certain proportion of individuals disappearing from the study sites successfully dispersed.

3.2.7 Dispersals and visits

In most cases, banded birds that disappeared were never seen again despite searches outside the study territories, and estimates of dispersal (particularly distance) are difficult to calculate. Immigrants moving into the study area may provide some clue to dispersal levels, but this mostly occurred when a primary male or female was replaced so the measure is reliant on survival rate. Therefore, I focus primarily on the potential for dispersal bias between males and females and the origin of individuals that filled vacancies within monitored groups. I also present data on the frequency of non-dispersal visits between territories.

3.2.8 Data handling and analysis

Comparisons were made between study sites and years for a number of social (e.g., group size, the number of nest attendants and the prevalence of cross-territorial provisioning) and reproductive measures (e.g., the number of nest attempts, multiple broods, nest success and group productivity). Data were examined

for departures from normality using frequency distributions, normal probability plots and the Shapiro-Wilks' test. Transformations were applied where required, but mostly did not improve the distribution of the data so I used a mixture of parametric, non-parametric and modelling methods. All data were back-transformed prior to presentation (consistent throughout the thesis unless indicated otherwise).

Data for group size and the number of nest attendants were discrete and had a Poisson distribution, so I used Poisson regression to determine group size and nest attendant differences between sites and years (including an interaction term for site \times year). Data on the percent contribution made by nest attendants to nestling provisioning were arcsine transformed and a one-way analysis of variance (ANOVA) was used to examine overall differences in provisioning contribution (homogeneity of variances was tested using Levene's test). Post hoc multiple comparisons were made using Tukey's honestly significant difference (HSD) test for unequal sample sizes. Changes in the provisioning rate of the primary male and female were analysed using simple linear regression after data were square root transformed. Scatterplots of residuals were examined for violations of regression assumptions.

As I re-sampled the same territories over 3 years, some groups (or individuals within groups) are represented more than once possibly leading to dependency in the data. To account for this in the analysis of group productivity, I initially used a mixed model approach incorporating random (group size) and fixed (site and year) effects. Evidence of dependency was determined by examining change in model deviance (distributed as χ^2) when the random effect was removed from a full model (following Legge 2000). Removal of the random effect did not result in a significant change in deviance suggesting no intra-group dependence between years. Therefore, I used Poisson regression to examine relationships between group productivity (which conformed to a Poisson distribution), group size, year and site. All modelling was conducted using S-Plus 2000 (Mathsoft 1999) and diagnostic procedures followed Nicholls (1989).

Juvenile and adult survival rates were compared between sites, years and group sizes using the computer program CONTRAST, which calculates a chi-square statistic for overall differences between values (see Sauer and Williams 1989 for a

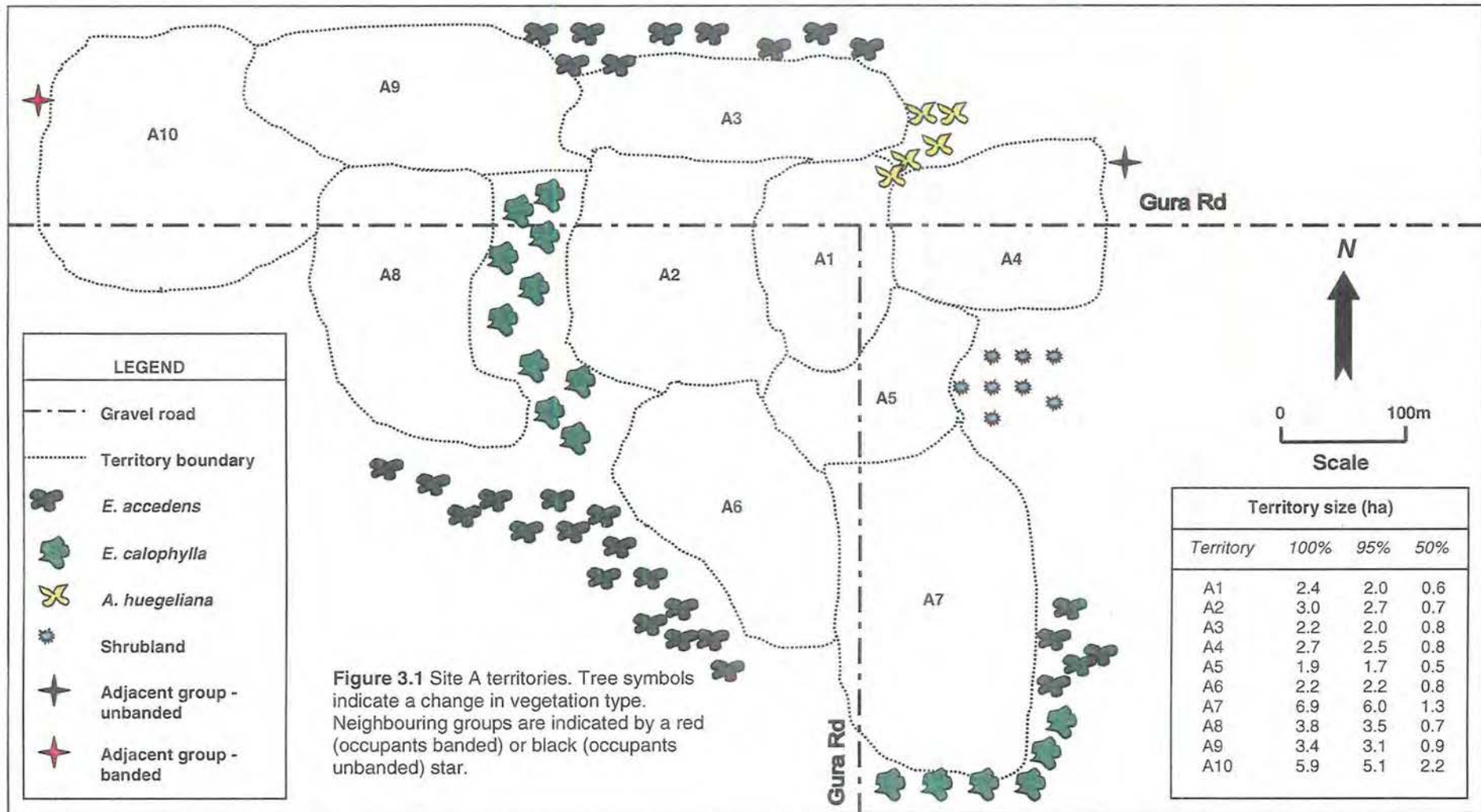
discussion of this method). In the interests of consistency, mean values (\pm one standard error) are presented throughout this thesis (except Appendix 2.1), acknowledging that non-parametric statistics test differences between medians or groups. I consider $P < 0.05$ as statistically significant and $P < 0.10$ as indicating a trend. In cases where multiple contrasts were made using the same data, a Bonferroni correction (α/m) was applied to the significance level, where $\alpha = 0.05$ (unless indicated otherwise) and $m =$ the number of contrasts made.

3.3 RESULTS

3.3.1 Territoriality and territory size

Rufous Treecreepers showed strong site fidelity. A total of 55% ($n = 60$) of primary males and females remained in the territory in which they were banded for the duration of the study. Territories were "all-purpose" (*sensu* Hinde 1956); used year-round for foraging and nesting. Territoriality was apparent, but variable. Neighbouring birds could engage in aggressive physical contact (e.g., clawing and pecking) or chase intruders from within territories, but during the breeding season territoriality was "relaxed" (*sensu* Noske 1982, 1991) in certain circumstances allowing individuals to feed nestlings in adjacent territories. The social organisation of the Rufous Treecreeper was not one of exclusive, vigorously defended territories and involved formations of interactive neighbourhoods.

Territories were generally contiguous and territorial boundaries appeared to remain stable for the duration of the study. I have plotted the location of each territory in each study site in Figures 3.1 – 3.3. Territories are represented as discrete units for ease of interpretation, acknowledging that boundary overlap may occur and territoriality may be relaxed during the breeding season. Territory size ranged from 1.6 – 6.0 ha (2.6 ± 0.18 , $n = 30$) based on the 95% MCP (Figures 3.1 – 3.3). There was no difference in territory size between sites (Kruskal-Wallis test, $H_{2,30} = 1.63$, $P = 0.44$). Relationships between territory size, group size and habitat quality are examined in Chapter 5.



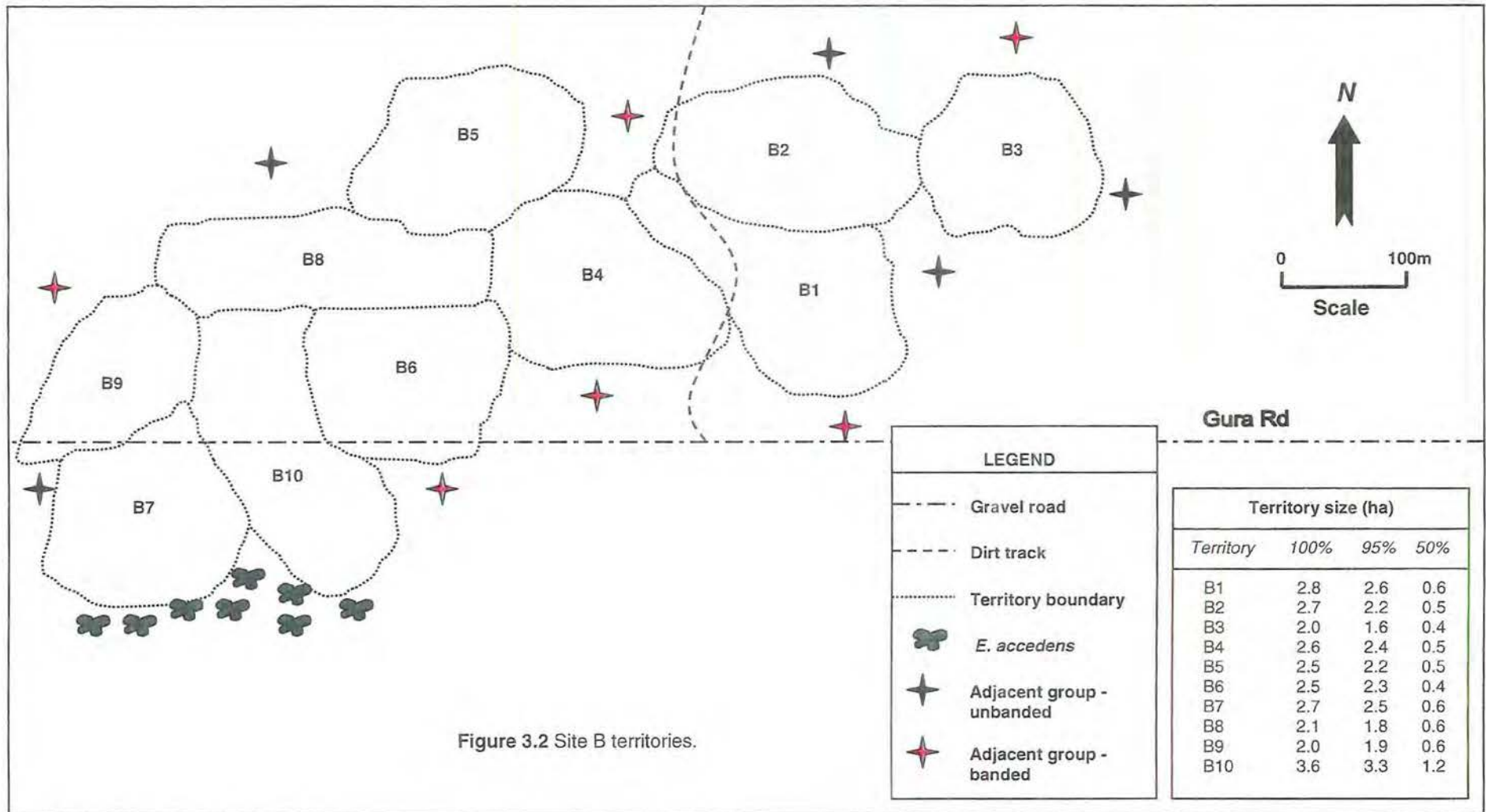


Figure 3.2 Site B territories.

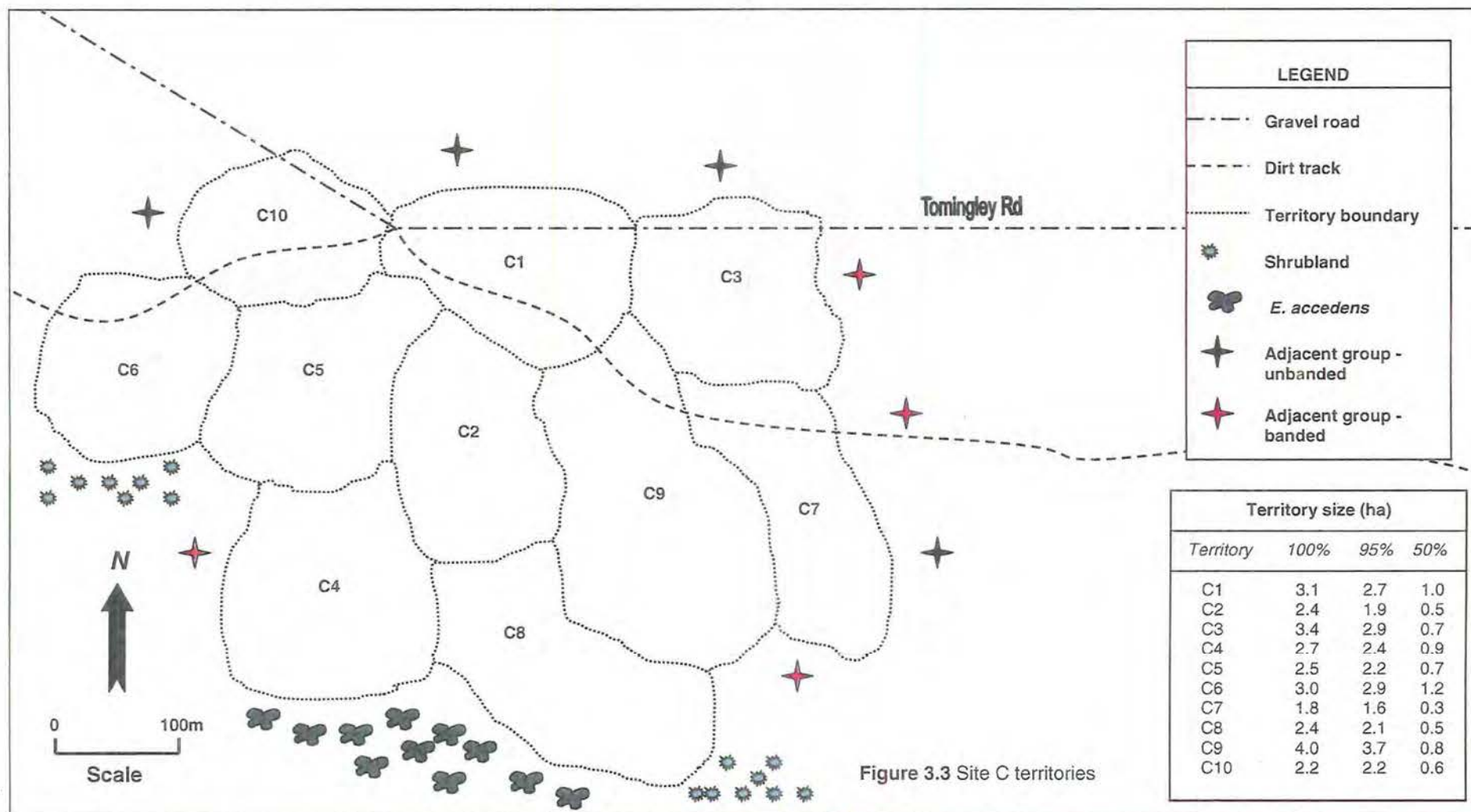


Figure 3.3 Site C territories

3.3.2 Sex ratio and group size

Based on the annual censuses at the beginning of the breeding season, the size of the study population for 1997, 1998 and 1999 was 83, 97 and 92 respectively. The adult sex ratio always favoured males, but a significant bias occurred only in 1999 (Table 3.1). There were no significant differences in the sex ratio of fledglings. Based on nest watches ($n = 112$), the sex ratio of helpers (excluding primary males and females and ensuring that the same individual was not double-counted) was strongly biased towards males ($\text{♂}:\text{♀}$ 95:35, Binomial test, $Z = 5.26$, $P < 0.001$).

Table 3.1 The sex ratio of adults and fledglings in each year of the study. The overall figure for adults is based on all birds banded in the study area. Significant differences marked with an asterisk (Binomial test, * $P < 0.05$).

	1997		1998		1999		Overall	
	♂:♀	Ratio	♂:♀	Ratio	♂:♀	Ratio	♂:♀	Ratio
Adults	45:38	1:0.84	57:40	1:0.70	58:34	1:0.59*	70:60	1:0.86
Fledglings	33:26	1:0.79	35:23	1:0.66	33:37	0.89:1	101:86	1:0.85

Group size ranged from two to seven individuals with pairs (41.1%) and groups of three (33.3%) being common (Figure 3.4). Average group size was $3.0 (\pm 0.12, n = 90$ group years). Group size differed significantly between sites, but not years, being highest at Site C (see Table 3.3). There was no site \times year interaction. Group composition varied; 45.6% of groups had more than one male and 23.3% of groups had more than one female (Table 3.2). All group members participated in a range of activities including territory and nest defence, and mobbing potential predators.

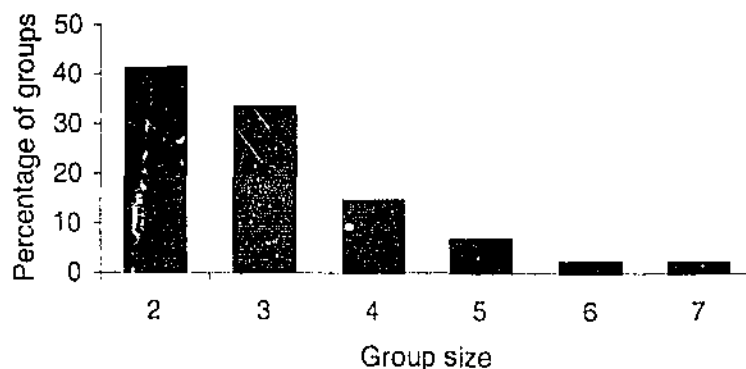


Figure 3.4 Distribution of group sizes ($n = 90$ group years).

Table 3.2 Composition of groups (values are percentages, $n = 90$ group years).

No. of females	No. of males				
	1	2	3	4	5
1	41.1	20.0	8.9	6.7	0.0
2	13.3	5.6	0.0	1.1	2.2
3	0.0	0.0	1.1	0.0	0.0

3.3.3 Nesting behaviour

The breeding season (defined as the period when eggs were laid) varied slightly between years, but was generally from August – December. Fledglings were recorded as early as October 6 and as late as February 10. Prior to egg laying, the primary female was often fed by the primary male and occasionally by helper males. I did not observe helper females feeding the primary female.

All group members assisted in nest building, but the primary female did the majority of work (68.5% of 146 visits). Visits to nests carrying nest material ranged from three to 32 per hour (14.6 ± 2.91 , $n = 10$). Nest maintenance (i.e., lining the nest with feathers, fur and other soft material) continued throughout the incubation and nestling period. All nests were in hollows, mostly in dead branches of Wandoo *Eucalyptus wandoo* trees (Chapter 4). When the length of a branch was completely hollow (i.e., there was no base), treecreepers would build up the hollow with strips of bark to create a platform on which to place the nest cup (Figure 3.5). The average depth of bark strips for accessible nests in my study areas (Dryandra and Yilliminning combined) was 21.5 cm (± 3.12 cm, $n = 17$).

Based on accessible nests that were found during the incubation stage (Dryandra and Yilliminning), clutch size ranged from one to three, but was predominantly two (82% of 34 clutches). Only the primary female incubated (based on 12 nest watches and other opportunistic observations). Incubation bouts (time spent in the hollow) ranged from 1 – 35 minutes (15.8 ± 1.87). While incubating, the primary female was fed by the primary male and occasionally by helper males.



Figure 3.5 A cross-section of a hollow (length = 1.1 m) used for nesting. The figure shows the platform of bark strips used to build up the hollow, and the nest cup placed on top.

3.3.4 Provisioning behaviour

Provisioning of nestlings

Provisioning of nestlings was conducted by all individuals resident on a territory ($n = 112$ nest watches). The number of nest attendants ranged from two to eight (3.7 ± 0.11 ; Figure 3.6) and did not differ between years, but did differ between sites being highest at Site C (Table 3.3). There was no year \times site interaction.

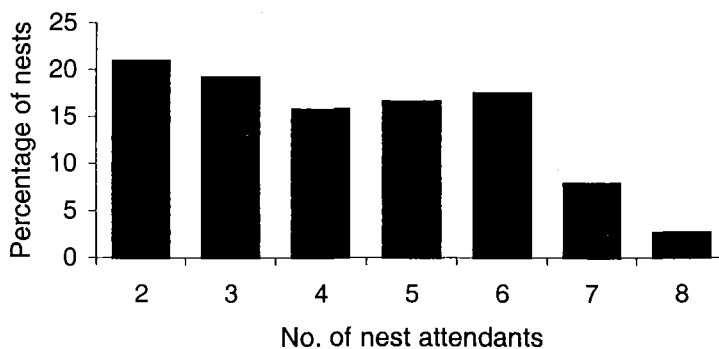


Figure 3.6 The number of nest attendants recorded provisioning nestlings ($n = 112$ nest watches).

The frequency distribution of number of nest attendants varied from that of group size with 60% of nests having four or more attendants (Figure 3.6). This was primarily influenced by two factors: larger groups (or those with more attendants at the first nest) were more likely to re-nest (Section 3.3.5), and non-resident birds sometimes provisioned nestlings in territories adjacent to their own, increasing the total number of attendants. In 20 (out of 90) group years, a group received help from non-resident individuals. Cross-territorial provisioning was slightly higher in 1997 and 1998 compared to 1999, but this difference was not significant, nor was there a significant difference between sites (Table 3.3).

Table 3.3 Comparisons between study sites and years for factors related to reproductive success (mean \pm s.e.). Site and year differences in group size and the number of nest attendants were analysed using Poisson regression (significance levels correspond to: * $P < 0.05$, ** $P < 0.01$). Count data were tested with chi-square, percentages were tested with a chi-square equivalent (Zar 1996). The chi-square tests involved multiple comparisons of the same data, so a Bonferroni adjusted significance level ($P = 0.025$) was used. A trend is indicated by $^{\dagger}P < 0.10$. Numbers in brackets are sample sizes.

	Site A	Site B	Site C	Site comparison
Group size (90)	2.5 \pm 0.10	3.0 \pm 0.19	3.6 \pm 0.27	$\chi^2_2 = 6.03^*$
Nest attendants (112)	2.7 \pm 0.13	3.4 \pm 0.17	4.8 \pm 0.23	$\chi^2_2 = 11.38^{**}$
Nest attempts	48	46	54	$\chi^2_2 = 0.70$
% nest success (148)	75.0	71.7	85.2	$\chi^2_2 = 2.88$
Cross-territorial ¹	3	7	10	$\chi^2_2 = 3.69$
Re-nesting ²	11	10	21	$\chi^2_2 = 5.28^{\dagger}$
Two broods ³	8	7	16	$\chi^2_2 = 4.72^{\dagger}$
	1997	1998	1999	Year comparison
Group size (90)	2.8 \pm 0.12	3.2 \pm 0.21	3.1 \pm 0.17	$\chi^2_2 = 1.12$
Nest attendants (112)	3.6 \pm 0.29	3.9 \pm 0.35	3.7 \pm 0.28	$\chi^2_2 = 0.94$
Nest attempts	45	47	56	$\chi^2_2 = 1.40$
% nest success (148)	77.8	76.6	78.6	$\chi^2_2 = 1.03$
Cross-territorial	8	9	3	$\chi^2_2 = 3.10$
Re-nesting	9	12	21	$\chi^2_2 = 5.58^{\dagger}$
Two broods	9	8	14	$\chi^2_2 = 2.00$

¹The number of groups receiving assistance from adjacent groups in provisioning nestlings.

²The number of groups re-nesting after a successful nesting attempt.

³The number of groups successfully fledging two broods in a season.

Provisioning rate per hour varied from eight to 50 (21.8 ± 0.91). It was influenced by the time of day, maximum daytime temperature, nest stage and number of nestlings, but not the number of nest attendants (Appendix 3.1). I calculated the percent contribution made by each nest attendant (attendant provisioning rate/total provisioning rate per hour) for nests where I was confident of the identity of the primary male and female ($n = 102$). I did not control for environmental or demographic influences on provisioning rate in these calculations, as I assumed that percent contribution would be similar despite differences in overall provisioning rate.

The percent contribution of the different nest attendant categories varied depending on the total number of nest attendants (Table 3.4). With no helpers, primary males and females contributed equally to provisioning nestlings (t -test for dependent samples, $t = 0.36_{22}$, $P = 0.72$). In Table 3.5, I have summarised the percent contribution of each nest attendant category. As these data are not independent, the contribution of primary males and females were compared separately with the other nest attendant categories and a Bonferroni adjusted significance level of $P = 0.025$ was used.

Regardless of the number of helpers, there were significant differences in the provisioning contribution made by nest attendants (Table 3.5). Post hoc multiple comparisons showed that resident male and female helpers generally contributed a similar amount to at least one of the primary sexes, and always contributed equally between themselves. Interestingly, non-resident females always contributed a similar amount to resident helpers, and quite often their contribution was comparable to primary males and females (sample sizes for non-resident females were small so these trends should be viewed with caution). Conversely, non-resident males almost always contributed less than primary males and females and often less than resident male helpers (Table 3.5). The data from Tables 3.4 and 3.5 indicate that male helpers were much more common, but in relative terms they contributed no more (and sometimes less) than female helpers.

Table 3.4 Percent contribution (mean \pm s.e.) to the provisioning of nestlings by the primary male (PM), primary female (PF), resident helper male (RM), resident helper female (RF), non-resident helper male (NRM) and non-resident helper female (NRF). Data are based on 102 nest watches. Numbers in brackets are sample sizes.

Status	No. of helpers						
	0	1	2	3	4	5	6
PM	48.5 \pm 3.34 (23)	39.2 \pm 3.49 (19)	28.4 \pm 3.22 (16)	27.7 \pm 3.03 (17)	23.7 \pm 2.91 (18)	13.6 \pm 2.81 (7)	14.8 \pm 7.4 (2)
PF	51.5 \pm 3.34 (23)	37.8 \pm 4.13 (19)	36.3 \pm 3.24 (16)	28.4 \pm 1.74 (17)	19.8 \pm 1.93 (18)	29.6 \pm 4.10 (7)	27.7 \pm 1.85 (2)
RM1		27.6 \pm 5.19 (9)	18.0 \pm 3.25 (11)	21.7 \pm 1.58 (8)	19.0 \pm 1.97 (15)	9.8 \pm 2.09 (7)	
RM2			17.0 \pm 6.51 (2)	17.4 \pm 2.16 (8)	16.9 \pm 2.42 (15)	12.7 \pm 3.06 (7)	
RM3				13.5 \pm 2.49 (8)	12.8 \pm 1.99 (9)	11.3 \pm 3.13 (5)	
RM4						11.0 \pm 5.15 (3)	
RF1		24.4 \pm 8.24 (6)	24.3 \pm 2.74 (8)	16.6 \pm 4.66 (4)	10.3 \pm 1.07 (11)	13.1 \pm 1.75 (7)	12.9 \pm 1.85 (2)
RF2						19.1 \pm 4.75 (2)	
NRM1		8.8 \pm 2.69 (4)	13.6 \pm 2.67 (7)	9.8 \pm 1.74 (9)	10.1 \pm 1.68 (14)	5.1 \pm 0.89 (4)	3.7 \pm 0.0 (2)
NRM2				9.7 \pm 1.55 (7)	6.7 \pm 0.0 (2)		3.7 \pm 0.0 (2)
NRM3				4.1 \pm 1.31 (2)			3.7 \pm 0.0 (2)
NRF1			10.8 \pm 2.97 (4)	19.2 \pm 5.40 (5)	17.4 \pm 7.91 (5)		16.6 \pm 9.95 (2)
NRF2					8.3 \pm 0.0 (1)		16.6 \pm 9.25 (2)

Table 3.5 The mean percent contribution of each nest attendant category to nestling provisioning. The contribution of primary males and females was compared separately with the other nest attendant categories using one-way ANOVA and Tukey's HSD for unequal sample sizes after data were arcsine transformed. A Bonferroni adjusted significance level of $P = 0.025$ was used. ANOVA significance levels correspond to: * $P < 0.025$, ** $P < 0.01$, *** $P < 0.001$. Means with the same letter are not significantly different.

No. of helpers	Percent contribution						<i>F</i>
	PM	PF	RM	RF	NRM	NRF	
1	39.2 ^a	37.8 ^a	27.6 ^{ab}	24.4 ^{ab}	8.8 ^b		PM 8.50 _{3,34} ** PF 4.42 _{3,34} *
2	28.4 ^{ab}	36.3 ^a	17.9 ^b	24.3 ^{ab}	13.6 ^b	10.8 ^b	PM 3.27 _{4,43} * PF 8.73 _{4,43} ***
3	27.7 ^a	28.4 ^a	17.5 ^b	16.6 ^{bc}	9.1 ^c	19.2 ^{ab}	PM 11.28 _{4,63} *** PF 15.97 _{4,63} ***
4	23.7 ^a	19.8 ^{ab}	16.7 ^{ab}	10.3 ^{bc}	9.6 ^c	15.9 ^{abc}	PM 7.38 _{4,85} *** PF 5.42 _{4,85} ***
> 4	13.9 ^{ab}	29.2 ^a	11.2 ^b	14.2 ^b	4.3 ^c	16.6 ^{ab}	PM 7.56 _{4,51} *** PF 17.34 _{4,51} ***

The data in Table 3.4 show a general decline in the provisioning contribution of the primary male and female with an increase in the number of helpers at the nest. I used simple linear regression to determine if there was a significant change in the provisioning rate (i.e., actual visits per hour not percent contribution) of the primary sexes with an increase in the number of helpers. In these analyses, I controlled for the number of nestlings, nest stage, time of day and maximum daytime temperature because these may influence provisioning rate (Appendix 3.1).

Both the primary male ($F_{1,32} = 46.29$, $P < 0.001$, Adjusted $R^2 = 0.578$) and primary female ($F_{1,32} = 32.38$, $P < 0.001$, Adjusted $R^2 = 0.487$) significantly reduced their provisioning rate as helper number increased (Figure 3.7a and b). The decline was slightly greater in males (slope of regression = -0.769 ± 0.11) compared to females (-0.709 ± 0.13), but this difference was not significant ($t_{64} = 1.2$, $P > 0.10$).

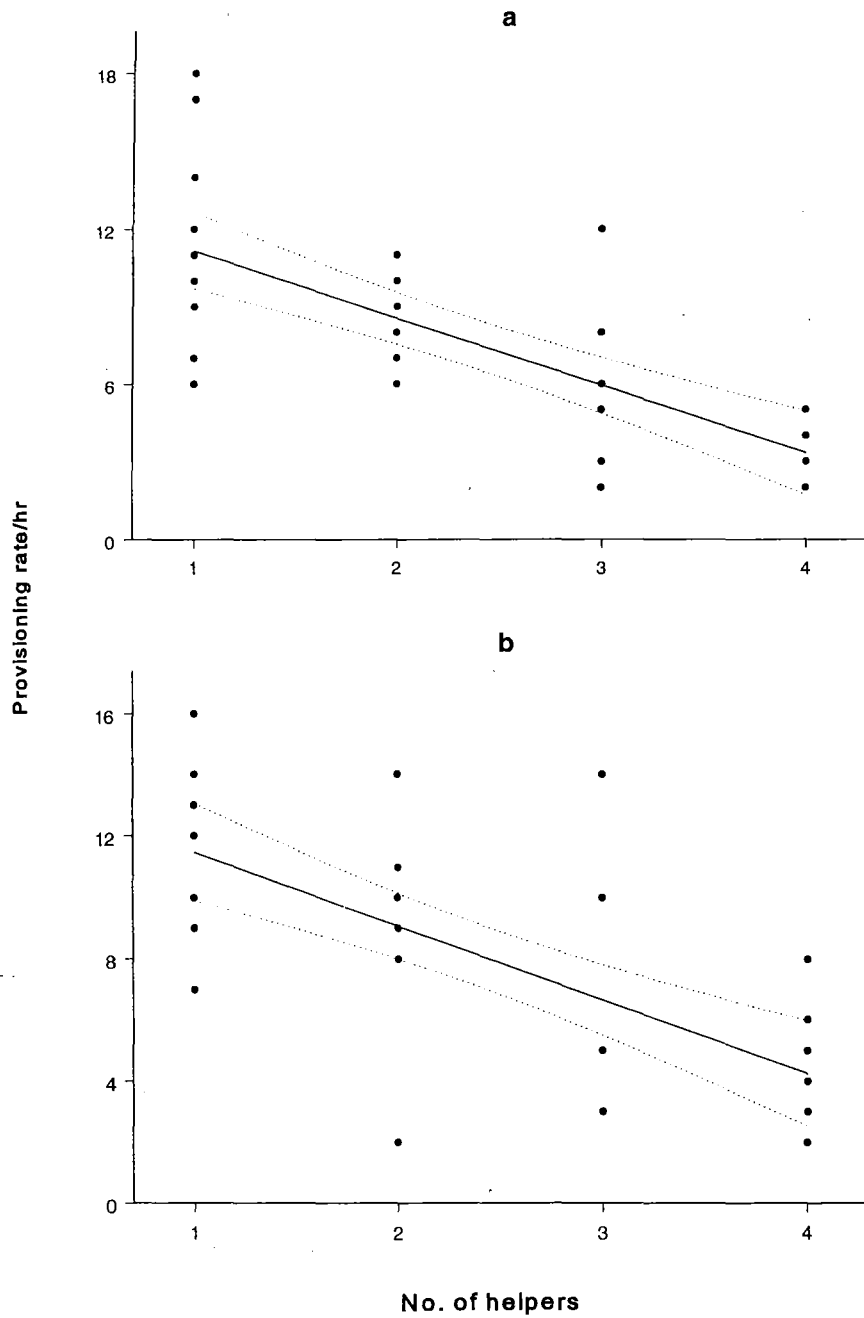


Figure 3.7 The decline in the provisioning rate/hr of the: a) primary male, and b) primary female with an increase in the number of helpers at the nest. Not every datum is shown ($n=34$) because cases with the same value are represented by a single point. The solid line is the line of best fit; dotted lines are 95% confidence intervals.

Relatedness of helpers

In 1998 and 1999, most of the resident helpers were banded offspring from the previous breeding seasons. Assuming that social parentage is comparable to genetic parentage an assessment of relatedness can be made. Of eight helper females of known origin, seven assisted at the nests of their parents (coefficient of relatedness 0.50) and one assisted her mother and stepfather (coefficient of relatedness 0.25). Of 36 helper males, 25 helped both parents, one helped his mother and stepfather, four helped their father and stepmother, and six (two territories with three helpers each) helped their father and sister. All non-resident helpers were of unknown relatedness to the individuals they helped.

3.3.5 Reproductive success

Nest success and multiple broods

A total of 77.7% of 148 recorded nesting attempts produced at least one fledgling. The number of nest attempts did not differ between sites or years, neither did the proportion of successful nests (see Table 3.3). Most groups (64.4%, $n = 90$ group years) nested twice within a season. Multiple broods were relatively common; 34.4% of groups raised two broods to fledging and 12.2% re-nested after successfully fledging the first brood, but failing in their second (Figure 3.8). There was no difference in nest success between first (75.3% successful, $n = 90$) and second (80.1%, $n = 58$) nests within a season (Fisher Exact test, $P = 0.69$).

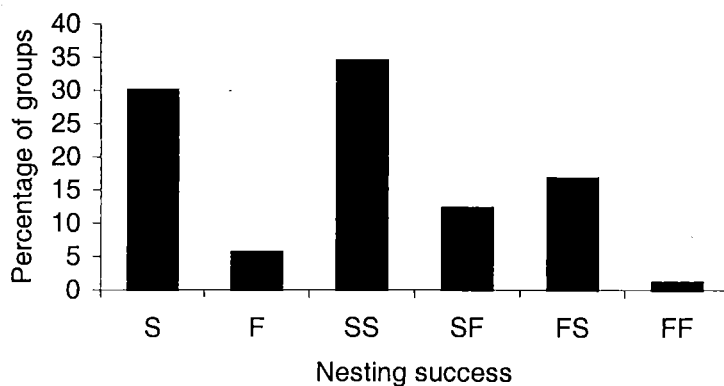


Figure 3.8 The percentage of groups with differing levels of nest success ($n = 90$ group years). S = succeed, F = fail. Multiple nesting attempts within a season are represented by two letters (e.g., SF = succeed in first nesting attempt and fail in second).

At Site C, there was a trend for more groups to re-nest after a successful nesting attempt and raise two broods to fledging within a season. The number of re-nesting attempts after a successful nest varied slightly between years, but there was no difference in the number of groups raising two broods (see Table 3.3). Re-nesting after a successful nest was more common for groups \geq three (58.5%, $n = 53$) compared to pairs (29.7%, $n = 37$, Fisher exact test, $P = 0.01$), and the former raised a higher percentage of multiple broods to fledging within a season (50.9%, $n = 53$ vs 10.8%, $n = 37$, Fisher exact test, $P = 0.001$). Groups \geq three also had a lower percentage of failed nests (7.5%, $n = 40$) than groups of three (30.2%, $n = 53$) and pairs (25.5%, $n = 55$; $\chi^2_2 = 7.27$, $P < 0.05$).

Group productivity

A total of 189 fledglings was produced over the 3 years of the study. The average number of fledglings produced per nest was 1.3 (± 0.04) and this did not differ between first (1.4 ± 0.09 , $n = 90$) and second (1.2 ± 0.10 , $n = 58$) nests within a season (Mann-Whitney test, $Z = 1.17$, $P = 0.24$). Mean group productivity was 2.1 (± 0.18 , $n = 90$ group years). Almost half (48.6%) of all nesting attempts produced two fledglings and only one nest produced three.

There was a significant difference in group productivity between sites (Poisson, $\chi^2_2 = 7.38$, $P < 0.025$) and between groups of different size ($\chi^2_2 = 6.50$, $P < 0.05$), but no effect of year ($\chi^2_2 = 1.34$, $P > 0.10$) and no significant interactions between these variables. Group productivity was highest at Site C and for groups of $>$ three individuals (Figure 3.9a and b).

Primary female experience

I compared a number of reproductive parameters for primary females who were assumed to have different levels of reproductive experience. Females nesting in 1998 and 1999 that also nested in 1997 and/or 1998 were considered to have had at least 1 years experience, and those individuals replacing a primary female (i.e., dispersing to, or inheriting a territory) in 1998 and 1999 were considered to have had no prior experience. This is true for at least the territory that the new females

occupied and is consistent with the observation that breeding dispersal appeared to be relatively infrequent in *Dryandra* (Section 3.3.7).

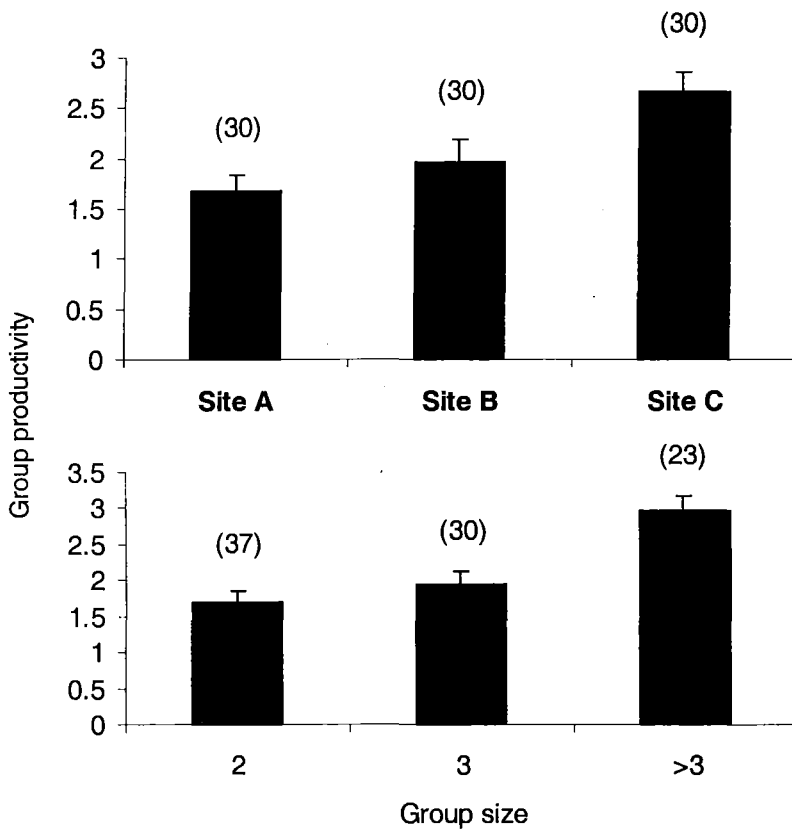


Figure 3.9 Differences in annual group productivity between: a) the three study sites, and b) different sized groups. Numbers above columns are sample sizes.

There were no significant differences in any of the reproductive measures compared between first year primary females ($n = 14$) and those with at least 1 years experience ($n = 46$), although all of the measures were slightly higher for experienced females (Table 3.6). Any differences between new and established females may also be confounded by group size differences because most (71.4%) new females began their reproductive life in pairs. This comparison does not consider any helping experience a new female may have had in a previous group, which may improve her reproductive success when she eventually becomes a breeder (Komdeur 1996). I removed individuals from the analysis who were known to have had helping experience ($n = 6$), but there were still no discernible differences in the reproductive output of established and new primary females.

Table 3.6 Measures of reproductive output for females with at least 1 years breeding experience and those assumed to have no prior experience (mean \pm s.e.). None of the differences are significant at $\alpha = 0.05$. Numbers in brackets are sample sizes.

Reproductive output	No experience (14)	≥ 1 year experience (46)
Nest attempts per female	1.3 \pm 0.12	1.9 \pm 0.06
Nest success (%)	73.7	78.6
Group productivity	1.5 \pm 0.24	2.4 \pm 0.18
Re-nesting after success (%)	46.7	57.8
Raising two broods (%)	33.3	37.8

3.3.6 Juvenile and adult survival

Juvenile survival

The mean number of fledglings per breeding group surviving to independence and juveniles surviving to the next breeding season were 1.6 (\pm 0.11) and 0.9 (\pm 0.12) respectively ($n = 90$ group years). Fledgling survival rate was quite high (0.76 \pm 0.04) and this rate increased slightly when only males were considered (0.80 \pm 0.06). Juvenile survival rate was 0.46 (\pm 0.03) and survival rate post-independence was 0.57 (\pm 0.04). These values were slightly higher for males only (0.54 \pm 0.05 and 0.62 \pm 0.05 respectively).

The mean number of fledglings surviving to independence and juveniles surviving to the next breeding season were highest at Site C and for groups $>$ three (these data are not independent of group productivity and were not tested statistically; Table 3.7). There was also a trend for fledgling and juvenile survival rates to be higher in groups $>$ three, but there was no difference between group sizes in survival rate post-independence. For males only, the trend was for all survival rate measures to be highest in groups $>$ three (Table 3.7).

Adult survival

Adult survival rate was 0.77 (\pm 0.06) for primary males and 0.75 (\pm 0.05) for primary females. The only significant difference occurred between sites for primary males with a very high survival rate at Site C (Table 3.8). However, there was a consistent trend in both sexes for survival rates to increase as group size increased.

Table 3.7 Differences between sites, years and group sizes in the number of fledglings and juveniles surviving, and fledgling and juvenile survival rates (mean \pm s.e.). The number of fledglings and juveniles surviving were not tested statistically owing to non-independence. Survival rates were compared using the computer program CONTRAST. A Bonferroni adjusted significance level of $P = 0.017$ was considered statistically significant, although all results with $P < 0.10$ are reported. Numbers in brackets are total number of group years.

	Overall				Males only			
	Fledglings surviving	Fledgling survival rate	Juveniles surviving	Juvenile survival rate	Juvenile survival rate post-independence	Fledgling survival rate	Juvenile survival rate	Juvenile survival rate post-independence
Site								
A (30)	1.2 \pm 0.14	0.71 \pm 0.07	0.6 \pm 0.15	0.39 \pm 0.04	0.53 \pm 0.05	0.71 \pm 0.07	0.42 \pm 0.07	0.55 \pm 0.05
B (30)	1.6 \pm 0.21	0.82 \pm 0.08	0.9 \pm 0.18	0.54 \pm 0.06	0.58 \pm 0.08	0.89 \pm 0.06	0.73 \pm 0.12	0.69 \pm 0.10
C (30)	2.1 \pm 0.24	0.74 \pm 0.06	1.2 \pm 0.30	0.44 \pm 0.05	0.59 \pm 0.10	0.79 \pm 0.11	0.47 \pm 0.06	0.61 \pm 0.09
							$\chi^2_2 = 12.37$	$P = 0.002$
Year								
1997 (30)	1.5 \pm 0.11	0.76 \pm 0.07	1.0 \pm 0.16	0.46 \pm 0.07	0.60 \pm 0.06	0.77 \pm 0.09	0.52 \pm 0.08	0.67 \pm 0.08
1998 (30)	1.5 \pm 0.16	0.75 \pm 0.08	0.8 \pm 0.13	0.44 \pm 0.09	0.53 \pm 0.05	0.83 \pm 0.10	0.55 \pm 0.09	0.58 \pm 0.07
1999 (30)	1.9 \pm 0.15	0.75 \pm 0.09	•	•	•	0.79 \pm 0.09	•	•
Group size								
2 (37)	1.3 \pm 0.15	0.73 \pm 0.05	0.7 \pm 0.17	0.49 \pm 0.09	0.61 \pm 0.04	0.75 \pm 0.08	0.53 \pm 0.09	0.64 \pm 0.09
3 (30)	1.3 \pm 0.17	0.68 \pm 0.06	0.6 \pm 0.14	0.32 \pm 0.08	0.46 \pm 0.03	0.75 \pm 0.08	0.43 \pm 0.06	0.50 \pm 0.06
>3 (23)	2.6 \pm 0.23	0.87 \pm 0.11	1.5 \pm 0.28	0.57 \pm 0.12	0.63 \pm 0.09	0.91 \pm 0.12	0.65 \pm 0.07	0.71 \pm 0.10
		$\chi^2_2 = 5.77$		$\chi^2_2 = 8.18$		$\chi^2_2 = 5.40$	$\chi^2_2 = 6.71$	$\chi^2_2 = 5.83$
		$P = 0.06$		$P = 0.02$		$P = 0.07$	$P = 0.03$	$P = 0.05$

Table 3.8 Differences between sites, years and group sizes (mean \pm s.e.) in adult survival rates (primary males and females only). Values were tested using CONTRAST. A Bonferroni adjusted significance level of 0.017 was used. Numbers in brackets are total number of group years.

	Males	Females
Site		
A (20)	0.60 \pm 0.11	0.70 \pm 0.10
B (20)	0.70 \pm 0.11	0.80 \pm 0.09
C (20)	1.00 \pm 0.00	0.75 \pm 0.09
	$\chi^2_2 = 20.66$	
	$P < 0.001$	
Year		
1998 (30)	0.77 \pm 0.08	0.83 \pm 0.07
1999 (30)	0.77 \pm 0.08	0.67 \pm 0.09
Group size		
2 (23)	0.71 \pm 0.09	0.71 \pm 0.09
3 (17)	0.76 \pm 0.09	0.76 \pm 0.09
>3 (20)	0.87 \pm 0.09	0.80 \pm 0.11
Overall	0.77 \pm 0.06	0.75 \pm 0.05

3.3.7 Dispersals and visits

Dispersal

Dispersal between territories occurred mostly when a vacancy became available as a result of the disappearance (probably death) of the primary male or female (see Figures 3.12 – 3.14). For primary males, dispersers from outside the study sites filled 35.7% of vacancies ($n = 14$) and dispersers from adjacent territories filled 57.1%. For primary females, 46.7% of vacancies ($n = 15$) were filled by dispersers from outside the study sites and 40% were filled by dispersers from adjacent territories (Table 3.9). For vacancies occupied by individuals from within the study sites ($n = 17$), 58.8% were filled by dispersers who had been helpers for at least 1 year. Breeding dispersal appeared to be relatively uncommon, as was inheritance of the natal territory (Table 3.9), although only five of the 29 breeding vacancies represented an opportunity for natal inheritance.

Table 3.9 The origin of individuals filling vacancies created by the disappearance of the primary male or female.

	Male	Female
No. of vacancies	14	15
Vacancies filled by		
Natal dispersal after helping	6	4
Natal dispersal of 1 st year bird	1	1
Breeding dispersal	1	1
Inheritance of natal territory	1	2
Dispersal from outside study sites	5	7

Only two territories lost their primary male and female at apparently the same time during the study and these were colonised by a new pair < 1 month after the disappearance of the original occupants. Two natal dispersals were by individuals < 12 months old who subsequently bred within their first year. Apart from dispersals to fill a breeding vacancy, on two occasions I recorded the movement of males to helping positions in adjacent territories. One was a first year male whose social parents had disappeared from the natal territory (subsequently colonised by a new pair) and the other was the primary male in a pair that occupied a low quality territory. These males remained in their adopted territory for at least 12 months and assisted in the feeding of nestlings.

Fledglings born in 1997 and 1998 were monitored each month until the end of the breeding season in 1999 to determine their fate. I then calculated the cumulative percentage of fledglings disappearing each month from their natal territory up to 12 months post-fledging (Figure 3.10). Approximately 84% of 51 fledgling females disappeared within 12 months of fledging (this includes 27.5% that disappeared before independence, which probably represents fledgling mortality). Conversely, only 46% of 66 males disappeared over the same time period (including 19.8% mortality). Excluding estimates of mortality and dispersals within the study sites, the percentage of females disappearing (54.9%) was significantly higher than males (22.7%, Fisher exact test, $P < 0.001$). The fate of disappearing individuals is unknown, but estimates of mortality before reaching independence suggest no significant sex bias in mortality rate and the higher disappearance rate of females is probably a result of sex-biased dispersal.

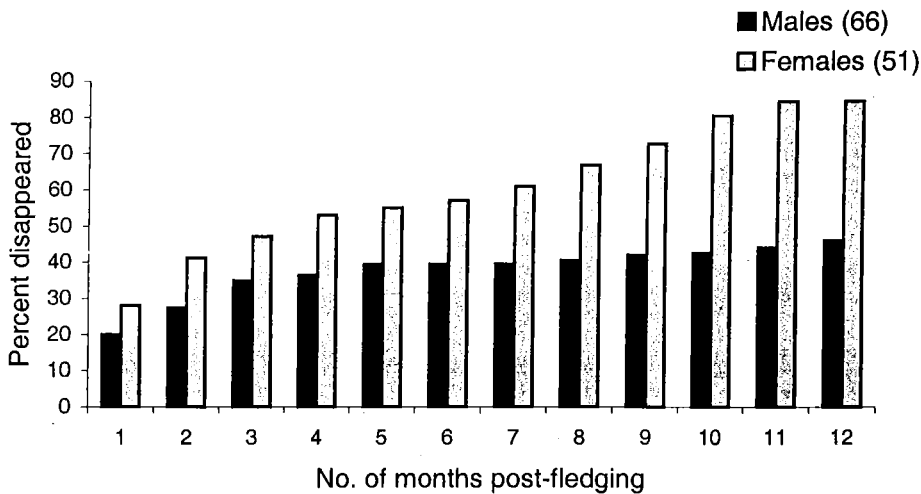


Figure 3.10 The percentage of juvenile males and females disappearing from their natal territory over a 12-month period. Numbers in brackets are sample sizes.

Of the 33 male fledglings born in 1997, 57.5% remained on their natal territory for at least 12 months and 30% remained for at least 2 years. Of the 26 female fledglings, 23.1% remained for at least 12 months and only 3.8% remained for 2 years.

Dispersal and territory quality

Komdeur (1992) found that territory quality influenced dispersal decisions in the Seychelles Warbler, as individuals born in high quality territories were more likely to remain as helpers rather than disperse to low or medium quality territories. For Rufous Treecreeper helpers, dispersal decisions may be influenced by the quality of the natal (originating) territory and the territory where a breeding vacancy occurs (destination), group size in each territory, the coefficient of relatedness between the helper and the offspring produced, and the difference in the number of young produced if the helper leaves the natal territory.

A quality index for the originating territory was calculated using the equation

$$\text{quality index } (q) = \frac{a}{b} + (cd_i - cd_j).$$

Here, a = the territory quality value derived from habitat structure (see Table 5.3 in Chapter 5), b = group size, c = the coefficient of relatedness between the helper and

any offspring produced in its originating territory, d_i is the number of offspring produced if the helper remains in its originating territory and, d_j is the number of offspring produced if it leaves.

The first part of the equation represents per capita territory quality and assumes that as group size increases, territory quality (e.g., food availability) for any individual decreases. This takes no account of any fitness benefits of group living. The bracketed section is the helper's inclusive fitness benefits arising from an increase in reproductive output as a result of its help (this section is modified from Stacey and Ligon 1987).

The above quality index pertains to a disperser's originating territory. To calculate an index for the destination territory, the bracketed section was replaced by cd_k where d_k is the number of offspring produced in the destination territory with group size k . I calculated a quality index for the originating and destination territories of all dispersers that obtained a primary (breeding) position in my study sites ($n = 14$). In these calculations, I used average group productivity values for groups of differing size and a coefficient of relatedness of 0.50.

Out of 14 dispersals where territory quality was known, 71.4% were to territories with a higher quality index than the originating territory. Of the four dispersals that were to a lower quality territory, two of these were by first year birds. This suggests that territory quality may influence dispersal decisions in treecreepers, but sample size is low and further data are required to assess this relationship.

Visits

Movements between territories that involved visits rather than dispersals were commonly observed during the breeding season when individuals would feed nestlings in territories other than their own. I recorded 42 visits (= individuals) from non-resident helpers for the 3 years of the study (based on banded birds of known origin). The majority of these (47.6%) were males who were helpers in their own territory (Figure 3.11). Non-resident helpers could also be primary males and/or females who had failed a nesting attempt (21.4%), helper females (16.7%) and occasionally primary males who had a nest of their own (14.3%). Primary females with their own nest were never recorded provisioning nestlings in a neighbouring

territory. Most (93%) non-resident helpers were from adjacent territories, but one was a primary male that crossed two intervening territories to help (see Figure 3.14).

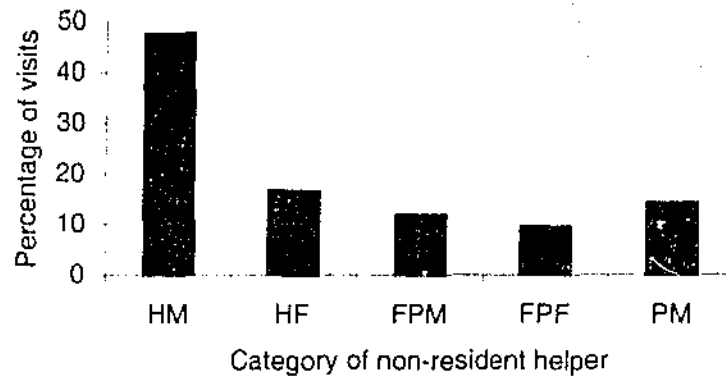
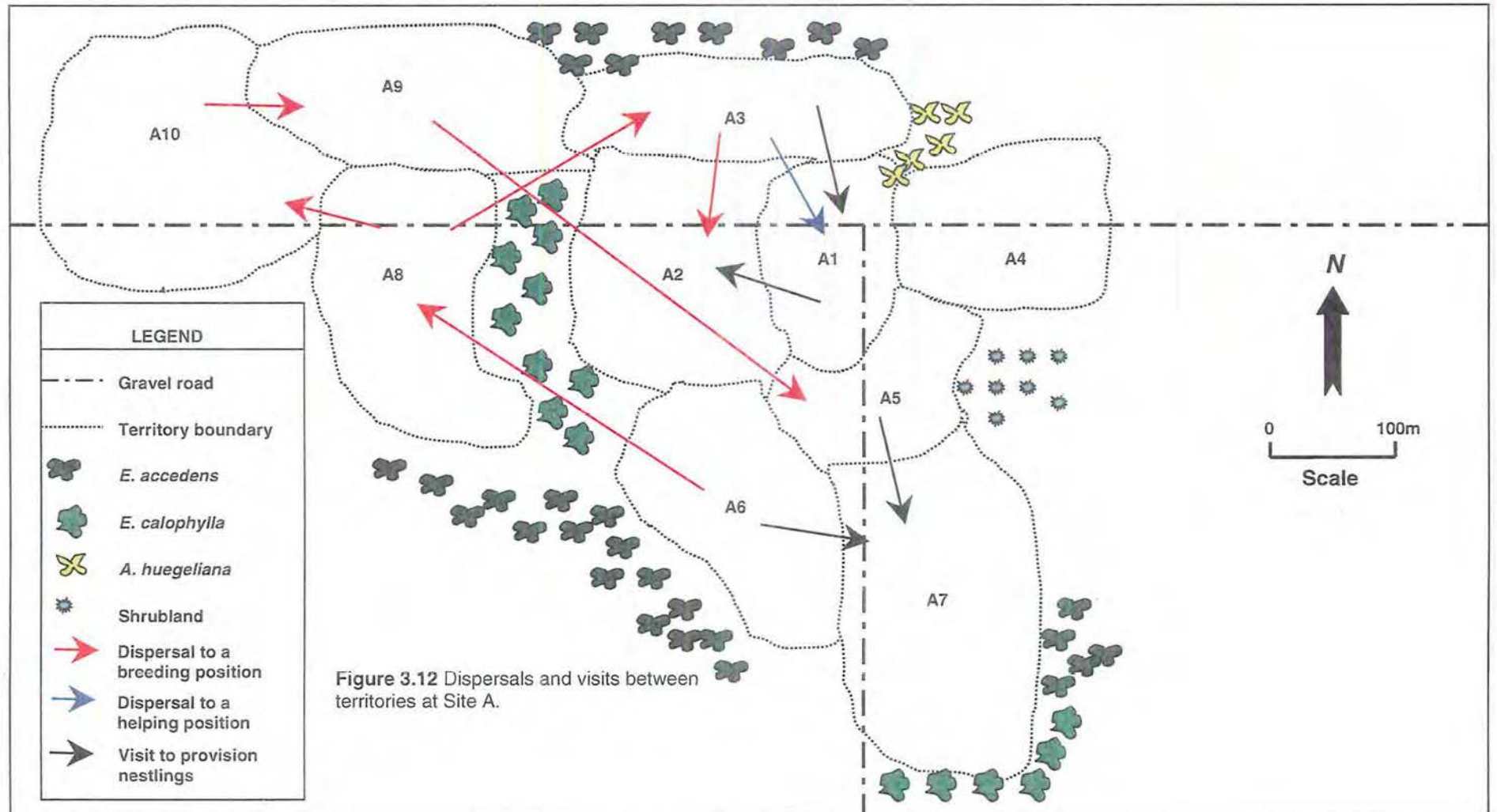


Figure 3.11 Categories of non-resident helpers observed feeding nestlings ($n = 42$). Abbreviations are HM and HF (helper male and female in own territory), FPM and FPF (primary male and female recently failed in a nesting attempt) and PM (primary male with nest).

A total of 14 territories received help from non-residents at least once during the three breeding seasons (Figures 3.12 – 3.14). These helping visits did not seem to be driven by reciprocation, which was only observed three times. There are a number of potential explanations for this behaviour (see Discussion), but interestingly, 70% of the 42 non-resident helpers came from territories that were of a lower quality than the ones they helped in (based on the territory quality value derived in Chapter 5). This suggests that cross-territorial helping may be a vehicle for non-residents to assess potential breeding vacancies in higher quality territories.



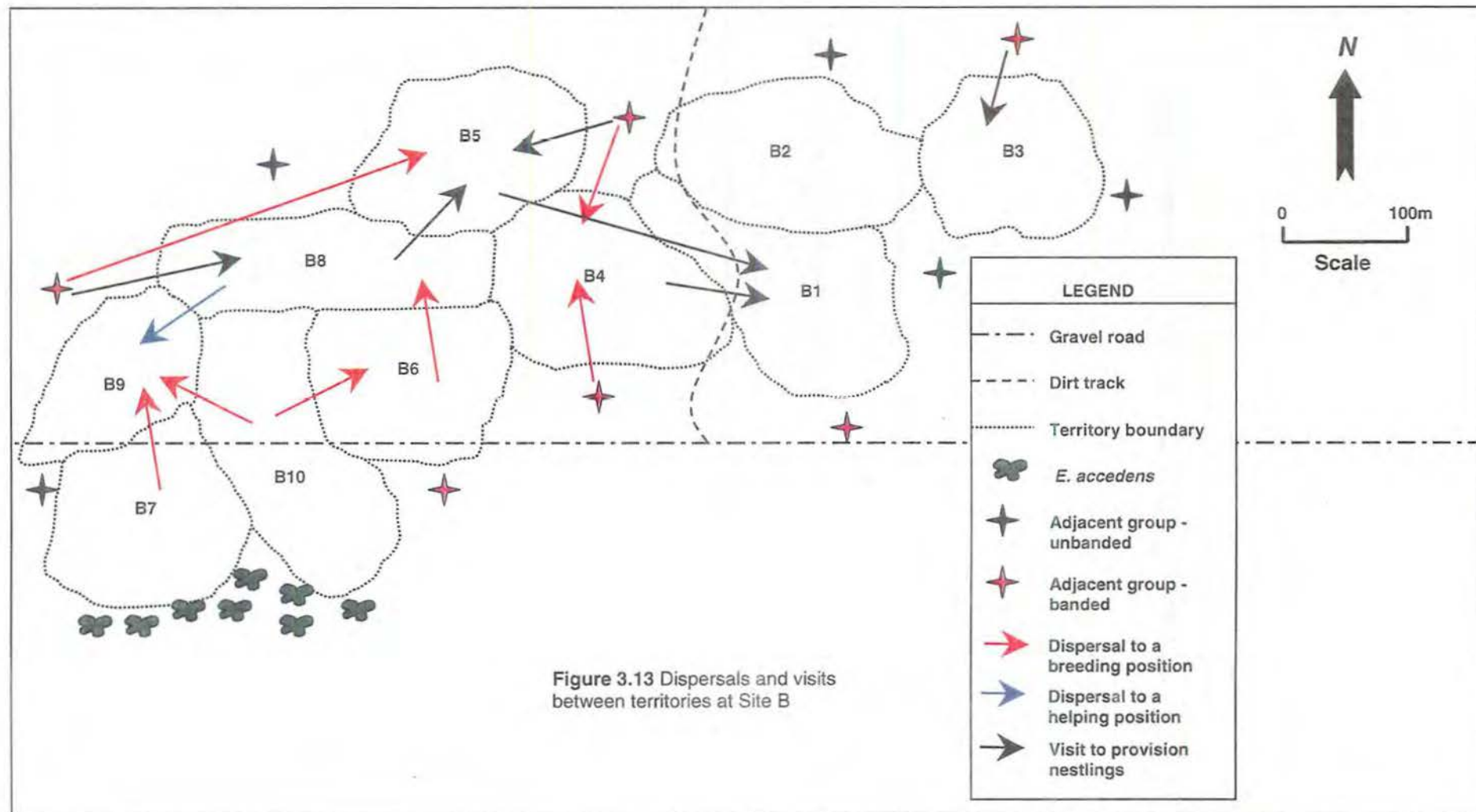
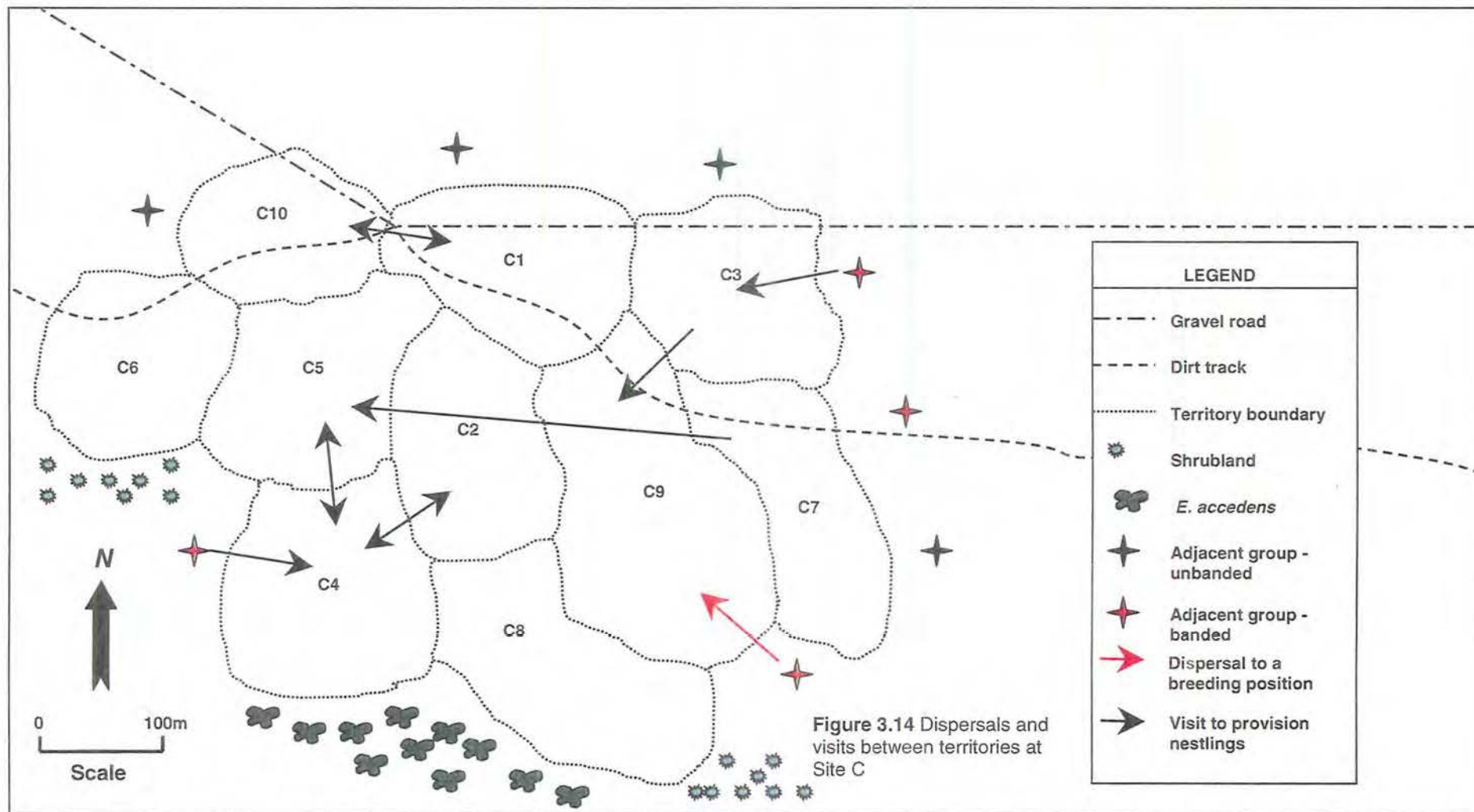


Figure 3.13 Dispersals and visits between territories at Site B



3.4 DISCUSSION

3.4.1 Territories and neighbourhoods

Treecreeper groups in Dryandra occupied all-purpose, year-round territories and all group members assisted in territory defence. During the breeding season, territorial behaviour between particular groups was relaxed allowing the cross-territorial provisioning of nestlings. Territories were not mutually exclusive in these circumstances and treecreepers may form "ecological neighbourhoods" (*sensu* Addicott et al. 1987) during this time. An ecological neighbourhood is defined by an ecological process (e.g., reproduction), a time scale appropriate to the process (e.g., at least one breeding season), and an organism's activity during the defined time period (e.g., provisioning of nestlings in neighbouring territories). Spatial scale relevant to the ecological process and an organism's activity is also important; most cross-territorial provisioning occurred between adjacent territories.

For the Rufous Treecreeper, ecological neighbourhoods comprised up to five interacting territories (Figure 3.14). Designation of a neighbourhood is constrained by the duration of a study, and for treecreepers, neighbourhood boundaries may change owing to the turnover of individuals. Longer-term data are required to provide a more complete picture of cross-territory interactions. Also, if a different ecological process is considered (e.g., dispersal), the spatial scale of a neighbourhood changes (see Section 3.4.6). For treecreepers, ecological neighbourhoods appeared to occur in a nested hierarchy defined by the relevant ecological process (Chapter 9).

3.4.2 Sex ratio and group size

Although a statistically significant difference was only recorded in 1 year of my study, there was a trend in all years for the sex ratio of adult birds to be biased towards males. This appears to be a consequence of female-biased dispersal. The sex ratio of fledglings slightly, but not significantly, favoured males in 1997 and 1998. Some studies of cooperatively breeding birds have found that, in certain circumstances, the sex ratio of offspring is biased towards the sex that is more likely to remain on the natal territory and help in subsequent breeding seasons (Gowaty and Lennartz 1985; Ligon and Ligon 1990b; Komdeur et al. 1997). These results

support the "repayment model" (Malcolm and Marten 1982; Emlen et al. 1986), which predicts that parents may bias the sex ratio of offspring to favour the more helpful sex. However, the usefulness of the repayment model may be restricted to only a few select cases and is difficult to test with short-term data (see review of Koenig and Walters 1999).

Treecreepers most commonly occurred in groups of two or three, but 25.6% of groups ($n = 90$) had four or more individuals. Contrary to the study of Rose (1996) and in accordance with the observations of Noske (1980), groups could contain more than one adult female (23.3%). Group size was positively related to territory quality (Chapter 5) and generally reflected prior reproductive success, as most helpers were young from a previous brood. Group members participated in nest-building, feeding the primary female, feeding and caring for nestlings and fledglings, and mobbing potential predators including the Yellow-footed Antechinus *Antechinus flavipes*, Carpet Python *Morelia spilota*, Southern Death Adder *Acanthophis antarcticus* and Sand Monitor *Varanus gouldii*.

3.4.3 Reproductive success

The breeding season for Rufous Treecreepers lasted for 4 months, although the period between when the first eggs were laid to when the last nestlings fledged could be up to 5.5 months. Clutch size was relatively small (1.94 ± 0.07 , $n = 34$), which appears to be characteristic among old endemic, resident passerines (Yom-Tov 1987; Rowley and Russell 1991). Small clutch size with low variation means that differences in group productivity are mostly a factor of the number of successful nests produced in a season.

Nest success was consistently high in each year of the study ($77.7\% \pm 0.58$) and was similar to that recorded by Noske (1991) for Red-browed Treecreepers *Climacteris erythroptera* (74%), but higher than the more closely related Brown Treecreeper *C. picumnus* (48%) observed during the same study. Although varying between sites, group productivity (2.1 ± 0.18) also appeared to be relatively high compared to Red-browed (1.12) and Brown Treecreepers (1.36; Noske 1991), but was slightly lower than the average (2.4) recorded for the southern temperate passerines examined by Rowley and Russell (1991).

Annual productivity for Australian passerines appears to be low compared to their Northern Hemisphere counterparts (Yom-Tov 1987; Rowley and Russell 1991; Rowley et al. 1991). In some species, low productivity may be a result of high levels of nest failure caused primarily by predation. Robinson (1990) suggested that small clutch sizes and multiple broods in Australian species are adaptations to high levels of predation, but predation does not appear to be a strong selective force for Rufous Treecreepers in Dryandra (Chapter 7). Allowing for a level of error in my estimates of nest success, predation rates on treecreeper nests in Dryandra were unlikely to exceed 25 – 30% (assuming all nest failures were from predation). It is more probable that the risk-spreading strategy (Payne 1977) of small clutch size and multiple broods is a response to the environmental variability (e.g., unpredictable changes in food availability) that may occur over a long breeding season (Burley 1980).

3.4.4 Juvenile and adult survival

Adult survival for Rufous Treecreepers (0.76 ± 0.04) was comparable to the average recorded for a number of southern temperate passerines (0.75; Rowley and Russell 1991) and for other cooperatively breeding treecreepers (0.78 – 0.79; Noske 1991), and did not differ between primary males and females. Fledgling survival rate to independence appeared to be relatively high (0.76 ± 0.04) compared to other cooperative and non-cooperative species (Cale 1999; Green and Cockburn 1999), as was juvenile survival to the next breeding season particularly if only males are considered. Although, fledgling and juvenile survival rates for Rufous Treecreepers were comparable to a recent study on the cooperatively breeding Red-winged Fairy-Wren in Karri *E. diversicolor* forest in southwest Western Australia (Russell and Rowley 2000). These survival rates are conservative because all disappearing birds are considered to have died.

There was little annual variation in any of the productivity or survival measures recorded for treecreepers in Dryandra (Tables 3.3 and 3.7), and population numbers were relatively stable over the 3 years of the study. However, there were differences between sites with Site C having consistently high productivity. This was primarily a factor of Site C having larger group sizes and higher quality

territories (Chapter 5). This result is important because it illustrates the spatial variability that can occur in a continuously vegetated landscape, even between sites in the same habitat type exposed to the same broad environmental conditions. Choosing any one of my study sites as a representation of the entire landscape would have been misleading.

Based on the data from my study, the demographic characteristics of the Rufous Treecreeper reflect the apparently typical traits of most resident, old endemic passerines. Clarke (1997) cautioned against extrapolating such results to all Australian passerines owing to a significant research bias favouring sedentary, cooperative species living in temperate regions.

3.4.5 Cooperative breeding behaviour

Why remain philopatric?

Ecological constraints and benefits of philopatry

In Dryandra, natality and juvenile survival exceeded primary male and female mortality and more potential breeders were being produced than there were vacancies to fill. Access to a primary (breeding) position rather than access to suitable mates appeared to be a constraining factor because a number of groups had multiple males and females that could potentially breed (based on two observations, treecreepers were able to reproduce in their first breeding season after fledging).

The fact that surplus individuals did not establish their own territory suggests that the availability of certain resources was also a constraining factor. Suitable nesting hollows do not appear to be limiting in Dryandra (Chapter 4) and the most likely resource constraint is the area required to support an all-purpose territory of suitable quality. Rufous Treecreepers in Dryandra preferentially used Wandoo woodland with particular structural characteristics (Chapter 4), and preferential habitat use was related to reproductive success and fitness (Chapter 5). An important component of habitat quality was the density of large Wandoo trees (Chapter 5), which were used disproportionately to their availability (Appendix 4.1). Therefore, the density of large Wandoo trees may be an important ecological constraint for this population of treecreepers.

Based on these observations, it is likely that preferred habitat in *Dryandra* is saturated and on the surface this appears to be a reasonable explanation for the natal philopatry exhibited by offspring. However, variation in territory quality, leading to philopatric benefits for certain individuals, may be just as (if not more) important in explaining philopatry in this population of treecreepers.

Experimental studies that have removed the breeding male and/or female from a territory have shown that the vacancies created are filled relatively quickly (a matter of hours or days) unless there is a shortage of one sex (Pruett-Jones and Lewis 1990; Marra and Holmes 1997). For Rufous Treecreepers, the data I have on the time span between a vacancy being created and the establishment of a new individual are constrained by the frequency of my visits to territories. Of the 29 vacancies recorded, two were filled within at least a week and 18 were filled within at least a month.

One notable exception was a female who solely occupied a territory for 6 months despite being surrounded by surplus males in adjacent territories. The territory she occupied was ranked the lowest quality of all 30 territories used in my study (see Chapter 5 for territory quality values). Her original partner dispersed to a helping position in an adjacent territory after failing to breed in 1997 and she eventually paired with an 8-month old male dispersing from an adjacent higher quality territory (hence his experience at determining territory quality was limited). This observation is not in accordance with the habitat saturation or mate limitation model, but supports the benefits-of-philopatry hypothesis (Stacey and Ligon 1987). This hypothesis is also supported by the fact that most dispersals of known origin (71.4%, $n = 14$) were to higher quality territories (Section 3.3.7).

Two further examples illustrate the importance of territory quality to natal philopatry. In Rufous Treecreepers, most female offspring reaching independence disappear (disperse) from their natal territory before the next breeding season. Those that remain should only do so if territory quality is high in accord with the benefits-of-philopatry hypothesis. I compared average territory quality between territories supporting philopatric helper females for at least 12 months ($n = 12$) and those where females reaching independence disappeared ($n = 12$). The difference in quality was in the predicted direction, but was not significant (mean quality of

territories with philopatric females 3.61 ± 1.14 vs those without 1.57 ± 1.24 , one-tailed Mann-Whitney test, $Z = 1.33$, $P = 0.08$).

A small proportion (26%, $n = 46$) of offspring born in 1997 and reaching independence remained on their natal territory as helpers for at least 2 years. In accordance with the benefits-of-philopatry hypothesis, these territories ($n = 7$) should be of a higher quality than those where independent helpers born in 1997 remained for 1 year or less ($n = 19$). This prediction was supported, with the average quality of territories supporting philopatric helpers for 2 years being significantly higher (6.27 ± 1.59 vs 1.72 ± 0.78 , one-tailed Mann-Whitney test, $Z = 2.34$, $P = 0.01$).

The above correlative relationships are weakened by the fact that an unknown proportion of disappearances represented death rather than dispersal. There are also a number of other important factors that may influence the dispersal decisions of helpers. Potential dispersers must be aware of the vacancies around them and of the quality of adjacent and nearby territories. This is a possible reason for the frequency of non-dispersal visits (see below). Competition with conspecifics for vacancies may also influence dispersal decisions. There is likely to be a trade-off between group size, territory quality and philopatry. Per capita quality (e.g., food availability) would decrease as group size increases, and only high quality territories could support large groups, as was found in my study (Chapter 5). If groups become too large, the primary male and/or female may aggressively exclude certain individuals from the territory. All of these factors interact to influence dispersal decisions and highlight the complex nature of only one component of cooperative breeding behaviour.

The above argument could be framed in terms of the ecological constraint hypothesis, whereby the availability of high quality territories is the constraining factor. This illustrates the potentially artificial dichotomy between the ecological constraints and benefits-of-philopatry models (Koenig et al. 1992; Mumme 1992; Emlen 1994), but it is useful to explore both the constraints to independent reproduction and the benefits of remaining as a helper or non-breeder. Other potential benefits to philopatric individuals include the inheritance of the natal territory, a competitive advantage in filling breeding vacancies in adjacent

territories, and the dynamics of group living (Rowley and Russell 1990; Russell and Rowley 1993). Group living may offer more effective predator surveillance, improved exploitation of patchily distributed resources, or the acquisition of skills needed for successful reproduction in the future (Koenig and Stacey 1990; Marzluff and Balda 1990; Komdeur 1996). Some studies have suggested fitness benefits from group cooperation for cooperative species, like the Rufous Treecreeper, that forage on the ground in open woodlands (Gaston 1977; Zack and Ligon 1985), but these benefits might also be available to non-cooperative, flock living birds (Clarke 1995). A useful approach would be to compare the survival rates of philopatric and non-philopatric individuals (Walters et al. 1992; Ekman et al. 1999), but this involves the difficult task of tracking dispersing birds.

Life history traits

In their review of the ecological constraints and life history hypotheses, Hatchwell and Komdeur (2000) concluded that both constraints and life-history traits probably act in concert to influence cooperative breeding in birds. The Rufous Treecreeper has many of the characteristic life history traits that are thought to predispose a species to cooperative breeding; high adult survival, small clutch size, low reproductive rates, reduced dispersal and increased sedentariness. The evolution of cooperative breeding in treecreepers is probably influenced by the synergistic effects of life history and ecological constraints, and a broader evolutionary model for this species is warranted (Hatchwell and Komdeur 2000). Although constraints and benefits may be opposite sides of the same coin, an expanded model that recognises the potential benefits of philopatry provides a more comprehensive assessment of the evolution of cooperative breeding.

Why do resident helpers help?

The benefits of helping

Stacey and Ligon (1987) suggested that once the decision to remain on the natal territory had been made the selective choice of providing care to offspring was problematic. However, it would be in the interests of philopatric individuals to care for nestlings if this increased the reproductive success of related breeders. In turn, this would increase the indirect fitness benefits to helpers. If philopatric individuals

are delaying breeding, the only way they can increase their own genetic representation in the population is to help raise a greater number of related kin. In Rufous Treecreepers, group size was positively related to reproductive output, consistent with many other species of cooperative breeders (Stacey and Koenig 1990). However, increased productivity and survival resulting entirely from helping behaviour is difficult to demonstrate owing to the confounding influences of parental and territory quality (Cockburn 1998). The regression approach I used in Chapter 5 indicated that group size provided no additional benefits to group productivity and fledgling survival once territory quality had been considered (there was a positive relationship with primary male survival rate – see below). Statistical procedures are generally poor substitutes for more rigorous experimental approaches where helper number or some component of territory quality is manipulated, but the results from these types of studies have been equivocal (Cockburn 1998) and a clear relationship between helping, territory quality and reproductive output is yet to be established.

If it is in the interests of resident, related helpers to help, then they may be more likely to contribute to activities like nestling provisioning at a similar rate to primary males and females, as was found in my study (Table 3.5). In some species (e.g., White-winged Chough *Corcorax melanorhamphos* and Seychelles Warbler), helping may improve future reproductive success by helpers gaining the skills required for successful reproduction (Heinsohn 1991, 1992; Komdeur 1996). This does not appear to be an important influential factor in the helping behaviour of Rufous Treecreepers. Most juvenile females disperse from the natal territory before the next breeding season. Juveniles born in the first brood of the season have the opportunity to help at a second brood, but many groups do not have successful second broods. Also, first year birds with no helping experience are able to disperse and successfully breed, although the comparative reproductive success of individuals with and without helping experience is yet to be determined.

The costs of philopatry and helping

Recent reviews have highlighted the need to assess the costs as well as the benefits of philopatry and helping (Cockburn 1998; Heinsohn and Legge 1999). Assuming resident helpers do not breed, a major cost of philopatry is foregoing

reproduction for 1 or more years. The decision to remain philopatric may be influenced by territory quality (see above), which is positively correlated with reproductive output and survival (Chapter 5). However, per capita quality may be reduced with an increase in group size. These interacting factors suggest a complex cost-benefit trade-off involving territory quality, the likelihood of future reproductive success, group size and inclusive fitness, which influence the dispersal decisions of helpers. This is further complicated by the possibility that the primary male and female may influence the decision to disperse (see below). The costs of philopatry and delayed breeding would increase over time, which is probably why few treecreeper helpers remained on their natal territory for more than a year.

For birds, indications that helping is costly has been suggested for species where related helpers do not contribute to nestling provisioning at the same rate as parents, where food availability is limited and helpers engage in deceptive “non-feeds”, or where there is a negative relationship between helper contribution and helper survival rate (Heinsohn and Legge 1999 and references therein). I was unable to detect any short-term costs associated with helping behaviour in Rufous Treecreepers. Resident helpers generally contributed at the same rate as primary males and females (Table 3.5) and helpers did not appear to engage in deceptive non-feeding.

For Rufous Treecreepers, there appear to be no real benefits to being seen to help, as has been suggested for species where gaining social prestige or forming social coalitions is important (e.g., Arabian Babblers *Turdoides squamiceps*, Zahavi 1995; White-winged Choughs, Heinsohn and Legge 1999). Social prestige in the natal group does not appear to drive helping behaviour in treecreepers because most helpers disperse after a year of helping. I also have no evidence of the formation of social coalitions. These observations do not discount the possibility that helping is a form of rent payment for being allowed access to the natal territory, but if provisioning of nestlings is a payment of rent, and this activity is costly, I predict that the contribution of resident helpers would be substantially less than that of the primary male and female. Importantly, the costs and benefits of helping may vary with changes in environmental conditions. When food availability is limited, helping

behaviour may be more costly and the contribution of helpers may be less (Chapter 6).

Why do non-residents help?

Non-resident Rufous Treecreeper helpers were either helpers in their own territory, failed breeders or occasionally primary males with their own nest. Helping by non-residents has also been recorded for the closely related Brown Treecreeper (Noske 1982). Helping by birds that failed in their own breeding attempt has been reported for White-fronted Bee-eaters (*Merops bullockoides*, Emlen 1990) and Long-tailed Tits (*Aegithalos caudatus*, Glen and Perrins 1988). In Bell Miners *Manorina melanophrys*, pairs with dependent young may act as helpers to another pair (Clarke 1984; Conrad et al. 1998).

The observations of non-residential help documented for Rufous Treecreepers are not unique, but raise interesting questions about the motivation for this type of helping behaviour. If individuals in neighbouring groups are related, then there may be an indirect fitness benefit for non-resident helpers similar to resident helpers. The proportional contribution to helping may be influenced by the level of relatedness (Hatchwell 1999 and references therein). Relatedness among territorial neighbours is a distinct possibility in treecreepers owing to a relatively high percentage of breeding vacancies being occupied by dispersers from adjacent territories (Table 3.9).

The interesting result from my study was that non-residents mostly helped in territories that were a higher quality than their own. It could be argued that groups in better quality territories produce more offspring to fill nearby vacancies and these groups have more potential helpers for future years. Another interpretation is that non-residents use helping behaviour as an avenue for assessing the quality of adjacent territories and the potential to obtain a breeding position. This is supported by the fact that most non-residential helpers were helpers in their own territory, and, for males at least, they generally contributed very little to nestling provisioning (Table 3.5) suggesting that the motivation for helping may have differed from that of resident helpers.

The above interpretation may not be applicable to primary males and females that help after failing in a breeding attempt. For these individuals, helping behaviour may be driven by relatedness, a payment for access to the resources of adjacent territories or an opportunity to improve reproductive skills to enhance future success.

Do primary males and females benefit from help?

In Rufous Treecreepers, the primary male and female reduced their provisioning contribution to nestlings as helper number increased, consistent with a number of other cooperative breeders (Brown et al. 1978; Curry 1988; Dickinson et al. 1996). A reduction in provisioning contribution may reduce the reproductive costs to breeders (Hatchwell 1999), allow primary birds to devote more time to predator surveillance (Austad and Rabenold 1985) or improve survival rates (Reyer 1984, Russell and Rowley 1988; Crick 1992). Primary female treecreepers with more helpers at the first nest of a season had a higher probability of re-nesting after a successful nest attempt, and group size was positively related to the number of successful broods in a season. In this way, helper number can increase breeder productivity. Russell and Rowley (1988) demonstrated that helper assistance in Splendid Fairy-wrens reduced the interval between broods, increasing the number of broods produced in a season. They also found that female survival rate was higher in groups with helpers compared to those without. A similar result was not recorded for primary female treecreepers, but primary male survival rate appeared to be influenced by group size even when territory quality had been considered (Chapter 5).

Many cooperative breeding studies approach the issue of philopatry and helping from the perspective of the helpers, and the influence of breeding birds on dispersal decisions has probably been understated (Cockburn 1996). Some studies have shown that parental aggression plays a role in excluding young from the natal territory (Mulder 1995). I have no data on parental aggression influencing dispersal decisions in treecreepers, but philopatry is likely to be a result of offspring deciding not to disperse and the primary male and female allowing them to stay. If parents are able to force offspring to leave the natal territory, the fact that they do not suggests

that there is a benefit to having philopatric young or that the costs of exclusion outweigh the costs of philopatry.

3.4.6 Dispersal

Dispersal in Rufous Treecreepers appeared to be female biased, especially for individuals < 1 year old, but few offspring remained on the natal territory for more than a year suggesting that the majority of males will also disperse within 2 years. Recorded dispersal distances were short (typically one to two territories, see Figures 3.12 - 3.14), but this undoubtedly underestimates the actual dispersal distance distribution of treecreepers (Koenig et al. 1996, 2000; Chapter 8).

The mating system model of Greenwood (1980) predicted that dispersal would be female biased when the mating system was based on resource defence. In this model, males defend resources to attract mates, and females disperse to avoid inbreeding and assess the quality of several males before settling. Hence, the reproductive strategies of the sexes differ. In Rufous Treecreepers, all group members participated in resource (territory) defence, but the primary male appeared to respond more readily to external threats (based on response to play back tapes). Also, the mating system appeared to be monogamous, but this requires genetic confirmation.

These observations tentatively support the mating system model of Greenwood (1980), but there are certain anomalies that require further interpretation. Firstly, there appeared to be no greater advantage to males remaining philopatric. Although my study was short, inheritance of the natal territory was comparable between males (7%) and females (13%). Dispersal to adjacent territories to fill vacancies was also similar between males (57%) and females (40%) suggesting no obvious benefit to males remaining philopatric and females dispersing.

It is possible that the primary female considers female offspring a threat and dispersal from the natal territory results from parental aggression. However, I have no evidence of plural nesting or egg-dumping, which may adversely affect the reproductive success of primary females and lead to female helper exclusion. Also, there were a number of groups where female offspring did not disperse.

If the slight bias towards the production of male offspring in 1997 and 1998 (Table 3.1) is representative of longer time spans, the opportunities to obtain a breeding vacancy may differ between the sexes. Females may disperse because they have a greater probability of finding a mate and breeding in their first year, whereas for males, it may be more profitable to remain as a helper to gain any indirect fitness benefits rather than becoming a non-breeding floater. These interpretations are preliminary and require further investigation.

3.4.7 Conclusions and caveats

There are a number of hypotheses associated with helping behaviour that I have not explored in detail in this study (see Clarke 1995 and Cockburn 1998). Most appear to have limited relevance to the Rufous Treecreeper. One that is worth mentioning is the unselected hypothesis of Jamieson (1986, 1991), which predicts that helping is a behavioural response by adult birds to feed begging young regardless of any relationship between adults and offspring. This hypothesis is not completely refuted by my observations. It could even be argued that non-resident helpers were simply responding to the begging calls of nestlings, as most non-residents resided in adjacent territories and would have been aware of begging offspring in neighbouring groups. If helping is a behavioural response to begging, I predict that cross-territorial feeding would be even more prevalent than that recorded in my study. Any one territory can have up to six neighbours all with begging young at some time and the unselected hypothesis does not explain why helping appears to be directed towards particular groups and not randomly to every adjacent territory.

In any observational study of cooperative breeding that does not include genetic data on the relatedness of individuals, conclusions about the motivational forces driving cooperation must be preliminary. In some cases, genetic evidence of mating systems and the relatedness of individuals supports conclusions based on behavioural data (Conrad et al. 1998; Quinn et al. 1999), but it is generally inadequate to assume that social and genetic parentage are the same. In the above discussion, I have assumed a low degree of extra-pair copulations and a monogamous mating system. A comprehensive genetic study of cooperative breeding in the Rufous Treecreeper would improve our knowledge of this species.

Appendix 3.1 VARIABILITY IN PROVISIONING RATES TO NESTLINGS IN THE COOPERATIVELY BREEDING RUFIOUS TREECREEPER

In press in Emu

Introduction

In cooperative breeders, more than two individuals often provision nestlings. Total provisioning rate may increase with the number of nest attendants (Emlen 1990; Mumme et al. 1990; Walters 1990), but in some cases, certain individuals (e.g., the breeding male and/or female) will reduce their effort so that provisioning rate to nestlings remains constant (Wilkinson & Brown 1984; Tidemann 1986; Russell & Rowley 1988; Wright & Dingemanse 1999). Hatchwell (1999) found that a positive relationship between the number of nest attendants and provisioning effort generally occurred in species where nestling starvation was frequent, whereas a reduction in effort by certain individuals was characteristic of species where nestling starvation was rare.

To assess this relationship adequately, it is important to consider other factors that may influence the provisioning of nestlings. Provisioning rate may be correlated with numerous variables including brood size, nestling weight, age and begging-signals, temperature, season and time of day (Brown et al. 1978; Wright 1998; Chamberlain et al. 1999).

The Rufous Treecreeper is a small (30 – 35 g; Appendix 2.1), cooperatively breeding (Rose 1996), insectivorous passerine occurring primarily in the temperate forests and woodlands of southwestern Australia (Blakers et al. 1984). In this study, I examined correlative relationships between treecreeper provisioning rate and selected environmental and demographic variables, and the number of nest attendants.

Methods

My study was conducted at three sites in Dryandra Woodland (32°45'S, 116°55'E), 160 km southeast of Perth, Western Australia. Each site was located in Wandoo *Eucalyptus wandoo* woodland and had 10 contiguous treecreeper territories (30 territories in total) in which most occupants (95%) were colour-banded as part of

a broader study on the ecology of the species. I conducted nest watches in the main breeding season (September – December) for 3 years (1997 – 1999). Birds were observed for 60 minutes per watch with a 22× telescope located 15 – 20 m from the nest. For each nest watch, I recorded the following variables that were used in the data analyses:

- a) site – A, B or C;
- b) year – 1997, 1998 or 1999;
- c) time of day – nest watches were conducted throughout the day from 0600 to 1600 hrs, the nearest hour was used as time of watch;
- d) day of season – the number of days from August 1, which was arbitrarily defined as the beginning of the breeding season;
- e) maximum daytime temperature – maximum temperature on day of nest watch recorded from a thermometer located in the study area;
- f) number of nestlings – determined by chick begging, observations of nestlings at hollow entrance, and number of fledglings (see below);
- g) nest stage – based on nestling age determined *a posteriori* from fledging date (see below) and classified as early (≤ 10 days post-hatching), mid ($11 < 20$ days) or late (≥ 20 days);
- h) nest number – Rufous Treecreepers may nest again after the first nest of a season fails (re-nesting) or succeeds (multibroodedness; Chapter 3), so I differentiated between the first and second nest of the season;
- i) number of nest attendants – total number of individuals provisioning nestlings (ranging from two to eight), determined by colour-band combinations; and
- j) provisioning rate per hour – based on visits where nest attendants brought food.

Rufous Treecreepers nest in tree-hollows, which generally prohibited direct observation of nest contents. Determining the stage of nesting and the number of nestlings is relatively easy when nestlings are near fledging because they can often be seen at the entrance of the hollow when begging for food. Nests at the early and mid stage were initially determined by observations of female behaviour (females would often brood recently hatched young), strength of chick begging and

knowledge of nest history (i.e., dates when individuals had been recorded nest building or incubating). Nest-stage categorisation was then confirmed by back-dating from fledging date based on the nestling period (28 days) defined by Rose (1996).

Based on 148 recorded nesting attempts, only one nest produced more than two fledglings (Chapter 3). Therefore, the number of nestlings appeared to be almost always one or two. For early and mid-stage nests, I determined if a nest had more than one nestling by listening for overlapping begging calls. The number of nestlings was confirmed in later watches where nestlings could be observed directly. If a nest was initially classified as having two nestlings, but only one nestling was observed at a later date it was not used in the analyses. Nests that failed before the number of nestlings could be confidently determined were also excluded.

One nest watch per nest attempt, per territory, per year was used in the analyses. First and second nesting attempts from the same territory were also included, as this allowed for examination of seasonal effects, and the number of nest attendants could differ between attempts. Provisioning rate data conformed to a Poisson distribution, so a General Linear Model (Family: Poisson, Link: Log) was used to examine the relationship between provisioning rate per hour (the dependent variable) and the environmental, demographic and nest attendant (independent) variables. Modelling and diagnostic procedures followed Nicholls (1989), and I used the S-Plus 2000 software package (MathSoft 1999). Significant correlations between independent variables were assessed using Spearman rank correlation.

Results

A total of 102 nest watches conducted over 3 years were included in the analyses. These were spread relatively evenly between years and sites. Provisioning rate per hour varied from eight to 50 (mean $21.8 \pm$ standard error 0.91). Changes in Poisson model deviance were used to assess the relationship between each independent variable and variation in provisioning rate. There were significant positive associations between nestling provisioning and number of nestlings and nest stage, and negative associations with time of day and maximum daytime temperature (Tables 1 and 2). Day of season was positively correlated with daytime

temperature ($r_s = 0.712$, $P < 0.001$), but the latter was associated with a greater change in model deviance.

Provisioning rate per hour was higher when there were two nestlings and increased with nest stage (i.e., nestling age; Figures 1a and b). Provisioning rates tended to be highest early in the day, but were relatively constant from approximately 0900 hrs onwards (Figure 1c). They were also higher when temperatures were mild (between 20 – 30° Celsius; Figure 1d). Importantly, there was no significant relationship between nestling provisioning and the number of nest attendants. Even with environmental and demographic variables controlled for, the total number of nest attendants was not significantly correlated with provisioning rate ($r_s = 0.001$, $P = 0.996$, $n = 34$).

Table 1 Significant change in model deviance (distributed as χ^2) with the addition of the independent variables listed ($P < 0.005$, $n = 102$).

Model	df	Change in deviance	Residual df	Residual deviance
Null			101	364.0
+No. of nestlings	1	92.6	100	271.4
+Nest stage	2	39.0	98	232.4
+Time of day	1	18.0	97	214.4
+Max. temperature	1	9.9	96	204.5

Table 2 The coefficients and standard errors (s.e.) of each variable included in the final Poisson model.

Variable	Coefficient	s.e.
Constant	3.050	0.187
No. of nestlings	0.376	0.054
Nest stage 1	0.159	0.033
Nest stage 2	0.083	0.016
Time of day	-0.032	0.006
Max. temperature	-0.014	0.004

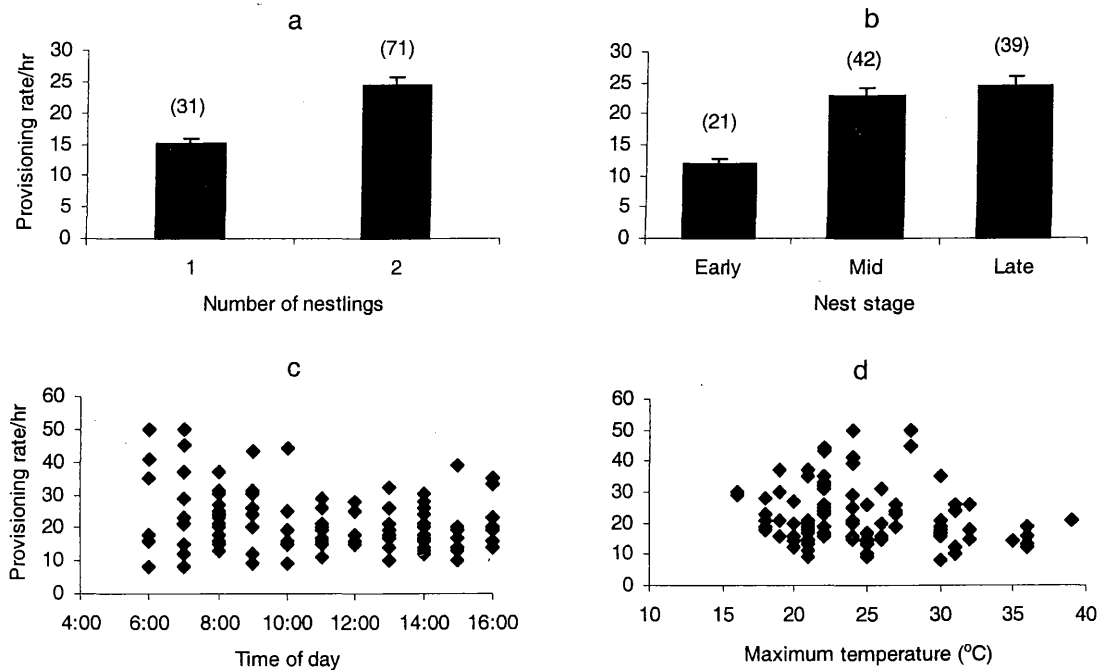


Figure 1 Relationship between provisioning rate/hr and; a) number of nestlings, b) nest stage, c) time of day, and d) maximum daytime temperature. Numbers in brackets above columns are sample sizes. Plots show original data, not controlling for other effects.

Discussion

For the Rufous Treecreeper, provisioning effort in *Dryandra* was compensatory rather than additive. As the number of nest attendants increased, the primary (assumed to be breeding) male and female reduced their contribution so that total provisioning rate remained relatively constant (Chapter 3). According to Hatchwell (1999), this suggests that nestling starvation is rare. Nest success was relatively high in *Dryandra* during my study (77.7%; Chapter 3), which provides some support for this conclusion. However, I have no data on the causes of nest failure.

There may be no positive association between provisioning rate and food intake of nestlings if an inverse relationship exists between number of feeding visits and prey size. The strong positive correlations between provisioning rate and nest stage (nestling age) and number of nestlings suggest that this is not the case for Rufous Treecreepers. Energetic demand would increase with the number of nestlings and probably with nestling age. Therefore, the associated increase in

provisioning rate probably reflects a positive relationship with food intake. This conclusion is supported by data from a small subset of nests ($n = 10$), which showed a positive correlation ($r = 0.72$) between provisioning rate and total prey biomass (Chapter 7).

Provisioning was highest early in the day and this probably represents a time of high energetic demand by nestlings owing to night-time food deprivation. Provisioning rate also tended to decrease when maximum daytime temperature exceeded 30° C. This may reflect a number of factors including a reduction in: a) the energetic requirement of nestlings with increased temperature; b) foraging effort by adults owing to heat stress; or c) invertebrate availability. As temperature was significantly correlated with day of season, a reduction in provisioning rate may also reflect seasonal variation in invertebrate availability.

A number of other factors may also be associated with variation in provisioning rate (e.g., nestling metabolic rate or rainfall; Brown et al. 1978). In addition to the variables identified in my study, these need to be considered when assessing relationships between provisioning effort and the number of nest attendants.

CHAPTER 4

A MULTI-SCALED ANALYSIS OF HABITAT USE

SUMMARY

In the wheatbelt of Western Australian, the Rufous Treecreeper occurs primarily in woodland, but we have no detailed knowledge on the specific habitat requirements of the species. This is fundamental to understanding the consequences of habitat modification on population viability. I examined the habitat use of the species at three spatial scales; landscape, woodland and territory, and developed predictive models of habitat use that were validated with new data.

Preferential habitat use by the treecreeper was exhibited at all spatial scales, supporting the assertion that multi-scaled analyses are required to adequately understand the habitat requirements of a species. At the landscape scale, Wandoo *Eucalyptus wandoo* woodland was used at a significantly greater rate than was predicted by the availability of this vegetation type. Territory use within woodlands was positively related to the density of hollow-bearing logs and nest sites, and tree age. Within an individual territory, nest sites (hollows) were preferentially used if they had a spout angle of $\geq 50^\circ$ and an entrance size of 5 – 10 cm.

Territory and nest-site models were derived using logistic regression from data collected in the Dryandra study area to predict the habitat use of the species. The predictive capability of these models was assessed with new data collected outside the study sites. The predictive capability of the territory model applied to the original data collected in Dryandra was 90%, but this was reduced to 70% when the model was applied to the new data, probably as a result of differences in habitat structure between sites. The nest-site model had a predictive capability of 67.8%. Nest sites appeared to be abundant in Dryandra and many of the unused hollows, which were compared with used hollows in the model, were probably suitable for nesting resulting in relatively low predictive success.

The Rufous Treecreeper preferentially used habitat with traits characteristic of old growth Wandoo woodland. Degradation of Wandoo through habitat modification (e.g., grazing, logging, fire and removal of deadwood) represents a significant threat to the persistence of treecreepers.

4.1 INTRODUCTION

4.1.1 Overview

In the Western Australian wheatbelt, the Rufous Treecreeper appears to occur primarily in Wandoo *Eucalyptus wandoo* and Salmon Gum *E. salmonophloia* woodlands (Ford 1971; Serventy and Whittell 1976; Kitchener et al. 1982). This relationship has not been quantified and there is only anecdotal evidence on specific habitat characteristics that may be important for the species. Explicit information on habitat requirements contributes to our understanding of how habitat change may affect the persistence of populations. In the first part of this chapter, I briefly review the theory of habitat selection and empirical studies of habitat use by birds. I then examine the habitat use of the Rufous Treecreeper at three spatial scales; landscape (woodland selection), woodland (territory selection) and territory (nest-site selection). Habitat use-temporal scale relationships are also considered for woodland selection. I use logistic regression to develop predictive models of territory and nest-site use, and validate the models with new data.

The specific aims of the chapter are to:

- a) determine if the Rufous Treecreeper preferentially uses particular woodland types;
- b) assess correlative relationships between structural habitat characteristics and territory and nest-site use;
- c) assess changes in species-habitat relationships with changes in spatial scale; and
- d) develop and validate predictive habitat models for Rufous Treecreepers in temperate woodland complexes characteristic of the western wheatbelt.

4.1.2 The theory of habitat selection

The relationship between organisms and where they live has long been studied in ecology. Lack (1933 cited in Morrison et al. 1992) is attributed as being one of the first to suggest that animals may "select" a place to live based on particular features of the environment. This gave rise to the concept of habitat selection and encouraged a number of researchers to examine the underlying

mechanisms of habitat choice in animals (Svardson 1949; Hildén 1965; Fretwell and Lucas 1970; James 1971). These studies have shown that where an animal lives is influenced by a number of factors including habitat structure, floristics, food availability, conspecifics, interspecific competition, predation risk and phylogenetic constraints (Hildén 1965; Southwood 1977; Butler 1980; Hutto 1985; Rotenberry 1985; Muller et al. 1997).

Correlative relationships between species distribution and habitat features may be confounded by fluctuations in climate, predator and competitor densities. Stochastic or deterministic extinction of populations may result in suitable habitat being unoccupied, whereas an increase in population density may reduce habitat selectivity resulting in species using a wider range of habitats than would otherwise be the case (Rosenzweig 1991).

The processes that drive habitat selection are often difficult to identify and are poorly understood, but the relationship between habitat use and population persistence remains an important problem in ecology (Morris 1987; Orians and Wittenberger 1991; Rosenzweig 1991; Pribil and Picman 1997; Clark and Shuter 1999). The first step in resolving this problem is to examine the relationship between the location of a species and particular habitat attributes to determine if habitat use is non-random. Correlative relationships between particular habitat features and species location may be useful in predicting a species distribution across landscapes (Lindenmayer et al. 1994; Fielding and Haworth 1995; Mladenoff et al. 1999; Franco et al. 2000). The second step in the study of habitat selection is to determine the variability of habitat features (identified in the first step) among used sites, and if this variability has any implications for fitness (e.g., reproductive success). This is discussed in Chapter 5.

4.1.3 Habitat use by birds

Studies of habitat use by birds have often demonstrated the importance of vegetation structure and floristics in determining distribution and abundance (Moen and Gutiérrez 1997; Shackelford and Conner 1997; Micheals and Cully 1998; Tibbetts and Pruett-Jones 1999). The structural characteristics of a habitat provide a bird with nest and roost sites, perches, foraging substrates and protection from

predators (Cody 1985; Ford 1989; Recher 1991). Birds may be associated with particular habitat types or show a close affinity with a certain plant species (Rice et al. 1984; Chan 1990; Adams and Morrison 1993; Storch 1993; McShea et al. 1995).

A number of habitat attributes may correlate with the presence of hollow-nesters like the Rufous Treecreeper. Studies in North America on cavity-nesting (= hollow-nesting) birds have shown that these species generally occur in older forests or woodlands that have a greater density of large trees, dead limbs or dead trees, hollows and logs (Sedgwick and Knopf 1990; Shackelford and Conner 1997; Hershey et al. 1998; Steeger and Hitchcock 1998; Hooge et al. 1999; Lahaye and Gutiérrez 1999; Savignac et al. 2000). In Australia, hollow abundance and woodland age are also considered influential in the habitat use of hollow-nesting birds (Saunders et al. 1982; Traill 1991; Bennett et al. 1994; Pell and Tidemann 1997).

Research on *Climacteris* species indicates that habitat characteristics such as tree species, type of bark, logs, ground cover, standing deadwood and the presence of hollows may be influential in the habitat use of treecreepers (Noske 1982, 1986; Recher et al. 1985; Ford et al. 1986; Brooker et al. 1990; Recher and Davis 1997). For the Rufous Treecreeper in particular, a foraging study by Luck et al. (Appendix 4.1) found that the ground layer and large trees were preferentially used as foraging substrates. Rose (1996) found that hollow logs were important refuges for recently fledged young. My study of the habitat use of the Rufous Treecreeper is based primarily on the structural characteristics of its habitat. I take no account of factors such as food availability or intra- or interspecific interactions, although these may be important in influencing the distribution of individuals (Mac Nally 1990).

4.1.4 Habitat use at three spatial scales

A hierarchical analysis

Scale plays a significant role in the examination of species habitat use (Wiens 1989b; Orians and Wittenberger 1991; Bergin 1992; Mac Nally and Quinn 1998). Studies conducted at only one scale are limited because different factors can influence habitat use at different scales (Wiens et al. 1987; Pribil and Picman 1997). A more useful approach is to investigate habitat use at multiple scales, preferably within a nested hierarchy (Maurer 1985; Wiens et al. 1987; Kotliar and Wiens 1990;

Bergin 1992). This multi-scale approach acknowledges the influence of spatial variation on species behaviour and recognises that there is no single correct spatial scale at which to conduct investigations (Morris 1987; Levin 1992; Otis 1997).

Single-scale studies of bird habitat use are common, with characteristic scales of investigation being habitat (or vegetation) type (Baines 1994; Hunt 1996), individual territories (McShea et al. 1995; Sodhi et al. 1999) or nest sites (Shields and Kelly 1997). However, many studies have taken a nested hierarchy approach to examining habitat use with scales of investigation ranging from landscape to nest tree (Moen and Gutiérrez 1997; Hall and Mannan 1999; Miller et al. 1999). Decisions about the appropriate scales of investigation should be based on the relevant ecological traits of the species of interest (e.g., home range size and dispersal ability) to reduce human bias in the selection process (Morris 1987; Orians and Wittenberger 1991).

The scales of investigation used in my study are relevant to specific ecological characteristics of the Rufous Treecreeper. At the broadest scale, I examined the relationship between the use and availability of different woodland types within my study area. The next (finer) scale of investigation is that of individual territory use within a woodland. In a true hierarchical analysis, territories would be nested within a single woodland type. This was not possible in my study because I compared used territories with non-used "pseudo-territories", and a given woodland type did not contain suitable numbers of these two categories for comparative analysis (see Section 4.3.2). At the finest scale of investigation, I examined the use of nest sites within territories.

The role of habitat modelling

Logistic regression is commonly used to develop predictive and explanatory statistical models of habitat use (Lindenmayer et al. 1991; Pearce et al. 1994; Boal and Mannan 1998; Ritter and Savidge 1999; Franco et al. 2000). In habitat studies, the method is appropriate when the dependent variable is dichotomous (e.g., the presence or absence of a species) and the aim of the research is to determine the association between the measured habitat (independent or predictor) variables and the location of a species.

Relationships derived from regression modelling are purely inferential. To strengthen interpretations of statistical inference it is important to assess the performance and validity of the models (Flather and King 1992). This generally occurs by applying various diagnostic procedures available with most computer statistical programs (Tabachnick and Fidell 1996). A particularly valuable, but infrequently used method of model assessment is to examine the predictive capability of habitat models when applied to new data (Straw et al. 1986; Lindenmayer et al. 1994; Mladenoff et al. 1999). This is especially important if the results of the model are to be used in a practical way for habitat management. In this study, I derive models of the habitat use of the treecreeper and assess the predictive capability of these models on independent data.

4.2 METHODS

4.2.1 Study areas

The majority of this study was conducted in the Dryandra study landscape (described in Chapter 2). Additional habitat data used to assess the predictive capability of the statistical (territory) model derived in Dryandra were obtained from the Julimar conservation reserve. Julimar is located approximately 90 km northeast of Perth and is a large (27,800 ha) reserve consisting primarily of a mixture of Wandoo, Jarrah *E. marginata*, Marri *E. calophylla* and Powderbark Wandoo *E. accedens* woodlands (Capill 1984).

4.2.2 Woodland type

Vegetation classification

The vegetation associations occurring in the Dryandra study landscape were broadly classified into seven types based on the vegetation maps of Coates (1993: see Chapter 2, Section 2.1.4). I chose to conduct presence/absence surveys in the four main woodland types because the other vegetation associations were unlikely to be used by the treecreeper (e.g., shrubland) or only covered a very small percentage of the study area (e.g., Marri and Sheoak *Allocasuarina huegeliana* woodland). Powderbark-Jarrah and Powderbark-Jarrah-Marri woodlands were combined and classified as one woodland type (referred to as Mixed woodland from here on) with

the other three woodlands classified by the predominant tree species as Wandoo, Powderbark Wandoo and Brown Mallet *E. astringens*. For Brown Mallet, presence/absence surveys were conducted mostly in the more extensive plantations (see Chapter 2), although some naturally occurring patches were also included.

Pilot study

In August 1997, I conducted a pilot study in Dryandra to determine the best methods for detecting Rufous Treecreepers at 30 locations that were known *a priori* to contain the species. The locations were surveyed between 0600 – 1200 hrs in fine weather conditions. All were accessible by dirt road or track and a vehicle was used to travel between sites. Immediately after arriving at a site, I stood next to the vehicle and used a stopwatch to determine the amount of time elapsed before visual (using 8 × 40 binoculars) or aural detection of a treecreeper. For the pilot study only, I attempted to visually locate all aurally detected individuals. I then measured the distance between the vehicle and the bird to establish a general association between strength of call and distance so that in the main study I could roughly estimate distance from observer for birds that were only located aurally.

For the 30 treecreeper locations, initial detection of the species was primarily aural (87%) with 90% of detections occurring within 5 minutes. Most (85%) aural detections were of birds ≤ 100 m from the observer with an apparent detection limit of approximately 150 m. This study was conducted primarily in one woodland type (Wandoo) and one season, and does not allow for differences in detectability between woodlands or seasons. This issue is addressed in Section 4.3.1.

Presence/absence surveys

To locate sample sites, I randomly selected sections of dirt roads and four-wheel-drive (4WD) tracks from a topographic map of the study area. Using a 4WD vehicle, I travelled a distance of 500 m from the beginning of each section of road. At this point, I classified the site into one of the seven broad vegetation associations based on the predominant overstorey species occurring within a 100 m radius of the vehicle. If a site was classified as one of the four main woodland types, it was marked on the map and in the field with flagging tape to facilitate re-location. I then

travelled another 500 m before locating the next sample site. This was repeated for each section of road.

I located 200 sites (50 per woodland type), which were surveyed for the presence of treecreepers on five occasions (once per season): mid-breeding season (November 1997), summer (January 1998), autumn (April 1998), winter (July 1998) and early breeding season (September 1998). Surveys were conducted in fine weather conditions between 0600 – 1200 hrs. The order of roads surveyed was randomised for each survey period.

At each sample site, I waited outside the vehicle for a maximum of 5 minutes listening for treecreeper calls and scanning the woodland with binoculars. If a treecreeper was detected, I recorded the time to detection and the approximate location of the bird. Each location was marked with flagging tape and its distance from the vehicle was measured by pacing. These marked locations were used to identify approximate areas of use of the species at any given site so more detailed habitat data could be collected (see Section 4.2.3). Detection times and distances were used to examine detectability differences between woodland types. This is important because differences in detectability may affect assessments of proportional habitat use (Thomas and Taylor 1990).

Data handling and analysis

I examined seasonal differences in the number of detections recorded overall and in each woodland type using chi-square. Differences in detection time and distance for each season and woodland type, for repeated measures on the same 200 sample sites, were analysed using repeated-measures analysis of variance (ANOVA) after data were \log_{10} transformed. To calculate the proportion of use for each woodland, I considered the species to be present at sites where detection frequency was \geq three (out of five surveys), and absent from sites with nil detections. Proportional availability (i.e., percent of the study area covered) of each woodland type was calculated using the GIS database of Dryandra vegetation (Chapter 2).

A chi-square goodness-of-fit test is commonly used to analyse habitat use-availability data (Neu et al. 1974; Thomas and Taylor 1990; Alldredge and Ratti 1992). If disproportionate use is established, simultaneous Bonferroni confidence

intervals can be calculated to determine which of the habitat types are being selected or avoided. This method has been criticised (Byers et al. 1984; Cherry 1998), as it is possible to have a significant chi-square value and find no evidence of selection or avoidance in the intervals, and vice versa. Cherry (1998) suggested that the calculation of confidence intervals only is sufficient to determine any relationships between habitat use and availability. Here, I calculate 95% Bonferroni confidence intervals to determine if any woodland type(s) are being preferentially used or avoided by the treecreeper.

Data represented as proportions that sum to one are not independent (the “unit-sum constraint”, Aitchison 1986; Aebischer et al. 1993), as is the case for the proportional use of woodland types by the treecreeper. To overcome this, proportions can be transformed to independent log-ratios using the equation

$$y_i = \ln(x_i/x_j).$$

Here, x_i is the proportion of vegetation type i and x_j is the proportion of vegetation type j , which is used as the denominator in each transformation. A habitat ranking matrix (from most to least preferred) can be constructed using the equation

$$\ln(x_{ui}/x_{uj}) - \ln(x_{ai}/x_{aj}).$$

Here, x_{ui} and x_{uj} are the used proportions of vegetation types i and j respectively, and x_{ai} and x_{aj} are the available proportions (see Aebischer et al. 1993 for more details). I used this method to confirm the results of the confidence interval analysis and to rank woodland types from most to least preferred.

Certain assumptions are implicit in the study of animal habitat use versus availability (Allredge and Ratti 1986, 1992; Thomas and Taylor 1990). In my study, I assumed that treecreepers were not restricted from using any particular woodland type, actual woodland availability was accurately classified with the GIS, and the location of an individual at any given sampling point was independent of other points. As sampling points were at least 500 m apart, and the average treecreeper territory size in Dryandra was 2.6 ha (Chapter 3), any given sampling point would be separated from the next nearest point by a distance of at least one territory.

4.2.3. Territory use

Field methods

Based on the results of the presence/absence surveys, I randomly selected 50 sites with treecreepers (\geq three detections) and 50 sites without (nil detections) from which to collect detailed habitat data. I estimated the species' area of use (referred to as territory from here on) at each site containing treecreepers based on the three or more flagged locations identified during the presence/absence surveys. This method of delineation is limited when compared to detailed territory mapping of a species, but the data collected were consistent with that obtained from the 30 intensely studied territories described in Chapter 3 (see Table 4.7).

For sites where treecreepers were absent, a pseudo-territory was established centred on a point located 100 m perpendicular to the road. The boundaries of territories and pseudo-territories extended from the centre point in a radius of 80 m. This covered an area of approximately 2.5 ha, comparable to the average size of a treecreeper territory in Dryandra.

In each territory and pseudo-territory, I collected detailed measurements of potentially important habitat attributes. The selection of attributes was based on prior knowledge of Rufous Treecreeper ecology, data from other studies on hollow-nesting birds, and observations of the species' behaviour at my study sites. I randomly located up to 10, 20 \times 20 m quadrats within the boundaries of each territory. The appropriate sample size for each woodland type was determined by plotting the mean and standard error of the most variable habitat characteristic measured (tree diameter at breast height (DBH)) against sample size until an asymptote was obtained. The number of quadrats differed for each woodland: Wandoo 10, Powderbark Wandoo eight, Brown Mallet five and Mixed woodland eight. The habitat characteristics measured and the methods used are described in Table 4.1.

Table 4.1 The habitat characteristics measured in each territory and pseudo-territory.

Habitat characteristic	Method of measurement
Tree density ha ⁻¹	Number of trees (≥ 2 cm DBH) per quadrat converted to density ha ⁻¹ . Multi-stemmed trees were considered a single tree if stems joined above the ground
Canopy tree density ha ⁻¹	As above for all trees estimated to be ≥ 10 m in height.
Subcanopy tree density ha ⁻¹	As above for all trees 5 m $<$ 10 m in height
Sapling density ha ⁻¹	As above for all trees $<$ 5 m in height
Wandoo density ha ⁻¹	As above for all Wandoo trees
Wandoo canopy density ha ⁻¹	As above for all Wandoo trees ≥ 10 m in height.
Density of hollow-bearing trees ha ⁻¹	As above for all trees with at least one hollow large enough to house a treecreeper. Trees were scanned for hollows from the ground using binoculars
Density of hollows ha ⁻¹	As above for all hollows large enough to house a treecreeper.
Density of hollow-bearing logs ha ⁻¹	As above for all logs (downed wood) with a hollow deemed suitable for treecreeper use (also see log biomass).
Tree size	Size was calculated for each tree as size class (sapling – 1, subcanopy – 2, canopy – 3) \times DBH. A mean value was assigned to each territory. DBH measurements were taken on the thickest stem to the nearest cm using a diameter tape.
Deadwood biomass	Percent amount of standing deadwood in each tree was subjectively estimated to the nearest 10%, and a biomass figure was calculated as % deadwood \times tree size. A mean biomass figure was then calculated for each territory.
Bark biomass	The thickest stem of each tree was sighted at eye level through binoculars at a distance of 25 m and percent amount of decorticated bark was estimated to the nearest 10%. Bark biomass was calculated as % bark \times tree size, and a mean value was calculated for each territory.
Log biomass	Downed wood was considered a log if ≥ 10 cm in diameter at the widest point. Only logs where $>$ 50% of total log length fell inside the quadrat boundaries were measured, fallen trees were considered a single log. A size value was calculated for each log as total log length \times length of log ≥ 10 cm in diameter. These values were summed for each quadrat and the total assigned to each territory.
% ground vegetation	Calculated for each territory as proportion of sampling points with ground vegetation (e.g., herbs and annuals).
% litter	As for ground vegetation. Litter classified as leaves, bark and woody debris $<$ 10 cm in diameter.
% bare ground	As for ground vegetation.
% shrub cover	As for ground vegetation. Woody stemmed shrubs were initially classified into height classes (i.e., dwarf $<$ 0.5 m, small 0.5 $<$ 1 m, medium 1 $<$ 1.5 m and tall \geq 1.5 m), but percent cover for each class was very low and values were pooled to provide total shrub cover.
% canopy cover	As for ground vegetation. Measured at each sampling point by sighting vertically through a 4 cm diameter monocular tube and recording the presence or absence of leaves.
S-W diversity index of ground cover	A Shannon-Wiener diversity index (Zar 1996) was calculated for all ground cover comprised of ground vegetation, litter and bare ground.
S-W diversity index of vegetation structure	As above for ground vegetation, shrub, sapling, subcanopy and canopy cover.

To calculate percent ground and shrub cover, each quadrat was dissected with four evenly spaced 20 m transects, and five sampling points per transect (20 per quadrat) were located at 5 m intervals (Figure 4.1). At each sampling point, a 10 mm diameter, 2 m high levy pole divided into 10 cm height classes was placed vertically and a substrate was recorded if it came in contact with the pole. Only one hit per substrate type or height class of shrub was recorded (i.e., presence or absence). The substrates ground vegetation, litter and bare ground were considered as mutually exclusive. Woody shrubs were classified into height classes (Table 4.1), which were not mutually exclusive from each other or from ground substrates (e.g., tall shrub, dwarf shrub and litter could be recorded at the one sampling point).

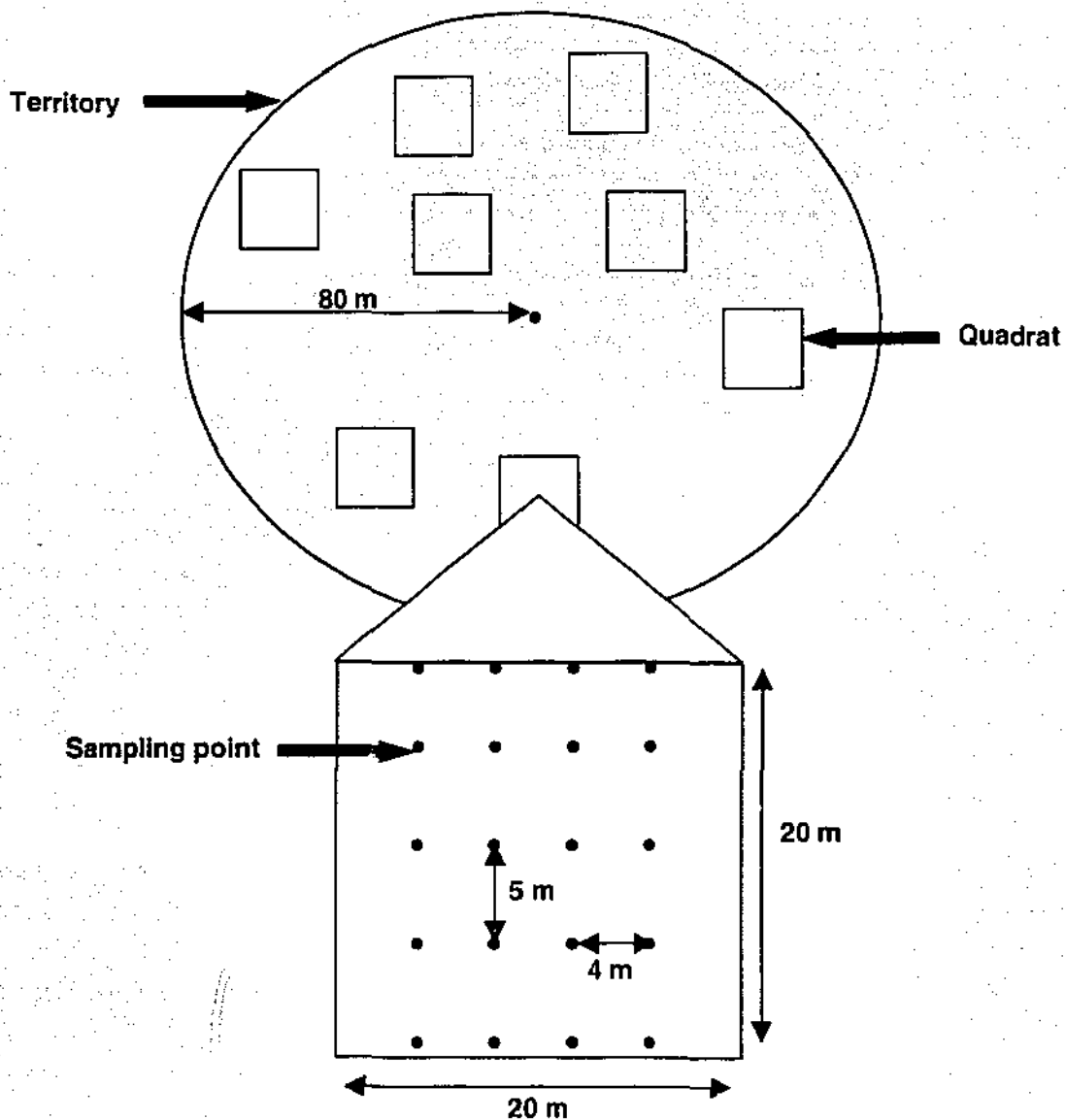


Figure 4.1 Sampling design used for collecting habitat data in each territory and pseudo-territory.

At Julimar, I located 50 sites (25 with treecreepers and 25 without) by randomly selecting road sections from a topographic map and stopping every 500 m to determine treecreeper presence. Classification of treecreeper absence from a site was based on a 30 minute survey of the immediate area. This was considered a suitable time period owing to the relative ease of detecting treecreepers. At each of the sites, habitat measurements were collected in the same manner as in Dryandra and were centred on the location of individuals at the sites containing treecreepers, and on a point 100 m perpendicular to the road at sites where treecreepers were absent. The Julimar survey was a snapshot of treecreeper habitat use in this area and is limited when compared to more detailed habitat surveying, but it is still a reasonable approximation of habitat use owing to the apparently high site fidelity of treecreepers (Chapter 3).

Data handling and analysis

Habitat variables that did not meet assumptions of normality were transformed (Table 4.7 contains a summary of transformations) after being examined using frequency distributions, normal probability plots and the Shapiro-Wilks test. I examined multicollinearity between variables using the Pearson correlation coefficient and considered $r \geq 0.70$ as the criterion for either omitting a variable or creating a composite variable using principal component analysis (Adler and Wilson 1985; Tabachnick and Fidell 1996). Principal component analysis is a data reduction technique that represents the relationship between highly correlated variables as new independent variables (principal components).

Automated, step-wise procedures are commonly used in regression analyses where the computer includes or removes variables from the regression equation based on a default cut-off level or one defined by the researcher. Automated methods have been criticised for various reasons particularly because, over multiple runs of the automated procedure on the same data set, the computer may select different predictor variables as explaining variation in the data (Henderson and Velleman 1981; James and McCulloch 1990). To avoid this problem, "interactive" (*sensu* Henderson and Velleman 1981) regression modelling is appropriate where the researcher analyses all possible subsets of variables and selects the best combination based on improvements in the fit and predictive power of the model. I

followed this approach in my study; modelling was conducted using SPSS 8.0 software (Norusis 1998).

Model fit and predictive capability were assessed using:

- a) significant changes in $-2\log\text{likelihood}$ with the addition or deletion of variables based on the goodness of fit statistic (Z^2 – distributed as χ^2) with suitable degrees of freedom (Tabachnick and Fidell 1996);
- b) the Hosmer-Lemeshow goodness-of-fit test;
- c) R^2 variance explained for each model; and
- d) the contingency table of predicted versus observed occurrences (using a cut-off level where predicted absence $< 0.5 \leq$ predicted presence) and the measures of error rate, sensitivity and specificity (Lindenmayer et al. 1991; Pearce et al. 1994; Table 4.2).

Table 4.2 Measures of error rate, sensitivity and specificity for model predictions (modified from Lindenmayer et al. 1991).

		Predicted occurrence		
		Present	Absent	
Observed occurrence	Present	a	b	a + b
	Absent	c	d	c + d
				N

a = number of sites where the Rufous Treecreeper was correctly predicted to be present.
b = number of sites where the Rufous Treecreeper was predicted to be absent, but was present.
c = number of sites where the Rufous Treecreeper was predicted to be present, but was absent.
d = number of sites where the Rufous Treecreeper was correctly predicted to be absent.
N = total number of sites.
Error rate = an estimate of the number of incorrect predictions made by the model, calculated as $(c + b)/N$.
Sensitivity = a measure of the ability of the model to predict the presence of the Rufous Treecreeper at a site, calculated as $a/(a + b)$.
Specificity = the ability of the model to correctly predict that the Rufous Treecreeper will not occur at a given site, calculated as $d/(c + d)$.

The predictive capability of the habitat model was assessed by calculating the probability of use for each site in Julimar based on the value of Logit (P) derived from the regression equation of the Dryandra model. Logit (P) is calculated as

$$\text{Logit}(P) = A + B_1X_1 + B_2X_2 + \dots + B_kX_k$$

with the constant A , coefficients B_j , and predictors X_j for k predictors (Tabachnick and Fidell 1996). A value of Logit (P) was calculated for each site in Julimar based on the constant and coefficients derived from the Dryandra model and the values of the predictor (habitat) variables measured in Julimar.

A probability of occurrence for each site in Julimar was then calculated as

$$\text{Probability of occurrence} = \frac{e^{[\text{Logit}(P)]}}{1 + e^{[\text{Logit}(P)]}}$$

where e is the base of the natural logarithm (2.718). A calculated probability of occurrence ≥ 0.5 (50%) was considered to predict the presence of the species with < 0.5 predicting the absence. These calculated probabilities were compared to the actual occurrence of treecreepers at the sites in Julimar to determine the predictive capability of the model. Error rate, sensitivity and specificity were calculated for the predicted versus observed occurrences.

4.2.4. Nest sites

Field methods

Nest tree and hollow measurements were collected in the 30 study territories in Dryandra and in habitat blocks outside the main study area, but still within the Dryandra woodland complex. The use of different nesting hollows attributable to the same female were not considered as independent and only one of these hollows (chosen randomly) was used in the analysis. Hollows used on multiple occasions were only measured once. The characteristics of each used nest tree and hollow were compared with an unused tree and hollow (unused for the duration of the study). The unused tree was the nearest hollow-bearing tree to the nest tree. An unused hollow was selected from this tree by counting the number of visible hollows and choosing a number at random. The characteristics measured and methods used are described in Table 4.3.

Data handling and analysis

The methods used for data analysis follow those described in Section 4.2.3. To assess the predictive capability of the logistic regression model, I derived a model based on 96 hollows (48 used and 48 unused) from my 30 study territories, and tested it against data collected outside the main study area ($n = 84$, 42 used and 42 unused).

Table 4.3 Nest-site characteristics measured at each used and unused site.

Nest-site characteristics	Methods of measurement
Tree DBH (cm)	Measured per Table 4.1
% deadwood	Percent amount of standing deadwood in the nest tree subjectively estimated to the nearest 10%.
Tree height (m)	Highest point of the nest tree measured using an inclinometer and calculated via trigonometry.
Number of hollows	Measured per Table 4.1
Hollow height (m)	Height of hollow entrance from the ground. Measured using extendable poles to a height of 8 m, or with an inclinometer.
Relative height of hollow (m)	Hollow height divided by tree height
Spout angle (°)	Measured as angle to horizon of branch or trunk which nest was placed in, estimated to the nearest 10°. Branch angle may not coincide with entrance angle (e.g., a front opening hollow in a trunk).
Size (cm)	Horizontal diameter of widest section of entrance hole measured externally using a 30 cm ruler fixed to the end of extendable poles and read through binoculars. For nests higher than 8 m, entrance size was estimated relative to the size of adult treecreepers by observing birds entering and leaving the nest (or just estimated for unused hollows). For hollows with more than one opening, I considered the entrance to the hollow to be the one that was used most frequently by the birds.
Aspect (°)	Compass direction to which entrance hole opened divided into nine aspect classes: north (337.5 < 22.5°); northeast (22.5 < 67.5°); east (67.5 < 112.5°); southeast (112.5 < 157.5°); south (157.5 < 202.5°); southwest (202.5 < 247.5°); west (247.5 < 292.5°); northwest (292.5 < 337.5°); vertical aspect (facing upwards).
% canopy cover	Measured by standing directly below the hollow, sighting vertically through a 4 cm diameter monocular tube and estimating percent field of view covered by leaves.

4.3 RESULTS

4.3.1 Woodland type

Detectability

There were no significant seasonal differences in the number of detections recorded for each woodland type or overall (Table 4.4), but there was a significant seasonal difference in the time to detection (Table 4.5). Detectability was lowest in summer, but occurred more readily during the breeding season probably as a result of the constant calling of nestlings and fledglings. There were no significant differences in detectability between woodland types and no woodland × season interactions (Table 4.5). Therefore, the data on habitat use versus availability should not be affected by detectability differences between woodlands.

Table 4.4 The number of detections in each season and for each woodland type ($n = 200$, 50 for each woodland). Chi-square values are not significant ($P > 0.10$).

Woodland type	Number of detections					χ^2
	Mid-breeding	Summer	Autumn	Winter	Early breeding	
Wandoo	43	46	46	44	43	0.20
Powderbark	7	5	10	9	7	0.98
Brown Mallet	6	7	13	10	10	2.90
Mixed woodland	5	4	7	7	5	1.28
Overall	61	62	76	70	65	2.31

Table 4.5 The time and distance to detection in each season and woodland type (mean \pm s.e.). There was no significant interaction between woodland type and season for time to detection ($F_{12,317} = 1.44$, $P = 0.15$) or distance to detection ($F_{12,317} = 0.82$, $P = 0.63$)

Season	Time (seconds)	Distance (metres)
	to detection	to detection
Mid-breeding	34.8 \pm 4.58	84.8 \pm 5.83
Summer	80.1 \pm 6.62	77.4 \pm 6.02
Autumn	61.4 \pm 6.90	68.6 \pm 5.28
Winter	53.5 \pm 8.11	73.3 \pm 5.23
Early-breeding	42.6 \pm 4.41	84.8 \pm 5.83
ANOVA	$F_{4, 244} = 8.81$ $P < 0.001$	$F_{4, 244} = 1.46$ $P > 0.10$
Woodland type		
Wandoo	49.5 \pm 3.82	75.7 \pm 3.38
Powderbark	57.8 \pm 11.92	84.4 \pm 9.57
Brown Mallet	53.2 \pm 7.97	80.3 \pm 8.28
Mixed woodland	62.6 \pm 6.37	83.5 \pm 4.66
ANOVA	$F_{3, 72} = 1.81$ $P > 0.10$	$F_{3, 72} = 0.83$ $P > 0.10$

Habitat use and availability

Rufous Treecreepers were recorded on three or more occasions at a total of 55 sites (Wandoo – 39; Powderbark Wandoo – six; Brown Mallet – six; Mixed woodland – four). Proportional use versus availability was significantly different for each woodland type (Table 4.6). Treecreepers were recorded most often in Wandoo woodland (70.9%) even though this comprised only 28.1% of the total vegetation cover in the study area. Use of the other three woodland types was lower than would be expected from their proportional availability. The ranking derived from the log-ratios of woodland availability confirmed the preference for Wandoo woodland (Table 4.6).

Table 4.6 Simultaneous Bonferroni confidence intervals ($\alpha = 0.05$) for observed versus expected use of the four main woodland types in Dryandra. Woodland rank was derived from a ranking matrix using the log-ratios of woodland use and availability (Aebischer et al. 1993).

Woodland type	Observed use	Expected use	Confidence intervals	Proportional use	Woodland rank
Wandoo	0.709	0.281(P_1)	$0.572 \leq P_1 \leq 0.882$	Higher	1
Powderbark	0.109	0.237(P_2)	$0.001 \leq P_2 \leq 0.217$	Lower	3
Brown Mallet	0.109	0.267(P_3)	$0.001 \leq P_3 \leq 0.217$	Lower	4
Mixed woodland	0.073	0.137(P_4)	$0.000 \leq P_4 \leq 0.131$	Lower	2

4.3.2. Territory use

Development of the territory model

Table 4.7 summarises the values of each habitat variable measured in Dryandra and Julimar. Before habitat modelling, I removed variables correlated ($r \geq 0.70$) with others in the data set or created composite variables using principal component analysis (see below) based on biological and statistical considerations. The variables SDEN, SCDEN, WDEN, DHBT, PGV and PLIT (see Table 4.7 for full variable names) were removed because they were nested within other habitat measures or because other variables provided more detailed information.

The highly correlated ($r > 0.75$) variables WCDEN, DHOL, TSIZ and DWBM were included in a principal component analysis. Two principal components were derived from this analysis that had an eigenvalue > 1.0 and explained 90.8% of cumulative variance in the data. WCDEN and DHOL had high factor loadings with the first principal component (0.88 and 0.87 respectively). This component was interpreted as the number of potential nest sites (as treecreepers primarily nest in hollows in Wandoo canopy trees) and formed the composite variable NSITE. The variables TSIZ and DWBM had high factor loadings with the second principal component (0.75 and 0.74 respectively). This component was interpreted as a measure of tree age (older trees are generally larger and have a greater biomass of standing deadwood) and formed the composite variable TAGE.

Table 4.7 The values (mean \pm s.e.) of each of the habitat variables measured in the Dryandra used and unused sites and the Julimar used sites (based on the presence/absence surveys), and the Dryandra study territories (described in Chapter 3). Numbers in brackets are sample sizes. The table also lists the transformations conducted prior to principal component analysis and logistic regression.

Habitat characteristic	Code	Sites				Transformation
		<i>Dryandra used (50)</i>	<i>Dryandra unused (50)</i>	<i>Julimar used (25)</i>	<i>Dryandra territories (30)</i>	
Tree density ha ⁻¹	TDEN	208.8 \pm 8.98	285.0 \pm 21.05	178.0 \pm 6.43	201.0 \pm 12.97	Square root
Canopy tree density ha ⁻¹	CDEN	89.1 \pm 3.94	103.2 \pm 11.80	53.0 \pm 4.34	77.4 \pm 3.78	Square root
Subcanopy tree density ha ⁻¹	SCDEN	70.7 \pm 3.72	85.0 \pm 12.47	55.8 \pm 2.24	67.9 \pm 5.14	Square root
Sapling density ha ⁻¹	SDEN	49.4 \pm 4.83	96.4 \pm 12.04	69.3 \pm 4.63	55.6 \pm 6.83	Square root
Wandoo density ha ⁻¹	WDEN	140.4 \pm 12.59	52.9 \pm 10.62	154.9 \pm 9.68	187.8 \pm 14.13	
Wandoo canopy density ha ⁻¹	WCDEN	53.9 \pm 4.46	6.3 \pm 1.53	36.7 \pm 2.12	70.4 \pm 4.35	
Density of hollow-bearing trees ha ⁻¹	DHBT	31.6 \pm 2.03	10.2 \pm 1.30	23.7 \pm 1.67	36.9 \pm 2.05	
Density of hollows ha ⁻¹	DHOL	91.1 \pm 6.70	23.5 \pm 3.23	85.1 \pm 7.46	110.7 \pm 7.37	
Density of hollow-bearing logs ha ⁻¹	DHLOG	20.3 \pm 1.37	10.4 \pm 0.98	17.0 \pm 1.20	22.7 \pm 1.62	
Tree size	TSIZ	66.5 \pm 2.48	47.5 \pm 3.22	59.5 \pm 2.48	65.5 \pm 3.19	
Deadwood biomass	DWBM	18.2 \pm 1.12	10.4 \pm 0.69	14.5 \pm 0.84	19.4 \pm 1.58	Log ₁₀
Bark biomass	BBM	15.8 \pm 0.93	8.3 \pm 0.83	16.0 \pm 0.88	18.9 \pm 0.81	
Log biomass	LBM	437.5 \pm 36.47	325.3 \pm 48.24	390.4 \pm 32.01	525.6 \pm 49.62	Square root
% ground vegetation	PGV	16.2 \pm 0.99	8.2 \pm 1.33	28.9 \pm 1.35	18.4 \pm 1.41	Arcsine
% litter	PLIT	67.4 \pm 1.31	74.1 \pm 1.84	53.7 \pm 1.07	67.7 \pm 1.69	Arcsine
% bare ground	PBG	16.4 \pm 0.93	17.8 \pm 1.09	17.4 \pm 0.81	13.9 \pm 0.90	Arcsine
% shrub cover	PSC	8.0 \pm 0.66	15.9 \pm 1.54	8.4 \pm 0.90	7.5 \pm 0.64	Arcsine
% canopy cover	PCC	50.4 \pm 1.37	50.2 \pm 1.97	52.9 \pm 2.14	51.4 \pm 1.83	Arcsine
S-W diversity of ground cover	SWG	0.8 \pm 0.02	0.6 \pm 0.03	0.9 \pm 0.01	0.7 \pm 0.02	
S-W diversity of vegetation structure	SWV	0.9 \pm 0.01	0.8 \pm 0.02	0.9 \pm 0.01	0.9 \pm 0.01	

The territory analysis was not structured as a true nested hierarchy because the 50 sites with treecreepers and the 50 sites without did not occur in the same woodland type (non-preferred woodlands did not have enough treecreeper sites and vice versa for Wandoo). Therefore, I included the dummy variable "woodland type" (i.e., Wandoo, Powderbark, Brown Mallet or Mixed) in the regression analysis to determine if this was a significant predictor of treecreeper territory use.

A total of 13 variables were analysed using interactive logistic regression to determine the most parsimonious model. The final model (Table 4.8) was highly significant ($\chi^2_3 = 94.16$, $P < 0.001$), explained 81.3% of variance in the data (Nagelkerke R^2), and was not significantly different from the statistically perfect model (Hosmer-Lemeshow goodness-of-fit $C_8 = 4.12$, $P = 0.846$). The presence of Rufous Treecreepers was closely related to the density of hollow-bearing logs (DHLOG) and the combined effects of tree size and standing deadwood biomass (TAGE), and density of Wandoo canopy trees and hollows (NSITE). The addition of further variables did not significantly improve model fit. The overall predictive capability of the final model was also very high (Table 4.9). The error rate was 10%, sensitivity 88% and specificity 92%. The model predicted the actual absence of the treecreeper from a site slightly better than it predicted actual presence.

Table 4.8 The habitat variables included in the final territory model showing values of the Wald statistic, levels of significance (sig.) and proportion of variance explained (R).

Variables	Coefficients	s.e.	Wald _{df}	sig.	R
Constant	-2.1071	0.8954	5.07 ₁	0.0243	
NSITE ¹	3.1780	0.8694	13.36 ₁	0.0003	0.2863
DHLOG	0.1944	0.0601	10.48 ₁	0.0012	0.2473
TAGE ²	0.9340	0.4812	3.76 ₁	0.0523	0.1129

¹Composite variable of WCDEN and DHOL.

²Composite variable of TSIZ and DWBM.

Table 4.9 The predictive capability of the final territory model showing the overall percentage of correct predictions and measures of sensitivity and specificity ($n = 100$).

		Predicted		
		<i>Present</i>	<i>Absent</i>	% correct
Observed	<i>Present</i>	44	6	88%
	<i>Absent</i>	4	46	92%
		<i>Overall</i>		90%

I plotted the relationship between the probability of occurrence of the treecreeper and the three habitat variables included in the model (Figure 4.2). For hollow log density, the probability of treecreeper occurrence dropped below 0.5 (50%) at a density of approximately 15 hollow logs ha^{-1} . The associations between probability of occurrence and the principal component scores (plotted as nest site index and tree age index in Figure 4.2) are difficult to interpret without the actual habitat measures, so I plotted probability of occurrence against WCDEN, DHOL, TSIZ and DWBM (Figure 4.3). Probability of occurrence dropped below 0.5 when the density of Wandoo canopy trees was $< 25 \text{ ha}^{-1}$ and hollow density was $< 50 \text{ ha}^{-1}$. The relationships plotted in Figures 4.2 and 4.3 are simplifications of the actual situation, as these habitat variables interact to influence probability of occurrence.

Structural differences between territories and pseudo-territories are further illustrated when comparing the means of Wandoo sites only (Table 4.10). Each of the significant habitat variables identified by the model (i.e., not factor scores) had higher mean values in sites containing treecreepers.

Table 4.10 Each significant habitat variable (mean \pm s.e.) included in the logistic regression model in territories (used) and pseudo-territories (unused) of Wandoo sites only. Numbers in brackets are sample sizes.

<i>Habitat characteristic</i>	Wandoo sites only	
	<i>Territories (36)</i>	<i>Pseudo-territories (12)</i>
TSIZ	67.4 \pm 2.94	32.0 \pm 2.13
DHOL	106.4 \pm 6.79	35.5 \pm 2.00
WCDEN	66.4 \pm 3.98	25.0 \pm 2.24
DHLOG	21.1 \pm 1.53	7.0 \pm 1.43
DWBM	19.3 \pm 1.37	8.8 \pm 0.54

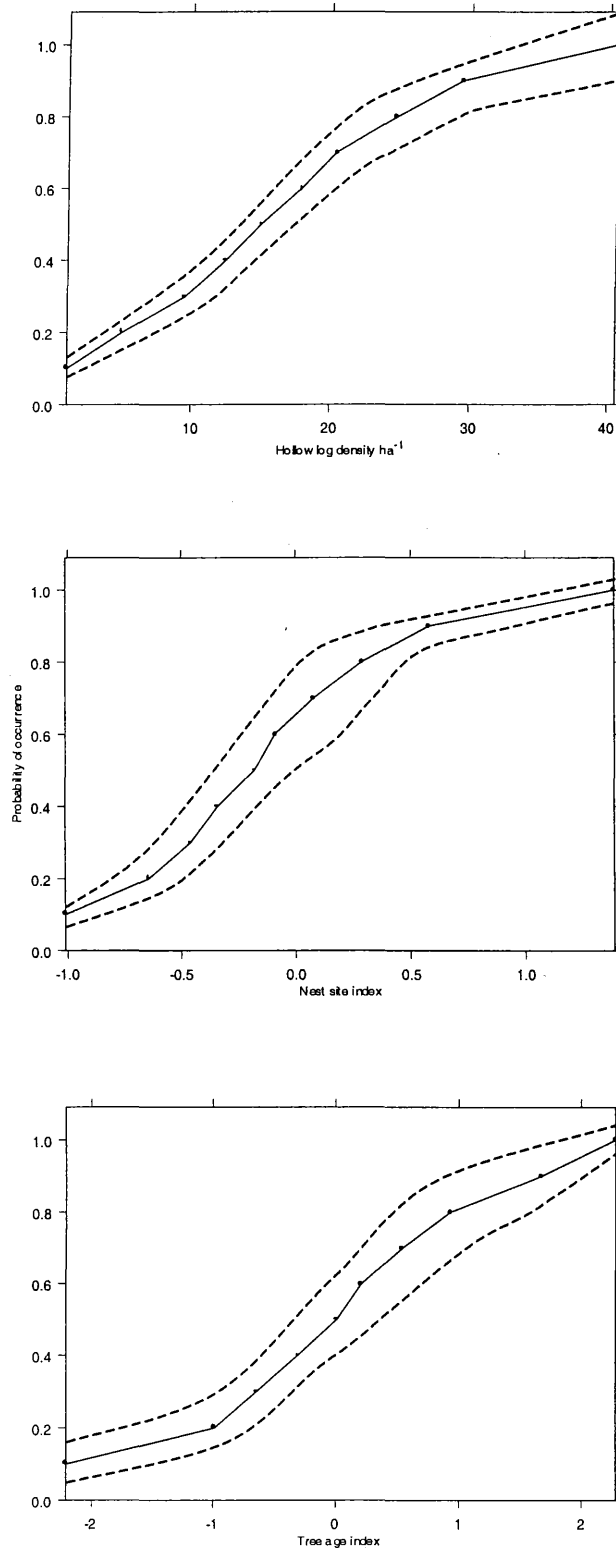


Figure 4.2 Relationship between the predicted probability of occurrence of Rufous Treecreepers and density of hollow-bearing logs, nest site index and tree age index (principal component scores) with other variables held at their mean. Dashed lines are 95% confidence intervals.

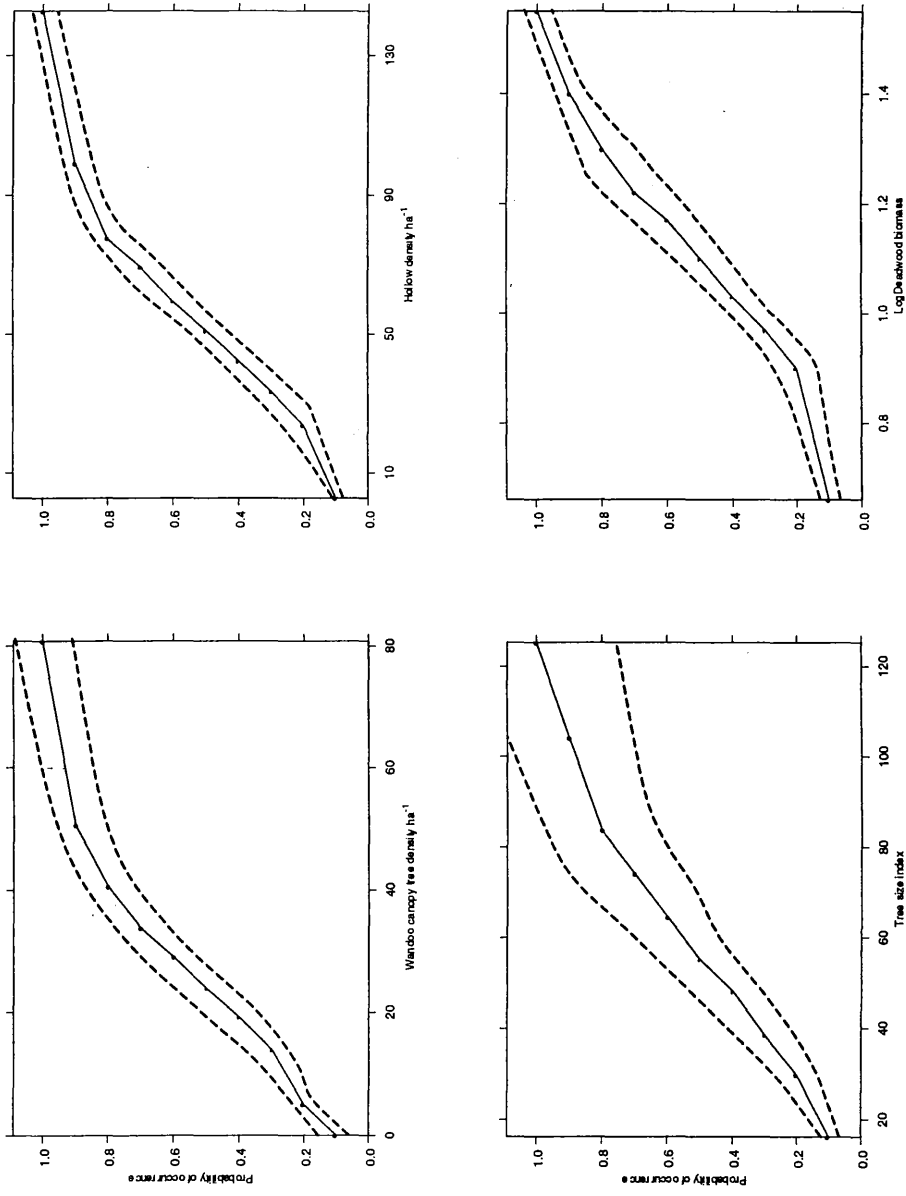


Figure 4.3 Relationship between the predicted probability of occurrence of Rufous Treecreepers and the density of Wandoo canopy trees and hollows, and tree size index and (log)deadwood biomass with other variables held at their mean. Dashed lines are 95% confidence intervals.

Validation of the territory model

The territory model derived from the sites in Dryandra was validated by comparing its predicted values with the new data collected in Julimar. Principal component analysis was used to create the composite variables NSITE and TAGE from the original variables WCDEN, DHOL, TSIZ and DWBM (\log_{10} transformed). The value of Logit (P) was calculated for each of the 50 sites in Julimar using the equation

$$\text{Logit } (P) = -2.1071 + 3.1780(\text{NSITE}) + 0.1944(\text{DHLOG}) + 0.9340(\text{TAGE}).$$

Based on the values of Logit (P), probability of occurrence values were calculated for each site using the equation in Section 4.2.3. These were compared to the actual presence or absence of treecreepers in the Julimar sites to determine measures of error rate, sensitivity and specificity (Table 4.11). The overall predictive capability of the Dryandra model applied to the new data was reasonably high, although error rate was 20% higher than in the original model. True absence was predicted more successfully (80%) than true presence (60%). This suggests that treecreepers were using a number of sites in Julimar that they would not be predicted to use based on the values from the Dryandra model. Relaxing the predicted presence/absence cut-off from 0.5 to 0.4 increases the overall correct predictions to 74%, and using the more conservative value of 0.6 reduces the overall percentage to 66%.

Table 4.11 The predictive capability of the Dryandra territory model when applied to the habitat data from Julimar. Table shows overall percentage of correct predictions and measures of sensitivity and specificity ($n = 50$).

		Predicted		
		<i>Present</i>	<i>Absent</i>	<i>% correct</i>
Observed	<i>Present</i>	15	10	60%
	<i>Absent</i>	5	20	80%
			<i>Overall</i>	70%

Owing to the difference in predictive capability of the Dryandra model, I conducted a separate logistic regression analysis on the 50 Julimar sites to determine if any other habitat variables were important in explaining the habitat use of treecreepers. In this analysis, I followed the procedures described in Section 4.3.2

and used the composite variables NSITE and TAGE. Interestingly, a different predictive model was derived from the Julimar data. This model included NSITE and PSC as the best predictors explaining the greatest amount of variance in the data. The model was highly significant ($\chi^2_2 = 96.14$, $P < 0.001$), explained 93.2% of variance (Nagelkerke R^2) and had an overall predictive capability of 94.3%. The relationship with percent shrub cover was negative, indicating that treecreepers were unlikely to occur at sites with a high shrub density.

4.3.3 Nest sites

Development of the nest-site model

A summary of the values of each nest-site characteristic is included in Table 4.12. None of the variables were highly (≥ 0.70) correlated and all were included in the logistic regression analysis. The final model included the variables SPNG and SIZE (Table 4.13). This model was significantly different from the constant-only model ($\chi^2_2 = 11.4$, $P < 0.01$) and not significantly different from the perfect model (Hosmer-Lemeshow goodness-of-fit $C_7 = 10.7$, $P = 0.151$), but it only explained 24.9% of variance in the data (Nagelkerke R^2). Treecreepers tended to use hollows as nest sites if the spout angle was $\geq 50^\circ$ (82% of hollows, $n = 48$) and the horizontal diameter of the entrance hole was 5 – 10 cm (72% of hollows).

Table 4.12 The values of each nest-site characteristic (mean \pm s.e.) and a summary of the transformations conducted prior to logistic regression analysis. Numbers in brackets are sample sizes. Aspect is not included in the table.

Nest-site characteristic	Code	Status		Transformation
		Used (90)	Unused (90)	
Tree DBH (cm)	DBH	46.8 \pm 1.89	47.6 \pm 2.24	
% deadwood	DWD	37.2 \pm 2.99	45.9 \pm 2.24	Arcsine
Tree height (m)	TRHE	16.3 \pm 0.48	15.5 \pm 0.58	
Number of hollows	NHOL	6.6 \pm 0.58	5.3 \pm 0.48	Square root
Hollow height (m)	HOHE	8.5 \pm 0.37	8.3 \pm 0.35	
Relative height of hollow (m)	REHE	0.5 \pm 0.21	0.6 \pm 0.03	
Spout angle ($^\circ$)	SPNG	67.9 \pm 2.53	50.2 \pm 3.30	Log ₁₀
Size (cm)	SIZE	7.2 \pm 0.31	9.1 \pm 0.65	
% canopy cover	CANC	37.6 \pm 3.39	36.1 \pm 3.40	

Table 4.13 The variables included in the final nest-site model showing values of the Wald statistic, levels of significance (sig.) and proportion of variance explained (R).

Variables	Coefficients	s.e.	Wald _{df}	sig.	R
Constant	-2.6087	1.1346	5.29 ₁	0.0215	
SPNG	1.8440	0.6691	7.60 ₁	0.0058	0.2051
SIZE	-0.0496	0.0425	4.15 ₁	0.0423	0.1246

The error rate, sensitivity and specificity of the final model were 32.2%, 81.3% and 54.2% respectively (Table 4.14). There were many hollows where the treecreeper was predicted to nest, but was not recorded nesting during the study. This result probably reflects the high number of potential nest hollows in my study area (based on the characteristics I measured) and the short duration of the study.

Table 4.14 The predictive capability of the final nest-site model showing overall percentage of correct predictions and measures of sensitivity and specificity ($n = 96$).

		Predicted		
		Present	Absent	% correct
Observed	Present	39	9	81.3%
	Absent	22	26	54.2%
		Overall		67.8%

Validation of the nest-site model

The predictive capability of the nest-site model developed from the data from the 30 study territories was assessed using data collected outside the main study area. The value of Logit (P) was calculated as

$$\text{Logit}(P) = -2.6087 + 1.8440(\text{SPNG}) + -0.496(\text{SIZE}).$$

Probability of use values were calculated and compared to actual use of nest sites for the new data set ($n = 84$). The overall predictive capability of the nest-site model when applied to the new data was similar to its original predictive capacity (Table 4.15). Once again the model predicted true presence a lot more successfully than true absence. A separate logistic regression analysis was run on the new data set to attempt to identify further variables that may explain nest hollow use of the treecreeper, but once again SPNG and SIZE provided best model fit.

Table 4.15 The predictive capability of the nest-site model derived from the 30 study territories when applied to data from outside the study area. Table shows overall percentage of correct predictions and measures of sensitivity and specificity ($n = 84$).

		Predicted		
		<i>Present</i>	<i>Absent</i>	% correct
Observed	<i>Present</i>	37	5	88.1%
	<i>Absent</i>	24	18	42.9%
		<i>Overall</i>		65.5%

4.4 DISCUSSION

4.4.1 Woodland type

The Rufous Treecreeper preferentially used Wandoo woodland in the Dryandra study area. Wandoo is also used by the species in other regions of the wheatbelt (Kitchener et al. 1982; Rose 1996) suggesting a close affinity with this woodland type. The importance of woodland habitat for birds in the wheatbelt is well recognised (Saunders and Ingram 1995; Arnold and Weeldenburg 1998). Wandoo woodland in particular harbours a number of species that have declined in the region since European colonisation (e.g., Yellow-plumed Honeyeater *Lichenostomus ornatus*, Western Yellow Robin *Eopsaltria griseogularis*, Crested Shrike-tit *Falcunculus frontatus*, Restless Flycatcher *Myiagra inquieta* and Jacky Winter *Microeca leucophaea*, pers. ob; Saunders and Ingram 1995). The preferential clearance of this woodland and associated woodlands (e.g., Salmon Gum) for agriculture is undoubtedly one of the main reasons why many of the bird species that use this habitat type are now uncommon in the wheatbelt.

Wandoo woodland was not used exclusively by treecreepers in Dryandra with the species being recorded in all other major woodland types. The Powderbark woodland sites used by the species were characterised by large trees, which are more likely to contain hollows for nesting (Figure 4.4). In Brown Mallet plantations, tree hollows were rare (a sample of > 1500 trees failed to yield a single hollow), although hollow-bearing stumps and logs were relatively common. This suggests two things: a) treecreepers may only use these plantations for foraging habitat; or b) they modify their nesting behaviour to use stumps and logs rather than tree hollows.

Nesting in hollow stumps or hollow logs on the ground has been observed in this species (Carnaby 1933; Serventy 1958).

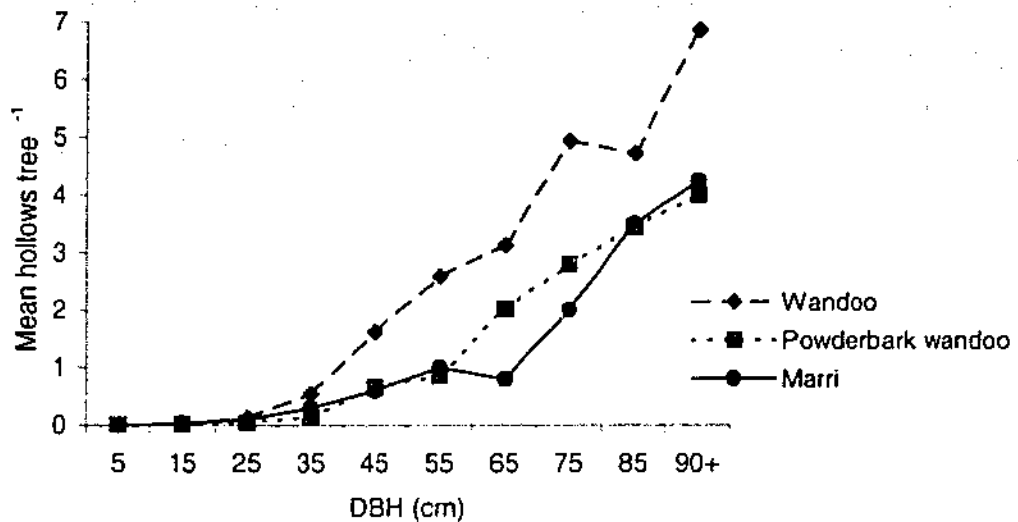


Figure 4.4 Relationship between the DBH of the three main hollow producing trees in Dryandra and the mean number of hollows per tree ($n = 2616$ – Wandoo, 1760 – Powderbark Wandoo and 348 – Marri).

In Dryandra, the survival rate of treecreepers during my study was relatively high and natality far outweighed adult mortality (Chapter 3). If these results are representative, the population density in Dryandra is likely to be high possibly resulting in reduced habitat selectivity (Rosenzweig 1991). Changes in the extent of use of non-preferred woodland types (e.g., Brown Mallet) may coincide with fluctuations in population density and the level of habitat saturation in Wandoo woodland.

Powderbark woodland and Brown Mallet plantations have a superficial structural resemblance to Wandoo. Both have a sparse understorey with a well developed litter layer and varying amounts of coarse woody debris. The treecreeper may prefer to use open habitats because it spends an extensive amount of time foraging on the ground (Appendix 4.1) and habitat openness may improve predator surveillance. Reduced visual occlusion may also assist in maintaining contact between group members and is a possible contributing factor to the evolution of cooperative breeding in this species (Cockburn 1996). Importantly though, the species uses a variety of habitat types throughout its distribution including the Jarrah and Karri *E. diversicolor* forests of the southwestern corner of Western Australia.

These forests are not as open as the woodland habitats used in the drier parts of its range and the habitat characteristics that correlate with the presence of the species in these regions are yet to be determined.

4.4.2 Territory use

Woodland type was not a significant predictor of treecreeper territory use because the species was recorded using woodland types other than Wandoo and was absent from some Wandoo sites. Territory use was correlated with particular structural characteristics of the woodland. Areas were preferred if they contained a high density of Wandoo canopy trees, hollows and hollow logs, large trees and a relatively large biomass of standing deadwood. This result is reinforced by the fact that Wandoo sites not containing treecreepers had lower mean values of these characteristics (Table 4.10).

The collinear variables Wandoo canopy density and hollow density were interpreted as representative measures of nest site availability, and tree size and deadwood biomass as measures of tree age. It could also be argued that all of the characteristics that correlated with treecreeper habitat use are surrogates for woodland age, and to a lesser extent lack of disturbance. Undisturbed, old growth Wandoo woodland would undoubtedly contain the important features identified in my study and probably represents extremely important habitat for the Rufous Treecreeper.

It is widely recognised that old growth habitat is important for hollow-nesting species (Saunders et al. 1982; Sedgwick and Knopf 1990; Pell and Tidemann 1997; Shackelford and Conner 1997). However, the relationship between tree size, age and the formation of hollows is a contentious issue (Mawson and Long 1994, 1997; Stoneman et al. 1997) and hollow formation for a particular tree species may vary throughout its range owing to different edaphic and climatic conditions (Saunders et al. 1982; Bennett et al. 1994). In Dryandra, the minimum DBH of a Wandoo tree that provided a nesting hollow for the Rufous Treecreeper was 20 cm with an average DBH of 46 (± 1.89) cm. Acknowledging potential limitations, Rose (1993) estimated that Wandoo trees of this size, in Dryandra, would be 60 and 150

years of age respectively. Therefore, younger stands of Wandoo may not be suitable breeding habitat for the treecreeper and other hollow-nesting species.

In addition to tree hollows, undisturbed, old growth Wandoo woodland contains other important structural characteristics that may influence treecreeper habitat use. The relatively high density of hollow-bearing logs is important for predator avoidance. Hollow logs are used extensively as shelter and protection from predators by fledgling and adult treecreepers (Chapter 5). This is probably one reason why the density of hollow logs was a better predictor of territory use than overall log biomass.

Large trees and a substantial amount of standing deadwood biomass may also be important determinants of treecreeper habitat use. Treecreepers preferentially selected larger trees for foraging, and standing deadwood was a common foraging substrate particularly in autumn (Appendix 4.1). Large trees are recognised as being important foraging and nesting resources for a number of Australian and Northern Hemisphere bird species (Kavanagh et al. 1985; Braithwaite et al. 1989; Sedgwick and Knoff 1990; Ford and Barrett 1995; Steeger and Hitchcock 1998; Flemming et al. 1999; Weikel and Hayes 1999).

How old must a woodland be before it provides all of these important characteristics? If the relationship between tree DBH and hollow formation is all that is considered, somewhere between 60 – 150 years appears to be the minimum age required for Wandoo woodland to be suitable for treecreeper use. However, the time between seedling establishment to the formation of hollow logs, especially logs in differing levels of decay, probably takes centuries (Abensperg-Traun and Smith 1993). The structural complexity of old growth woodland (combining elements such as litter depth, moss and lichen cover, woody debris and logs, bark structure, standing deadwood and hollows) is also likely to take, at a minimum, hundreds of years to develop. This has significant implications for habitat restoration in degraded regions like the Western Australian wheatbelt, where habitat recovery is likely to be a long-term process.

An important caveat to the results presented here is that I only considered structural characteristics in my habitat models. These characteristics had strong correlations with the presence of Rufous Treecreepers, but they may not be the

actual variables influencing the habitat use of the species (i.e., they may be surrogates for other important factors such as food availability). Also, I did not consider species interactions (e.g., competition and predation), which may affect habitat use (Mac Nally 1990). Identifying the actual variables influencing a species' distribution requires comprehensive data collection and may be difficult if these variables are consistently correlated with other habitat characteristics. There appeared to be no obvious interspecific interactions affecting the habitat use of the treecreeper in Dryandra.

4.4.3. Nest sites

In the majority of cases, hollows used for nesting by the treecreeper had specific characteristics (i.e., a spout angle $\geq 50^\circ$ and an entrance size between 5 – 10 cm) and the nest-site model did a reasonable job at predicting the kind of hollows that the species was likely to use. The relatively poor performance of the model in predicting true absence from a hollow was probably influenced by two major factors: a) potential nest hollows are abundant in Dryandra; and b) the short duration of my study.

In the Northern Hemisphere, the population density of secondary cavity-nesting species (i.e., those that do not excavate their own cavity) is often considered to be limited by the availability of cavities (Newton 1994; Pribil 1998). However, some experimental and observational studies suggest this is not always the case (Waters et al. 1990; Welsh and Capen 1992) and variability between studies probably reflects differences in habitat structure and age. Research on hollow-nesting birds in Australia has found that hollow abundance is probably not a factor limiting population density (Saunders 1979; Saunders et al. 1982). In my study area, hollow density was relatively high ($91 \text{ ha}^{-1} \pm 6.70$) and the average treecreeper territory (2.6 ha) probably contained many potential nest hollows. These data should be interpreted with caution because the method I used for identifying hollows (i.e., scanning trees from the ground with binoculars) is limited. Hollows facing skywards are likely to be missed and, conversely, holes in branches that appear to be hollows from the ground may only be shallow depressions.

An abundance of suitable hollows would weaken statistical power in identifying important characteristics influencing hollow selectivity (Pribil 1998). The relatively short duration of my study places another limitation on the interpretation of treecreeper hollow use because a certain proportion of hollows that were not used during the study may be used in the future. Also, I only measured the external characteristics of hollows owing to the difficulty of direct access. Treecreepers probably require hollows with particular internal characteristics (e.g., depth of hollow).

Despite these limitations, the statistical correlations between treecreeper hollow use and spout angle and entrance size probably reflect important biological relationships. An angle of $> 50^\circ$ ensures that the nest cup is close to parallel with the ground, thereby providing a relatively stable platform on which to lay the eggs (see Figure 3.5 in Chapter 3). An entrance size of 5 – 10 cm allows easy hollow access by adult birds, reduces predation risk by larger nest predators such as the Common Brushtail Possum *Trichosurus vulpecula*, and ensures greater protection of the nest from adverse climatic conditions (e.g., rain) than hollows with larger entrance sizes.

4.4.4 Spatial scale and habitat use

The Rufous Treecreeper uses a range of woodland and forest types throughout its distribution. However, within any given region or landscape the species may preferentially use a particular habitat type, as was found in my study. At a finer spatial scale, territory and nest-site selection, and foraging behaviour may be influenced by structural characteristics of the habitat. The focus of my study was on spatial rather than temporal scale variation, although I did identify temporal (seasonal) differences in the use of foraging substrates within territories (Appendix 4.1).

Non-random habitat use at multiple spatial scales indicates that investigations confined to a single scale are misleading and a hierarchical approach should be adopted (Kotliar and Wiens 1990; Figure 4.5). Potential scales of habitat use probably represent a continuum, but partitioning into discrete units facilitates interpretation (Wiens et al. 1987).

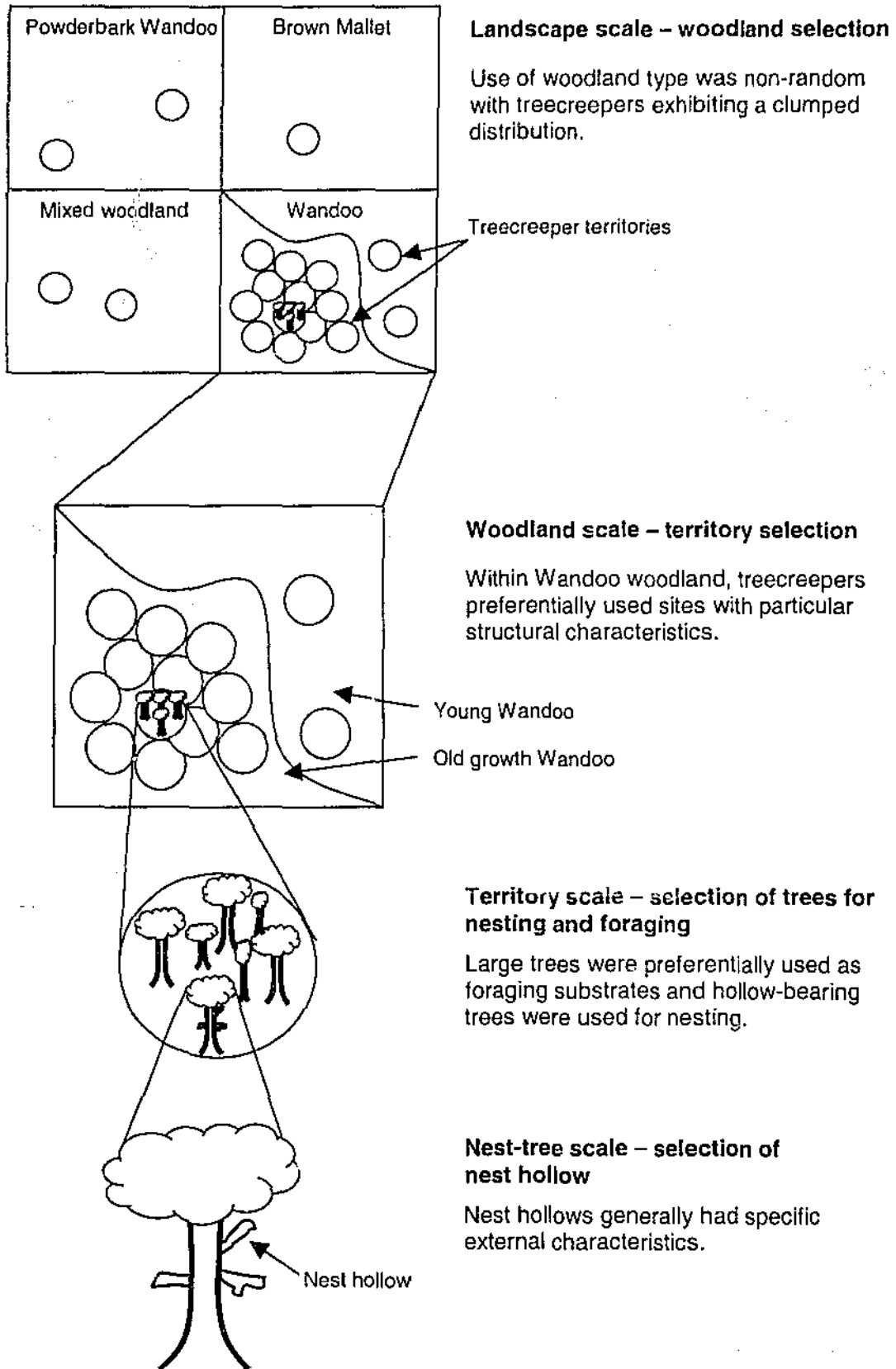


Figure 4.5 A hierarchical analysis of Rufous Treecreeper habitat use. Non-random use was exhibited at each spatial scale.

For the Rufous Treecreeper, interpretations of habitat use are scale dependent and different selection processes operate at different scales, as has been found for other bird species (Bergin 1992). Orians and Wittenberger (1991) suggested that nest-site selection drives habitat use decisions at larger spatial scales because individuals are committed to a nest site for the duration of the nesting attempt. The availability of nest sites is often recognised as one of the most important limiting factors in the habitat use of birds (Sedgewick and Knopf 1990; Bergin 1992; Matsuoka et al. 1997). However, for sedentary species that occupy all-purpose territories, which must provide suitable nesting *and* foraging habitat, territory choice is a key factor. This is particularly the case for Rufous Treecreepers in Dryandra because breeding birds occupy territories for extended periods, territory quality is positively correlated with reproductive success (Chapter 5), and potential nest sites do not appear to be limited.

4.4.5 The performance of habitat models

Misclassification of suitable and unsuitable habitat is inevitable in any habitat modelling procedure (Fielding and Haworth 1995). This may reflect a number of factors including inherent problems in the model, a level of flexibility in the habitat use of the species being studied, failure to identify important habitat characteristics, or temporal variation in habitat use. Misclassification in the Dryandra territory model was a result of treecreeper presence in non-Wandoo sites that shared structural similarities with the species' preferred habitat, or absence in apparently suitable Wandoo sites. Absence from suitable habitat may reflect stochastic or deterministic localised extinction of groups or neighbourhoods.

When applied to the Julimar data, the territory model derived in Dryandra predicted true absence more successfully than true presence. Out of the 25 sites that contained treecreepers, 40% were considered unsuitable habitat by the model and all of these were in Wandoo woodland. In addition to the factors listed above, this result may reflect limitations in the survey method (i.e., a single, snapshot survey), small sample size, regional variation in habitat use or differences in land-use history. Compared to Dryandra, Wandoo patches in Julimar have been extensively logged and there is a dearth of large, presumably older trees. Logging activities would also

result in the removal of downed wood contributing to the structural differences between the Wandoo woodlands of Julimar and Dryandra (Table 4.7).

In contrast to the Dryandra model, the subsequent logistic regression analysis conducted on the Julimar data identified shrub cover as an important predictor of treecreeper habitat use. Sites containing treecreepers had lower percent cover than those where the species was absent, but percent shrub cover in the Julimar and Dryandra used sites was similar (Table 4.7). The probable reason that this variable was included in the Julimar analysis was that most of the sites without treecreepers had a relatively high percent cover of shrubs, whereas in Dryandra most non-preferred sites had sparse shrub cover similar to Wandoo woodland. Hence, used and non-used sites may differ in a number of ways and these differences may vary from one region to another reflecting landscape heterogeneity.

Importantly, structural differences in used and non-used sites may be readily identified by procedures such as logistic regression, but these differences may vary from region to region confounding interpretations about which characteristics actually influence the habitat use of a species. To improve our understanding of bird-habitat relationships, modelling should be an iterative procedure whereby the development, validation, refinement and re-validation of models is an ongoing process until consistent patterns in habitat use are identified. For example, nest-site abundance was considered a significant predictor of treecreeper habitat use in Dryandra and Julimar (Section 4.3.2) and future habitat modelling may confirm its importance in other wheatbelt landscapes.

Species like the Rufous Treecreeper that show strong site fidelity may continue to use particular habitat types even after these habitats have been modified. Current distribution may reflect past species-habitat associations, and there may be a time lag between date of modification and the eventual disappearance of a species (Knick and Rotenberry 2000). Species may also exhibit resilience thresholds where modified habitat remains suitable up to a point. These possible relationships further complicate interpretations of habitat modelling and validation, but testing the predictive capability of habitat models between closely related sites in the same region limits the generality of any conclusions and their value to conservation managers.

***Appendix 4.1 SEASONAL AND LANDSCAPE DIFFERENCES
IN THE FORAGING BEHAVIOUR OF THE RUFOUS TREECREEPER***

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In press in Pacific Conservation Biology

Summary

The insectivorous Rufous Treecreeper has declined in abundance in the agricultural regions of southwestern Australia. Examining its foraging behaviour is fundamental to identifying important foraging resources and how landscape change (e.g., fragmentation and disturbance) may influence foraging effectiveness. We studied seasonal and landscape differences in the foraging behaviour of the treecreeper in the wheatbelt of Western Australia. Foraging data were collected in autumn and winter in a large, unfragmented landscape and in a highly modified agricultural landscape (winter only) with grazed and ungrazed woodland remnants.

The ground layer was the most common foraging location used by the species, but there were seasonal differences in foraging behaviour in the unfragmented landscape. In autumn, treecreepers foraged primarily on trees (56% of observations) with a shift to mostly ground foraging in winter (72 – 74%). The species also preferentially foraged on larger trees. Foraging behaviour differed between the two landscapes within the same season. Treecreepers foraged less on the ground in the agricultural landscape (52%), but this difference is attributed mainly to the low percentage of ground foraging in ungrazed (43%) compared to grazed (60%) remnants.

In winter and early spring, the ground layer is an important foraging substrate for the Rufous Treecreeper and other woodland birds. Changes to the ground layer and associated invertebrate communities through habitat disturbance (e.g., weed invasion) may be detrimental to the foraging effectiveness of ground-foraging insectivores. This is a potential contributing factor to the decline of these species in the agricultural regions of southern Australia.

Introduction

Woodland bird species are declining in abundance in the agricultural regions of southern Australia (Saunders and Curry 1990; Barrett et al. 1994; Robinson and Traill 1996; Recher 1999) and recent research suggests that ground-foraging insectivores may be particularly affected (Reid 1999). The Rufous Treecreeper, an insectivorous bird species dependent on the temperate forests and woodlands of southern Australia, has declined dramatically in abundance since the advent of agriculture and urbanisation (Storr 1991; Saunders and Ingram 1995). This is especially the case in the wheatbelt of Western Australia where low-lying, open woodlands often used by the species (e.g., Wandoo *Eucalyptus wandoo* and Salmon Gum *E. salmonophloia*) have been preferentially cleared for agriculture (Kitchener et al. 1982; Saunders and Curry 1990; Hobbs and Mooney 1998).

Studies of foraging behaviour that determine the importance of different foraging resources are vital in developing conservation strategies to ensure the persistence of avian species (Recher 1991). Community-level foraging studies have included descriptions of the foraging behaviour of the Rufous Treecreeper. A study by Wykes (1985) conducted in Jarrah *E. marginata* forest found that the species was primarily a bark-forager, although it exhibited seasonal shifts in its use of foraging substrates. Recher and Davis (1998), who collected data in the same Wandoo woodlands that comprise our study area, recorded 70% of their observations as ground foraging. However, Recher and Davis confined their study to a single season (early spring) thus precluding the examination of seasonal variation in foraging behaviour. Our study complements this research, as we present foraging data for autumn and early-mid winter, which will add to our knowledge of seasonal differences in the use of foraging substrates by this species.

Another important component of our study is the analysis of landscape differences in foraging behaviour. We compared foraging behaviour between a continuously vegetated, relatively undisturbed landscape and a highly modified agricultural landscape with small remnants of grazed and ungrazed woodland. This analysis is part of a broader study on landscape differences in the ecology of the Rufous Treecreeper, which considers the effects of landscape alteration on social organisation, habitat selection, reproductive success and dispersal. Comparative

studies such as these contribute significantly to our understanding of the effects of habitat alteration on a species behaviour and ultimately population persistence.

The specific aims of our study were to examine:

- a) the foraging manoeuvres, locations and substrates used by the Rufous Treecreeper;
- b) within landscape and within season differences in foraging behaviour;
- c) seasonal differences in foraging behaviour in the unfragmented landscape; and
- d) landscape differences in foraging behaviour.

Study Sites

Our study was conducted in two different landscapes in the western wheatbelt of Western Australia. There are varying definitions of “landscape” based primarily on the spatial or organisational properties of a given area (see Wiens 1997 and references therein). Our use of the term is species specific and refers to a scale that is relevant to the spatial organisation of the Rufous Treecreeper.

The first landscape was located in Dryandra Woodland approximately 160 km southeast of Perth (centred on 32°45'S, 116°55'E). Dryandra is made up of 17 blocks of native vegetation and is one of the largest, most diverse and relatively undisturbed bushland areas in the wheatbelt (Department of Conservation and Land Management 1995). As part of the broader study on the ecology of the Rufous Treecreeper, an 8,500 ha study area was delineated in the largest block (12,283 ha) of continuous habitat. Vegetation in the study area consists mostly of open eucalypt woodland with Wandoo, Powderbark Wandoo *E. accedens* and Brown Mallet *E. astringens* as the predominant species (see Coates 1993 for a more detailed vegetation description).

Three study sites (2 – 5 km apart) were established in this larger area. Each site was located in Wandoo woodland and had 10 contiguous territories (30 territories per landscape) containing colour-banded, resident treecreepers. The ecological traits of the treecreepers in these sites differed in certain aspects (e.g., reproductive success) and we considered it appropriate to examine foraging differences between sites.

The second landscape was in the Yilliminning agricultural district (centred on 32°54'S, 117°24'E) located approximately 35 km east of Dryandra. A 10,000 ha study area was delineated comprised of remnant woodland habitat (e.g., Wandoo, Brown Mallet, Salmon Gum and Morrell *E. longicornis*) embedded in a matrix of agricultural land used primarily for cropping and sheep grazing. This study area also contained 30 treecreeper territories with colour-banded residents. These territories were distributed among 10 woodland remnants (nine remnants < 100 ha, one remnant < 250 ha) with 15 territories each in grazed and ungrazed woodland. "Grazed" remnants were located in paddocks that were subject to annual or biannual grazing by sheep. "Ungrazed" remnants had been free from stock grazing for at least 15 years. We differentiated between grazed and ungrazed remnants because grazing may significantly alter vegetation structure (Wilson 1990) potentially influencing the foraging behaviour of birds.

Methods

Study design

Our study was conducted in two parts. In 1998, PE collected data at the three study sites in Dryandra from June 1 – 12 and July 6 – 17. In 1999, AC collected data in Dryandra from May 3 – 14 (autumn) and in Dryandra and Yilliminning from June 7 – 18 and July 12 – 23 (winter). For the first part of the study (1998), we tested for differences between the three study sites and the 2 months (within landscape and season variation). For the second part (1999), we examined seasonal differences in foraging behaviour within Dryandra, and landscape differences within the same season (winter). When analysing landscape differences, we recognised three habitat contexts: "Dryandra" (unfragmented and ungrazed); "ungrazed" (fragmented and ungrazed); and "grazed" (fragmented and grazed).

Foraging observations

Foraging observations were made between 0730 – 1630 hrs in fine weather conditions. Data were collected in the treecreeper territories containing colour-banded birds and in adjacent territories to increase sample size. Visits to the three study sites in Dryandra and the grazed and ungrazed sites in Yilliminning were conducted on a systematic, rotational basis in morning (0730 – 1200 hrs) and

afternoon (1200 – 1630 hrs) shifts. Additional visits were made to some study sites to ensure a similar number of observations for each and an even distribution between morning and afternoon visits.

Territories within a site were also visited on a systematic and rotational basis. In each territory, a single foraging observation was taken regardless of the number of territory residents (Rufous Treecreepers live in groups of between two to seven individuals; Chapter 3). The observer then moved to the next territory. With this method, a period of at least 60 minutes elapsed before the same territory was visited again. After locating a bird, the observer waited for 30 seconds before taking a foraging datum to avoid recording mostly conspicuous behaviours that may have initially attracted the observer's attention (Recher and Gebski 1990).

Single observations were taken from foraging birds because sequential observations are generally not considered as statistically independent (Morrison 1984; Hejl et al. 1990). However, as we revisited sites and territories, we inevitably recorded multiple observations from the same individuals (generally we could not identify individual birds when collecting foraging data) resulting in pseudoreplication problems (Ford et al. 1990). We attempted to address this limitation by increasing the number of territories (and individuals) sampled and maximising the number of foraging observations recorded at each site. The number of individuals from which foraging observations could potentially be obtained was approximately 150 at Dryandra and 100 at Yilliminning.

Foraging manoeuvre, location and substrate

For each observation, we recorded foraging manoeuvre, location and substrate. A foraging manoeuvre was recorded if it was considered that an individual had obtained or attempted to obtain a prey item (following Recher et al. 1985). Rufous Treecreepers have two main foraging manoeuvres; glean (obtaining prey from the substrate surface often while moving rapidly) and probe (inserting bill into the soil, litter or ground vegetation, under bark or in crevices in trees or logs). They have also been observed hawking and hang-gleaning (GL pers. ob; see Recher et al. 1985 for a description of foraging manoeuvres).

Foraging location was divided into five categories, which corresponded approximately to foraging height: 1) ground (< 0.1 m); 2) log (mostly < 1 m); 3)

trunk (the main stem of primarily eucalypt trees, mostly $0.1 \text{ m} < 5 \text{ m}$); 4) branch (other than the main stem of a tree, mostly $5 \text{ m} < 10 \text{ m}$); and 5) canopy (upper branches and foliage, mostly $\geq 10 \text{ m}$). Foraging substrates were divided into four categories: 1) ground (ground vegetation $< 0.1 \text{ m}$ in height, leaf and bark litter, and woody debris $< 0.1 \text{ m}$ in diameter); 2) deadwood (standing deadwood and logs $\geq 0.1 \text{ m}$ in diameter); 3) bark (smooth, decorticating or fissured bark on the trunks and branches of woody vegetation – primarily eucalypt trees); and 4) foliage (branchlets, leaves, buds and flowers). For each foraging observation recorded on trees, we identified the species used, differentiated between live and dead substrates and measured the diameter at breast height (DBH) of the largest stem.

Vegetation measurements

In Dryandra and Yilliminning, data were collected on vegetation structure from 10, 20 m \times 20 m randomly located quadrats in each territory. Sample size was determined by an asymptotic relationship (i.e., the number of quadrats required per territory to stabilise the mean and standard error of the most variable habitat characteristic measured). In each quadrat, species, DBH of the largest stem, and height class (sapling $< 5 \text{ m}$, subcanopy $5 < 10 \text{ m}$ and canopy $\geq 10 \text{ m}$) were obtained for every tree. A 2 m high levy pole divided into 0.1 m height classes was used to measure ground and shrub cover at 20 evenly spaced (5 m) sampling points within each quadrat (a total of 200 samples per territory divided by two to give percent cover). At each sampling point, the pole was placed vertically and a substrate was recorded if it came in contact with the pole (i.e., presence/absence). The substrates were litter (leaves, bark and woody debris $< 0.1 \text{ m}$ in diameter), ground vegetation (herbs and annuals) and bare ground (each of these were considered as mutually exclusive), and dwarf ($< 0.5 \text{ m}$), small ($0.5 < 1 \text{ m}$), medium ($1 < 1.5 \text{ m}$) and tall ($\geq 1.5 \text{ m}$) woody shrubs (these were not mutually exclusive from each other or from the ground substrates, for example, litter, dwarf shrub and tall shrub could be recorded at the same sampling point).

Data handling and analysis

We used multiway frequency analysis (MFA) to examine differences in the foraging behaviour of the treecreeper. This analysis assesses relationships between

three or more categorical variables by comparing observed and expected use in each category. It can be considered an extension of the two-way χ^2 test of association, which is appropriate when there are only two categorical variables. In our analysis, we used MFA to “screen for effects”, as described by Tabachnick and Fidell (1996 p. 245), which involves examining differences between levels of a particular variable and interactions between variables (the extension of MFA, loglinear modelling, was not used). MFA computes a likelihood ratio statistic, G^2 , which is distributed as χ^2 . Therefore, we used χ^2 tables to evaluate significance.

We conducted three analyses. The first MFA tested for within season and within landscape differences in foraging behaviour in Dryandra 1998. The categorical variables in this analysis were foraging manoeuvre (two levels – glean and probe), foraging location (four levels – ground, log, lower tree < 5 m and upper tree \geq 5 m), site (three levels) and month (two levels – June and July). Foraging substrate was not used as a variable because it was highly correlated with foraging location. Specifically, we examined whether, based on our foraging observations, observed use of foraging manoeuvre and location differed from expected use (assuming equal use of manoeuvre and location), and if foraging behaviour differed between sites and months (i.e., were there any interactions between these four factors). For example, the treecreeper may favour gleaning, but only when it is foraging on the ground and only at site three in June.

In the second analysis, we examined seasonal differences in foraging behaviour for data collected in Dryandra in 1999. The categorical variables were season (autumn and winter), foraging manoeuvre and foraging location (the same levels as described above). The final analysis examined differences in foraging behaviour (manoeuvre and location) between the three habitat contexts for data collected in Dryandra and Yilliminning in winter 1999. In each analysis, foraging location was reduced to four levels to limit the number of cells with no observations and to ensure that the total number of observations was at least five times greater than the number of parameters generated by multiplying categorical variables by levels (Noon and Block 1990; Tabachnick and Fidell 1996). As we re-sampled the same sites, and data for Dryandra winter were used in two analyses (multiple

contrasts), we considered a more conservative value of α (0.01) to represent statistical significance.

We calculated Bonferroni confidence intervals (see Neu et al. 1974; Byers et al. 1984; and Cherry 1998 for a discussion of this method) to determine if treecreepers were using a particular size class of tree for foraging. Only data from Dryandra (1998 and 1999) were used in this analysis and all measurements are from Wandoo trees (the most common tree in the study sites). Based on DBH measurements, the tree-size classes were small (< 0.11 m), medium ($0.11 < 0.24$ m) and large (≥ 0.24 m). These correspond approximately to the height class of trees (i.e., 87% of saplings were in the small, 84% of subcanopy trees were in the medium and 87% of canopy trees were in the large size class).

Data represented as proportions that sum to one are not independent (the “unit-sum constraint”, Aitchison 1986; Aebischer et al. 1993). This is the case for the proportional use of the different tree-size classes in Dryandra. To overcome this, proportions can be transformed to independent log-ratios using the equation

$$y_i = \ln(x_i/x_j).$$

Here, x_i is the proportion of tree-size class i and x_j is the proportion of tree-size class j , which is used as the denominator in each transformation. Also, a ranking matrix (from most to least preferred) can be constructed using the equation

$$\ln(x_{ui}/x_{uj}) - \ln(x_{ai}/x_{aj}).$$

Here, x_{ui} and x_{uj} are the used proportions of tree-size class i and j respectively, and x_{ai} and x_{aj} are the available proportions (see Aebischer et al. 1993 for more details). We used this method to confirm the results of the confidence interval analysis and to rank tree-size classes from most to least preferred.

Proportions of litter, bare ground and ground vegetation are also not independent and were transformed to log-ratios before analysis. We used multiple analysis of variance (MANOVA) to test for an overall difference in ground and shrub cover (arcsine transformed) between the three habitat contexts. This difference was significant ($F_{8,104} = 21.06$, $P < 0.001$); therefore, we used univariate analysis of variance (ANOVA) to determine differences in each cover type, and Tukey’s honestly significant difference (HSD) test for unequal sample sizes to determine differences between each habitat context.

Results

Within season and landscape differences in foraging behaviour

A total of 360 observations (120 per site, 180 per month) were recorded for the surveys conducted in June and July in Dryandra. There were significant differences in foraging manoeuvre and location, and significant interactions between manoeuvre \times month and manoeuvre \times foraging location \times month (Table 1). Rufous Treecreepers used glean (76%) rather than probe (24%) as their primary foraging manoeuvre (these proportions are consistent with all of the data collected in our study). The significant interactions involving manoeuvre, month and foraging location indicate a change in foraging behaviour between months. Treecreepers probed more in July (38%) than June (10%) and this difference is associated mostly with an increase in probing on the ground (from 5% in June to 31% in July).

Table 1 Within season differences in foraging behaviour in Dryandra 1998. Results indicate that observed use of particular foraging manoeuvres (glean vs probe) and locations (ground, log, lower tree and upper tree) differed from expected use. Interactions indicate that foraging manoeuvre differed between months, but only for particular foraging locations (see text).

Main effects and interactions	G^2	df	P
Manoeuvre	44.8	1	< 0.001
Foraging location	196.1	3	< 0.001
Manoeuvre \times Month	19.4	1	< 0.001
Manoeuvre \times Month \times Foraging location	16.4	3	< 0.001

The significant difference in foraging location can be attributed to the majority of our observations being recorded as ground foraging (Figure 1a). Only 21% of foraging observations were on trees and 5% on logs. For all of the data collected, treecreepers were rarely recorded foraging directly on logs. When not foraging on the ground, treecreepers used bark (10%) and deadwood (14%) as their primary foraging substrates (Figure 1b).

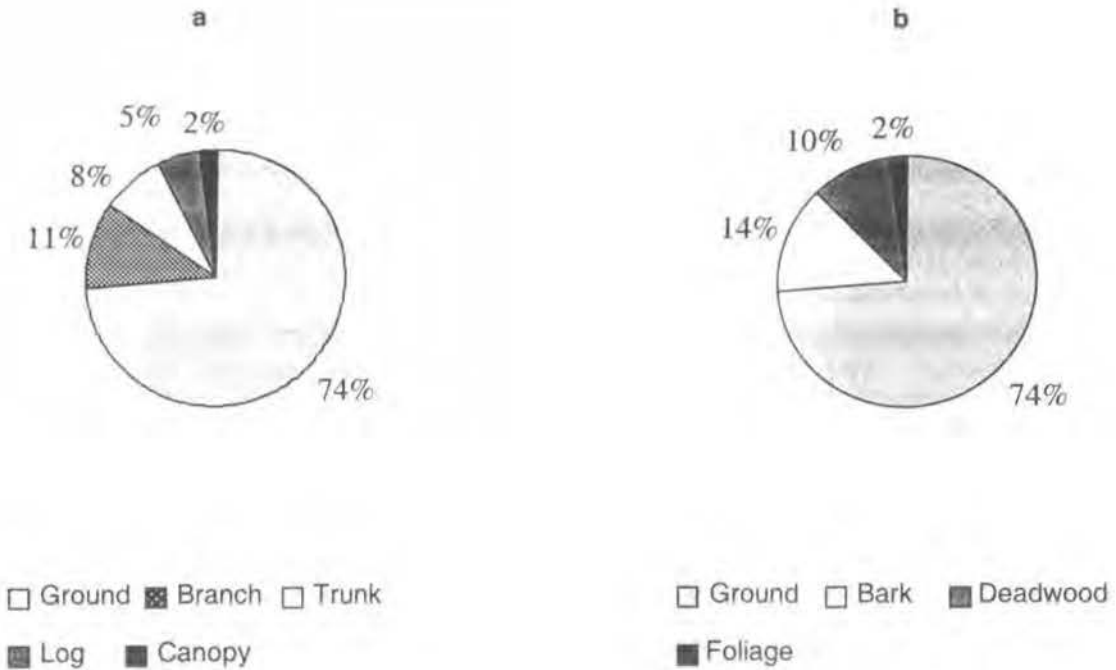


Figure 1 Percent use of: a) foraging locations, and b) foraging substrates in Dryandra in winter 1998 ($n = 360$).

Seasonal differences in foraging behaviour

As there were no significant differences between sites in Dryandra (1998), we pooled the data for all sites within a particular season in 1999. To increase sample size, we also pooled the data for June and July (treated together as “winter”) even though the previous analysis showed a difference in foraging manoeuvre between months. This was because we were primarily interested in differences in foraging location rather than manoeuvre. A total of 156 foraging observations were collected in autumn and 150 in winter in Dryandra.

There were significant differences in foraging manoeuvre and location (Table 2), as the majority of observations were of treecreepers gleaning on the ground. There was also a significant interaction between season and foraging location (Table 2). In autumn, 56% of our observations were of treecreepers foraging on trees (trunk, branch or foliage) and only 38% were of ground foraging, whereas in winter, ground foraging increased to 72% (Figure 2a and b). Treecreepers used bark and deadwood in relatively even proportions within a given season, although overall use of these substrates was greater in autumn (Figure 3a

and b). Also in autumn, the use of foliage as a foraging substrate (7%) was the highest recorded in our study.

Table 2 Seasonal differences in foraging behaviour in autumn and winter in Dryandra 1999. Results for foraging manoeuvre and location per Table 1. The interaction indicates that foraging location differed between seasons (see text).

Main effects and interactions	G^2	df	P
Manoeuvre	78.1	1	< 0.001
Foraging location	69.7	3	< 0.001
Foraging location × Season	17.7	3	< 0.001

Landscape differences in foraging behaviour

Another 300 foraging observations (150 each in ungrazed and grazed remnants) were collected in Yilliminning during winter to compare with data collected in Dryandra in the same year and season. In addition to the significant differences recorded for foraging manoeuvre (more gleaning than probing) and location (foraging primarily on the ground), there was a significant interaction between foraging location and habitat context (Table 3). Treecreepers foraged less on the ground in Yilliminning than Dryandra (Figure 2b, c and d). The proportion of ground foraging was lowest in ungrazed woodland (43%), but relatively similar between grazed woodland (60%) and Dryandra (72%). In ungrazed remnants, treecreepers used bark as their primary foraging substrate (45%) rather than using bark and deadwood in relatively even proportions, as was recorded at other sites (Figure 3b, c and d).

Table 3 Landscape (habitat context) differences in foraging behaviour between Dryandra and Yilliminning in winter 1999. Results for foraging manoeuvre and location per Table 1. The interaction indicates that foraging location differed between habitat contexts (see text).

Main effects and interactions	G^2	df	P
Manoeuvre	97.6	1	< 0.001
Foraging location	115.6	3	< 0.001
Foraging location × Habitat context	14.9	3	< 0.01

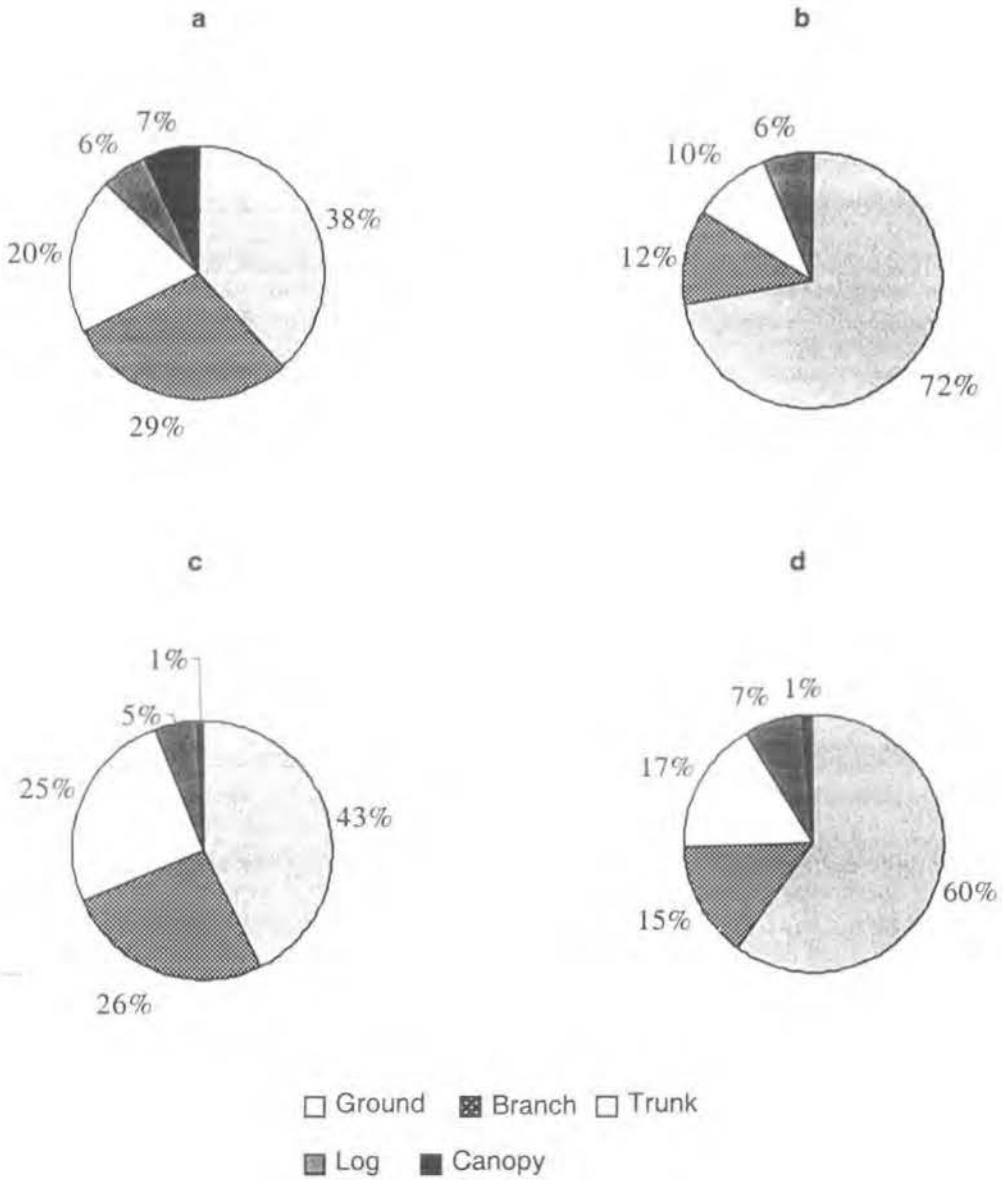


Figure 2 Foraging locations used in: a) Dryandra autumn ($n = 156$), b) Dryandra winter ($n = 150$), c) Yilliminning ungrazed winter ($n = 150$), and d) Yilliminning grazed winter ($n = 150$) in 1999.

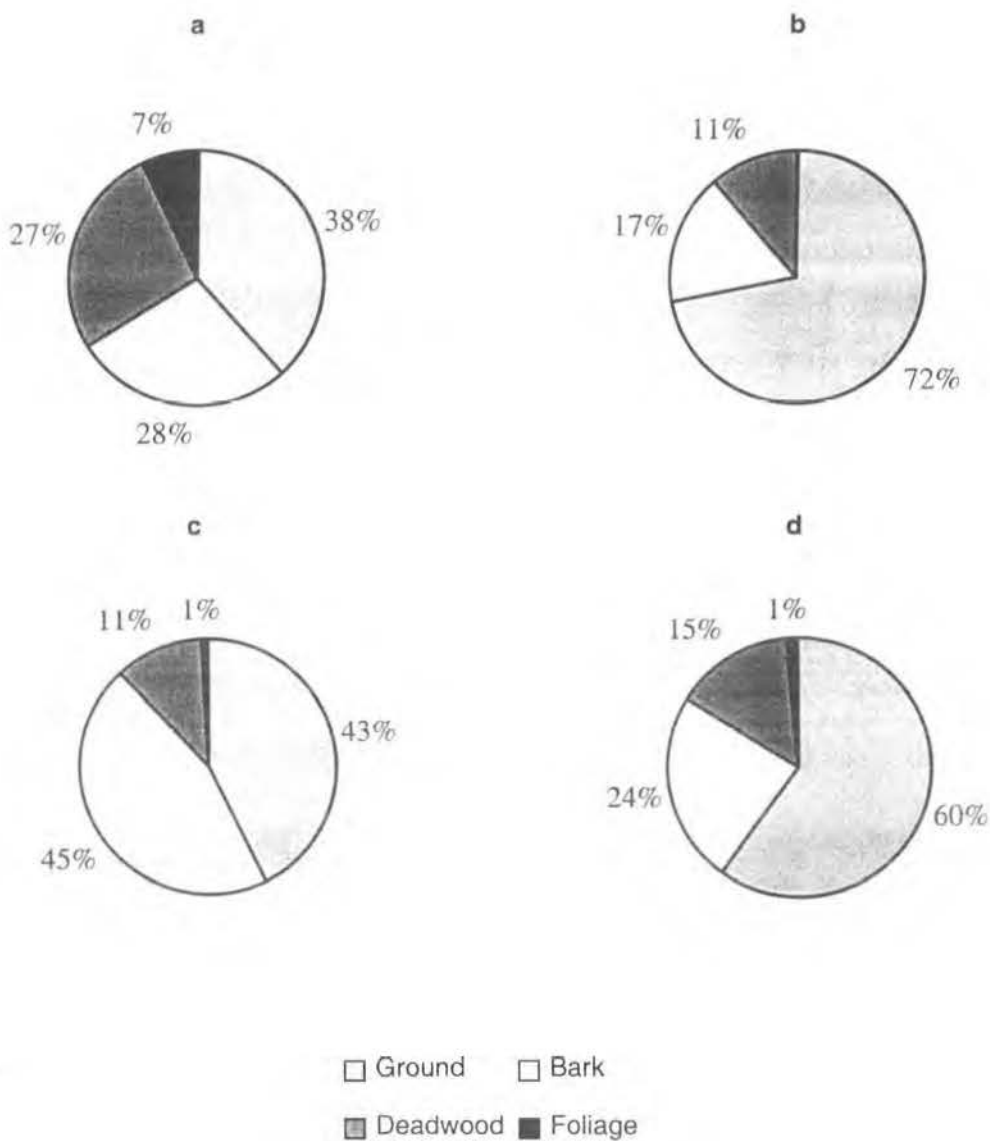


Figure 3 Foraging substrates used in: a) Dryandra autumn, b) Dryandra winter, c) Yilliminning ungrazed winter, and d) Yilliminning grazed winter in 1999.

Tree use

We obtained DBH measurements from 2256 Wandoo trees in the 30 territories in Dryandra and 197 foraging records of treecreepers on this eucalypt. Based on the availability of our pre-defined size classes, the proportional use of small and medium-sized wandoo trees was less than expected and large trees more than expected (Figure 4). This result was confirmed by the ranking matrix of log-ratios, which ranked large wandoo trees as the most preferred and small wandoo trees as the least. The proportional use of size classes at Yilliminning was almost the same as that recorded in Dryandra (i.e., small: 9.4%; medium: 32%; large: 58.6%).

Compared to the Dryandra territories, which contained predominantly Wandoo trees, the Yilliminning territories had a greater diversity of eucalypt species. However, treecreepers did not preferentially forage on any particular species. The availability-use of the three most common species (Wandoo, Morrell and Salmon Gum; availability $n = 1648$, use $n = 72$) was 55.6%-48.3%, 22.7%-15.4% and 10.8%-14.5% respectively.

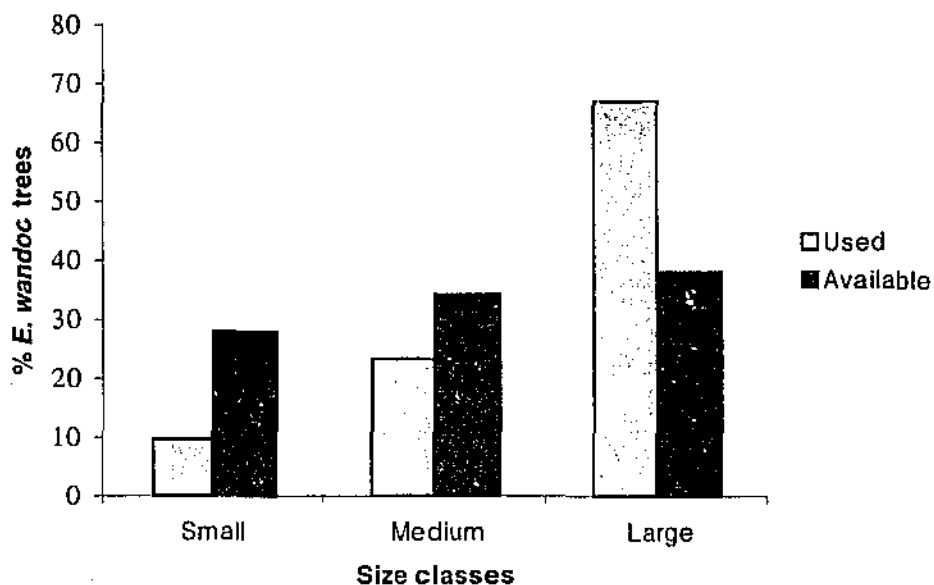


Figure 4 Percentage of Wandoo trees available ($n = 2256$) and used ($n = 197$) in each tree-size class at Dryandra (small; < 0.11 m, medium; $0.11 < 0.24$ m, large; ≥ 0.24 m). Confidence intervals indicated that small and medium trees were used less than expected (small trees: observed use 0.10, expected use (p) 0.28, confidence intervals $0.05 \leq p \leq 0.14$; medium trees: observed use 0.23, expected use 0.34, confidence intervals $0.17 \leq p \leq 0.30$) and large trees were used more than expected based on availability (observed use 0.67, expected use 0.38, confidence intervals $0.60 \leq p \leq 0.74$). The ranking matrix of log-ratios confirmed this result.

Ground and shrub cover

There was a significant difference in the percent cover of litter ($F_{2,55} = 18.5$, $P < 0.001$), bare ground ($F_{2,55} = 78.9$, $P < 0.001$), ground vegetation ($F_{2,55} = 20.0$, $P < 0.001$) and shrub cover ($F_{2,55} = 15.6$, $P < 0.001$) between each habitat context (the different height classes for shrubs were combined because percent cover was too low to justify separating the classes; Figure 5). Post hoc comparisons indicated that Dryandra had a significantly higher percent cover of litter, ground vegetation and shrubs than grazed sites (Tukey's HSD, $P < 0.01$), and a higher percent cover of litter than ungrazed sites ($P < 0.001$; Figure 5). Ungrazed sites had a higher percent cover of bare ground and ground vegetation than Dryandra ($P < 0.02$), and a higher percent cover of ground vegetation and shrubs than grazed sites ($P < 0.02$). A lack of shrub and ground vegetation cover illustrates the effects of extensive grazing and, as might be expected, grazed sites had a higher percent cover of bare ground than Dryandra and ungrazed sites ($P < 0.001$; Figure 5).

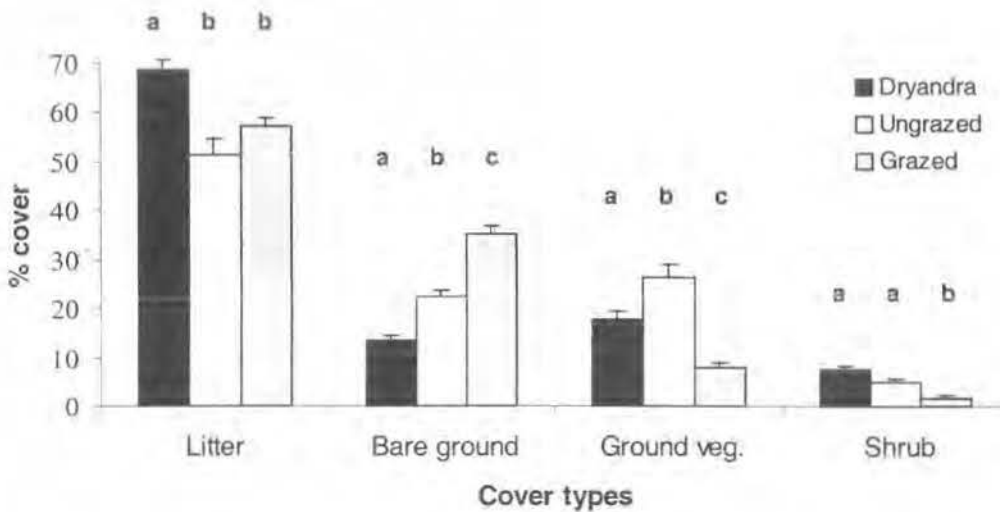


Figure 5 The percent cover of the different cover types in each habitat context ($n = 60$). Values with the same letter (above the columns) are not significantly different between each context (determined using Tukey's HSD, see text for details).

Discussion

Foraging manoeuvre, location and substrate

Gleaning was the most frequently recorded foraging manoeuvre used by the Rufous Treecreeper in our study, in common with all other Australian treecreepers (Noske 1982; Noske 1985; Recher et al. 1985; Ford et al. 1986; Brooker et al. 1990; Recher and Davis 1997). Rufous Treecreepers also foraged by probing into the crevices of trunks, branches and logs, and under decorticating bark. Although there were seasonal differences in foraging location, Rufous Treecreepers were frequently recorded foraging on the ground. This is also a common foraging location for the closely related Brown Treecreeper *Climacteris picumnus* (Noske 1979; Ford et al. 1986; Walters et al. 1999), but other Australian treecreepers appear to be mostly arboreal (Noske 1985; Recher et al. 1985; Ford et al. 1986; Holmes and Recher 1986; Brooker et al. 1990; Recher and Davis 1997). Ground foraging by Rufous Treecreepers may be more prevalent in open woodland habitats where detection of predators is easier. In the Jarrah forest of the southwest of Western Australia, which generally has a higher shrub density than Wandoo, Wykes (1985) recorded approximately 25% ground foraging for the species in all seasons.

The foraging substrates used by the Rufous Treecreeper generally represent the most common substrates available in the woodland habitat of our study areas. There are large areas of open ground much of it covered with litter or low ground vegetation that would provide suitable microhabitats for a range of invertebrates. Bark and deadwood are also common substrates that were frequently used by treecreepers. At a finer scale, treecreepers preferentially foraged on larger Wandoo trees. Preferential use of larger trees by bark-foraging birds has been recorded in a number of studies (Flemming et al. 1999; Weikel and Hayes 1999). Large trees have a greater surface area and would probably harbour a greater biomass of invertebrates. Therefore, it would be energetically efficient to spend more time foraging on this substrate.

Logs have been recognised as an important foraging location for Rufous Treecreepers (Recher 1991), but we rarely recorded direct foraging on this substrate even though logs are common in our study areas (e.g., mean log density in Dryandra was $41 \text{ ha}^{-1} \pm \text{s.e. } 2.11$; Chapter 4). This probably misrepresents the importance of

logs and coarse woody debris to the species. Logs in varying degrees of decay provide many microhabitats for invertebrates, assist in the accumulation of litter, and return nutrients to the soil (Lindenmayer et al. 1999 and references therein). These factors may influence the high percentage of ground foraging by Rufous Treecreepers.

Seasonal differences in foraging behaviour

There were seasonal differences in the foraging behaviour of treecreepers with a greater use of trees in autumn and a shift to primarily ground foraging in winter. The prevalence of ground foraging appears to continue into the early breeding season (GL pers. ob; Recher and Davis 1998) with an increase in tree foraging occurring around late spring – early summer (GL pers. ob.). Seasonal shifts in foraging location have been recorded for a number of Australian bird species (Recher 1989; Ford et al. 1990; Robinson 1992) and for bark-foraging birds in the Northern Hemisphere (Morrison et al. 1987; Lundquist and Manuwal 1990).

A move to primarily ground foraging by insectivores during winter has generally been associated with seasonal changes in the distribution, abundance and/or availability of invertebrates (Ford et al. 1990; Robinson 1992). In eucalypt woodlands in eastern Australia, Ford et al. (1990) found that arthropod abundance did not decline seasonally as much on the ground as on bark and foliage. Ground arthropods may be relatively more common in winter than other arthropod groups (Recher et al. 1983), but some studies show that bark-dwelling arthropods are also relatively abundant in winter (Loyn 1985; Recher and Holmes 1985).

Much of the current research on prey abundance has been conducted in eastern Australia and these data may not be applicable to western eucalypt woodlands owing to differences in the seasonality of invertebrate communities (Recher et al. 1996). Correlations between the foraging location of insectivorous birds and invertebrate abundance and availability need to be established through extensive sampling of the invertebrate fauna. This has been done in some studies with equivocal results (Ford et al. 1990; Adams and Morrison 1993). The high temporal and spatial variability in invertebrate distribution and abundance also means that exhaustive sampling is required, which was beyond the scope of our study.

Landscape differences in foraging behaviour

There was a difference in the use of foraging locations between landscapes in the same year and season. Ground foraging was more prevalent in Dryandra (72%) than Yilliminning (52%) with the converse for tree foraging (Dryandra 22%, Yilliminning 43%). This difference is largely attributable to the results obtained in ungrazed woodland. Reasons for this difference are unclear, but we propose the following hypotheses that require further testing.

Hypothesis 1: Differences in the percent cover of litter, bare ground and ground vegetation

Percent ground cover differed between the three habitat contexts. Ungrazed woodland had the lowest percent cover of litter (52%, although not significantly different to grazed remnants at 57%) and the highest percent cover of ground vegetation. These differences may have induced a lower percentage of ground foraging by treecreepers in the ungrazed habitat. Increased cover of ground vegetation in particular would make it difficult for species that prefer open areas for foraging. However, interestingly, ungrazed woodland had a significantly higher percent cover of bare ground (22%) than Dryandra (11%) and other factors besides overall percent cover may have influenced the behaviour of the species. This hypothesis could be tested by altering the percent cover of the different ground cover types and monitoring changes in treecreeper foraging behaviour.

Hypothesis 2: Differences in species assemblage and structure of ground vegetation

In Dryandra, ground vegetation is comprised almost entirely of native species that are mostly herbaceous and grow low (< 0.1 m) to the ground. In contrast, the ungrazed woodland remnants at Yilliminning contained a greater proportion of exotic species, particularly tall (\approx 0.5 m) grasses and pasture weeds (e.g., wild oats *Avena* spp. and veldt grass *Ehrharta* spp.) that penetrated into habitat fragments from adjacent agricultural land. Differences in plant species composition may change the distribution or abundance of ground invertebrates or the composition of invertebrate communities. The presence of taller vegetation can make the ground a less attractive place to forage, as it can hinder predator

surveillance. Differences in vegetation structure may also reduce the availability of invertebrates to ground-foraging birds, even if abundance and species richness remain the same as undisturbed sites. Altering ground vegetation structure (e.g., height), as opposed to percent cover, may be useful in testing this hypothesis. Comparing invertebrate species assemblages between weed infested and undisturbed sites could reveal patterns of community change and the potential effects on ground-foraging insectivores.

Hypothesis 3: Adverse changes to ground invertebrate communities in ungrazed remnants

A number of studies have examined the effects of habitat fragmentation and grazing on the invertebrate communities of remnant woodland in eastern and western Australia (Abensperg-Traun 1992; Abensperg-Traun et al. 1996; Bromham et al. 1999). These studies generally detail complex relationships between the distribution, abundance and composition of invertebrate communities and levels of habitat disturbance. Notably, Bromham et al. (1999) found that ungrazed woodland had a higher diversity of ground invertebrates when compared to grazed woodland and pasture. There is no clear indication of how changes to ground invertebrate communities in ungrazed, fragmented woodland remnants may influence the behaviour of ground-foraging birds. Comparing bird foraging behaviour and invertebrate abundance and diversity in the same temporal and spatial context would contribute to our understanding of this relationship.

Hypothesis 4: Sampling artefact

It is possible that our result is a sampling artefact. As ungrazed remnants had taller ground vegetation, observations of ground foraging may have been obstructed resulting in a lower percentage compared to more open sites. If this is the case, researchers may need to follow individual birds for extended periods to get a clear indication of the proportional use of the various foraging substrates.

As the ground layer is an extensively used foraging substrate for the treecreeper, the inability to exploit this resource may have detrimental consequences. We have no data to suggest that the individuals in the ungrazed

remnants were adversely affected. In fact, nest success and fledgling productivity were higher in ungrazed compared to grazed remnants (Chapter 7).

The proportional use of foraging substrates by treecreepers in Dryandra and grazed sites was relatively similar, but this gives no indication of differences in foraging effort (e.g., time spent foraging) or the level of reward (i.e., food intake) per effort. In a similar study to ours, Walters et al. (1999) compared the foraging behaviour of Brown Treecreepers in two areas with different levels of fragmentation. They hypothesised that birds may spend a greater amount of time foraging in the more fragmented landscape owing to lower food availability, but the results of their study did not show any differences in the time spent foraging or the proportional use of ground or trees as foraging substrates. Interestingly, Walters et al. (1999) recorded similar levels of ground foraging (65%) to our study, with both of their study areas subject to livestock grazing.

In summary, it appears that the effects of habitat alteration on the foraging effectiveness of Rufous Treecreepers may be complex. Grazed woodland appears to be structurally suitable for foraging by having large areas of open ground, but the diversity of invertebrate species may be reduced in these remnants (Bromham et al. 1999). Conversely, ungrazed remnants subject to weed invasion may be structurally unsuitable for ground-foragers resulting in the under-utilisation of this resource.

Conservation and management

Our study highlights important considerations for the conservation of not only the Rufous Treecreeper, but other woodland birds. In Wandoo woodlands, the ground layer is an important foraging substrate particularly during critical times of the year such as the beginning of the breeding season. Recher and Davis (1998) found that in early spring in Dryandra, 61% of species took more than 20% of their prey from the ground. These included a number of species that are considered threatened by habitat alteration (e.g., Western Yellow Robin *Eopsaltria griseogularis*, Hooded Robin *Melanodryas cucullata* and Jacky Winter *Microeca fascinans*). Many ground-foragers are insectivores and it is vital that the ground layer is maintained in such a way that it provides suitable microhabitats for invertebrates and remains a functioning component of the ecosystem.

Large trees are recognised as being important habitat components to bird species in Australia (Braithwaite et al. 1989; Ford and Barrett 1995) and elsewhere (Sedgwick and Knopf 1990; Steeger and Hitchcock 1998), and the results of our study concur with these findings. The preferential use of larger trees by Rufous Treecreepers gives some indication of the appropriate structural and age characteristics of woodland habitat suitable for this species. In Dryandra, Rose (1993) estimated that Wandoo trees with a DBH of ≥ 0.24 m (the lower limit of our "large" size class) are approximately 80 years old. Also, hollows suitable for use by Rufous Treecreepers (an obligate hollow nester) generally occur in trees estimated to be 150 years old (Chapter 4; Rose 1993) and younger stands of Wandoo may not have the appropriate structural characteristics needed to support this species.

In highly modified agricultural landscapes, passive management of vegetation remnants (e.g., fencing from grazing) may not be sufficient to maintain them as habitat suitable for particular species. Fenced remnants are still susceptible to degrading processes like weed invasion, which may result in bird species (particularly ground-foragers) modifying their foraging behaviour, possibly influencing foraging effectiveness. Active management (e.g., weed removal) is required to maintain the integrity of these ecosystems. There is also a need for further research on the effects of habitat alteration on foraging behaviour, as this may contribute to our understanding of processes that threaten the persistence of species living in human-dominated landscapes.

CHAPTER 5 *HABITAT QUALITY AND FITNESS*

SUMMARY

In cooperative breeders, reproductive success may be positively correlated with group size (Chapter 3), but this relationship may not be independent of habitat quality. I determined the relationship between the reproductive success and survival of the Rufous Treecreeper and habitat quality at two spatial scales; nest site and territory. The structural characteristics of the habitat identified as important predictors of the nest-site and territory use of the treecreeper (Chapter 4) were used as independent measures of habitat quality.

At the nest-site scale, hollow characteristics that were positively correlated with the probability of a hollow being used had no relationship with the nest success of treecreepers. Preferred nest sites did not yield greater success. This result may reflect the relatively unrestricted access to suitable nest sites in *Dryandra* or difficulties in identifying important nest-site characteristics.

In contrast, the structural characteristics of the habitat that predicted territory use in treecreepers (territory quality) were positively correlated with each measure of fitness (annual productivity and survival) except primary female survival rate. Territory quality was also positively correlated with group size and provisioning rate to nestlings, which in turn were correlated with certain fitness measures. These correlations suggest a complex interaction between territory quality, group size and fitness.

I used regression modelling to determine if group size was significantly correlated with fitness once territory quality had been considered. With territory quality entered first in each model, group size was not related to any fitness measure except primary male survival rate. In most cases, group living did not appear to offer additional fitness benefits over and above that of territory quality. This relationship is complex and requires further investigation, but the quality of territories occupied by Rufous Treecreepers appears to be a significant factor for breeding group fitness.

5.1 INTRODUCTION

5.1.1 Overview

In Chapter 4, I demonstrated that Rufous Treecreepers exhibited non-random use of habitat at multiple spatial scales. This was the first step in defining habitat selectivity. The second step is to determine if preferential habitat use has consequences for fitness (e.g., reproductive success and survival). Clark and Shutler (1999) argue that a third step is required that links the pattern and process of habitat selection with adaptive habitat choice through the theory of natural selection.

In this chapter, I explore the relationship between habitat quality and measures of fitness at the territory and nest-site scale. In particular, I determine if variability in fitness is correlated with the structural characteristics of treecreeper habitat identified as significant predictors of habitat use by the models developed in Chapter 4. Adaptive habitat choice at the nest-site scale is explored by examining changes in hollow use within and between years. Variability in fitness is usually considered at the individual level, but in this thesis it generally applies to a cooperatively breeding group.

The aims of this chapter are to examine the relationships between:

- a) the structural characteristics of nest hollows and nest success (nest-site quality);
- b) nest fate and the fidelity of females to hollows within and between years, and fidelity and subsequent nest success (adaptive nest-site selection);
- c) the structural characteristics of territories and various fitness indices (territory quality); and
- d) fitness, territory quality, group size and the provisioning rate to nestlings.

5.1.2 Habitat quality

Defining quality

In avian species, habitat "quality" may be determined by food abundance, availability of nest sites, suitability of foraging substrates and protection from predators. It is generally recognised that habitats vary in quality and that high quality sites, which enhance fitness, should be preferentially used over poorer quality sites (Fretwell and Lucas 1970; Morris 1987; Rosenzweig 1991; Ens et al. 1992; Yosef

and Grubb 1994; Muller et al. 1997). However, associations between habitat features and fitness may be difficult to demonstrate because normally productive habitats may be temporarily unsuitable owing to the spatial and temporal dynamics of the system being studied (Orians and Wittenberger 1991).

Defining habitat quality is generally undertaken by correlating temporal and/or spatial variability in fitness with temporal and/or spatial variability in particular habitat characteristics (e.g., vegetation cover or food abundance). A useful approach is to determine if certain habitat features are associated with preference for and success in particular sites (Matthysen 1990). In birds, fitness measures may include nest success (the proportion of clutches that produce offspring), the number of fledglings produced per nest and the number of fledglings produced per season for breeding pairs or groups (Braden et al. 1997; Dunk et al. 1997; Langen and Vehrencamp 1998; McKee et al. 1998; Wilson and Cooper 1998; Roberts and Norment 1999). These indicative measures of success may not be correlated (Murray 2000) and it is preferable to collect the most detailed data possible (e.g., annual productivity) to provide a closer approximation of actual fitness. Broadening fitness indices to include juvenile survival and recruitment may also strengthen interpretations of habitat quality.

Nest-site quality

In hollow-nesting birds, nest-site selection may affect fitness through microclimate variability, accessibility of nest to predators, or protection from adverse climatic conditions (e.g., rain or wind). These factors are influenced by hollow entrance size, orientation and angle, nest height and depth of nest cup from hollow entrance (Inouye et al. 1981; Nilsson 1986; Gutzwiller and Anderson 1987; Hooge et al. 1999). Although habitat selection theory predicts that preferred nest sites should correlate with higher reproductive success, results from studies of nest-site selection have been equivocal. In some cases, particular nest-site features used more frequently by a species correlate with higher reproduction (T. E. Martin 1998; McKee et al. 1998), but there are many examples where there is little relationship between these factors (Murphy et al. 1997; Pribil 1998; Wilson and Cooper 1998). A study of the cavity-nesting Acorn Woodpecker *Melanerpes formicivorus* found that

only one out of five preferred nest-site characteristics yielded higher reproductive success (Hooge et al. 1999).

There are a number of potential reasons for the lack of a relationship between nest-site selection and success. Researchers may fail to identify important traits that are both preferred and yield greater success. Interspecific competition for nest sites may limit optimal nest-site selection (Brawn 1988; Li and Martin 1991). Conversely, if high quality nest sites are abundant and available to all individuals in the breeding population, there will be no correlation between nest-site selection and success (Pribil 1998). This highlights the importance of comparing used sites with random (available) sites to ascertain the level of preference and the potential abundance or scarcity of nest sites (Pribil 1998: Chapter 4).

Nest fate and hollow fidelity

In a review of nest-site selection studies, Clark and Shutler (1999) found that 61% of studies ($n = 270$) examined pattern that could be attributed to the theory of natural selection (comparing used sites with available sites), 54% examined evidence for the process of natural selection (comparing traits of successful and unsuccessful nests), but few (10%) determined if the process of natural selection resulted in subsequent adaptation in nest-site use. For example, preferential use of nest sites with specific habitat characteristics would be consistent with pattern predicted by natural selection, higher reproductive success in these preferred nest sites would be indicative of natural selection process, and changes in nest-site location after reproductive failure would suggest an adaptive response, particularly if this change resulted in subsequent nest success.

Clark and Shutler (1999) argued that more studies should frame questions about nest-site selection within the context of the theory of natural selection. It is relatively easy to examine pattern and process arising from natural selection, but subsequent adaptation may be difficult to test without long-term data of closely monitored and individually marked populations. Despite having collected data for only three breeding seasons, my observations of Rufous Treecreeper nest-site use are conducive to at least an initial investigation of nesting adaptation driven by the process of natural selection. The use of nest hollows by breeding birds varied from

using a single hollow for all nesting attempts (up to a maximum of six attempts) to using a maximum of four hollows. Multiple nesting attempts by individually marked females that remained in the study sites for more than 1 year allowed me to examine the relationship between nest fate and hollow fidelity. There may be a higher probability of a female using a different hollow if the initial nest fails.

Territory quality

In territorial birds, there is relatively strong evidence for variability in territory quality reflected by changes in fitness (Conner et al. 1986; Newton 1989; Matthysen 1990; Braden et al. 1997; Langen and Vehrencamp 1998; Davenport et al. 2000). Preferential use and defence of high quality sites is particularly important if territories are commonly occupied for extended periods (e.g., generations), provide most ecological requirements (e.g., foraging and nesting sites) and do not vary dramatically in quality over time (Matthysen 1990).

Assessments of territory quality commonly correlate structural or floristic characteristics of territories with success (Hunt 1996; Braden et al. 1997; Huhta et al. 1998; Roberts and Norment 1999). This procedure is relatively simple and may result in strong correlations, but more direct measures of territory quality can yield greater information. Differences in food abundance may be more indicative of variation in quality, but temporal and spatial variability in food abundance, and difficulties in accurately measuring useable resources, can preclude the detection of a clear relationship between abundance and quality. Also, abundance does not necessarily reflect availability and researchers must have a detailed knowledge of the specific dietary requirements and foraging limitations of the species they are studying. Encouragingly, a number of studies have found that the abundance of invertebrate prey may be positively correlated with preferred structural characteristics suggesting that measures of habitat structure provide proximate assessments of food abundance (Conner et al. 1986; Smith and Shugart 1987; Huhta et al. 1998).

Territory size is another potential measure of habitat quality (Smith and Shugart 1987). Habitats that support a high density of comparatively small territories suggest some underlying relationship with resource abundance and quality, but

without complementary data on reproductive success this relationship may be spurious (Van Horne 1983; also see Chapter 6). Some studies have found a negative correlation between food abundance and territory size, or documented shifts in territorial boundaries with changes in abundance (Smith and Shugart 1987; Temeles 1987; Eberhard and Ewald 1994). Sherman and Eason (1998) argued that this relationship depends on the flexibility of territory boundaries and is unlikely to occur in territorial species with contiguous territories and inflexible territorial boundaries.

Analyses of the relationship between territory quality and reproductive success in cooperative breeders must also consider the confounding effect of group size, which is often positively correlated with reproductive output (Chapter 3). In Rufous Treecreepers, a further complication occurs when individuals provision nestlings in territories adjacent to their own. This potentially confounds the relationship between the quality of a given territory and its reproductive output because individuals from adjacent territories may bring food from their own territory to provision nestlings (Chapter 3).

5.2 METHODS

5.2.1 Study sites

My analysis of the relationship between nest-site and territory quality and fitness was confined to the 30 study territories in Dryandra (all within Wandoo *E. wandoo* woodland). As these territories occurred in the same continuously vegetated landscape, landscape metrics (e.g., patch size) were not considered in this analysis. It was also beyond the scope of my study to examine differences in habitat quality between the various woodland types occupied by the treecreeper in Dryandra.

5.2.2 Nest-site quality

For the three breeding seasons combined, I recorded 148 nesting attempts in 76 hollows in the 30 study territories. The structural characteristics of each nest were measured following the methods described in Chapter 4 (Section 4.2.4). Nest fate was classified as successful (fledging at least one nestling) or unsuccessful (failing to fledge a nestling).

To examine the relationship between hollow attributes and nest success, I used only the first nest attempt in each breeding season (eggs laid before mid-October) to limit any effects associated with multiple nest attempts (within years) and season. Nesting attempts by the same female in different years (using either the same or a different hollow) results in pseudoreplication. For these cases, I chose a single nesting attempt (= hollow) at random. Nesting attempts by new primary females (i.e., replacing the original primary female) were considered appropriate replicates if a different hollow was used from the original female. Only one nesting attempt was chosen at random if these new females nested in the following season.

In Chapter 4, I established that the probability of hollow use by the treecreeper was related to spout angle and hollow entrance size. To determine if preferential use of hollows, as defined by these characteristics, was related to nest success, I used the value of Logit (P) as an independent indicator of hollow quality. Logit (P) was calculated from the regression equation in Chapter 4 (Section 4.3.3) with the values of the predictor variables (spout angle and size) coming from the successful and unsuccessful nests considered here. The value of Logit (P) correlates with the probability of a nest site being used and my aim was to determine if probability of use correlates with greater nest success. I used logistic regression with nest success as the dichotomous dependent variable and the value of Logit (P) as a predictor variable to determine the strength of this relationship.

5.2.3 Nest fate and hollow fidelity

To explore the relationship between nest fate and hollow fidelity, I determined the proportion of successful and unsuccessful hollows that were used again within and between years. Patterns of hollow use were only considered for multiple nesting attempts by the same female. Within year patterns were pooled for the three breeding seasons (1997 – 1999) because low sample size precluded analysis of annual differences. For between year patterns, if a female re-nested in the same hollow in any given year, but only produced fledglings in one of these nesting attempts, the hollow was considered successful for that year. I also determined the proportion of subsequently successful nesting attempts for females that used either

the same or a different hollow when re-nesting after an initial failure, to explore evidence for adaptive selection.

5.2.4 Territory quality

I measured structural habitat characteristics in each of the 30 study territories using the methods outlined in Chapter 4 (Section 4.2.3). Based on the territory model from Chapter 4, I determined the value of Logit (P) for each territory using the regression equation from the model and the values of the predictor variables from the new habitat data. Principal component analysis was used to derive factor scores for the habitat variables Wandoo canopy density (WCDEN) and density of hollows (DHOL – combined to create the composite variable nest-site (NSITE)), and tree size (TSIZ) and deadwood biomass (DWBM – combined to create the composite variable tree age (TAGE)). DWBM was \log_{10} transformed before analysis. Factor loadings between the original habitat variables and the first two principal components were 0.83, 0.74, 0.94 and 0.95 respectively. The value of Logit (P) was then used as an indicator of territory quality (higher values representing higher quality territories).

To examine the relationship between territory quality (TQ) and fitness, the following measures were recorded in each territory for each breeding season (see Chapter 3 for more details; the abbreviations in brackets are used in tables of results):

- a) group productivity (GP) – the total number of fledglings produced per breeding group per season;
- b) fledgling survival (FS) – the total number of fledglings surviving to independence;
- c) recruitment (RT) – the total number of juveniles surviving to the next breeding season;
- d) primary male survival rate (MSR) – the probability of a primary male surviving from one breeding season to the next; and
- e) primary female survival rate (FSR) – as for primary male.

Cross-territorial provisioning of nestlings confounds the relationship between the quality of a given territory and group productivity and possibly

fledgling survival. I removed the years when the occupants of a given territory received help from territorial neighbours and chose a single year at random as a representative measure of group productivity and fledgling survival for each territory. This was suitable because there were no significant differences between years for any fitness measure (Chapter 3). I used 1998 – 1999 as a representative year for recruitment (i.e., juveniles born in 1998 remaining on the natal territory until the beginning of the 1999 breeding season) because averaging across years would confound relationships with group size (see below).

I also examined the interrelationship between territory quality, fitness and the following “social” measures (see Chapter 3 for more details):

- a) group size (GS) – the number of adult birds in a territory at the beginning of each breeding season;
- b) provisioning rate (PR) – the number of visits per hour by adult birds bringing food to nestlings; and
- c) territory size (TS) – 95% minimum convex polygon.

To compare group size with group productivity and fledgling survival, I used group size values from the representative year, as chosen above. For recruitment, I used group sizes from 1998 because group sizes from 1999 are not independent of recruitment (i.e., juveniles recruited in 1999 were included in the measure of group size). Group sizes were averaged for 1997 – 1998 to compare with primary male and female survival rates.

Provisioning rates were used as a surrogate measure of food availability in a given territory. These were averaged across the years when groups did not receive help from adjacent territories (provisioning rates did not differ between years – Appendix 3.1). I also controlled for brood size (= two), stage of nesting (= mid – late), time of day (later than 0900 hrs) and maximum daytime temperature (< 30° Celsius) because these may influence provisioning rates (Appendix 3.1).

Group productivity and fledgling survival differed between the three study sites in Dryandra (Chapter 3), but this appeared to be related to differences in group size (Chapter 3) and territory quality (see Section 5.3.3). Therefore, the relationships between quality, group size and fitness were consistent for all sites and data were pooled to improve sample size.

Spearman rank correlation coefficients were calculated between all variables to examine the interrelationships between the social measures, territory quality and fitness. As this involved multiple contrasts of the same data, I adjusted the significance level using a Bonferroni adjustment (α/m , where α is the significance level and m is the number of contrasts made). Owing to small sample sizes, I used a significance level of 0.1 in this calculation to reduce the level of Type II errors.

The distribution of data for group productivity, fledgling survival and recruitment were discrete, asymmetrical and conformed to a Poisson distribution. Poisson regression was used to examine the relationship between these measures and territory quality, provisioning rate and group size. The survival rates for primary males and females were mostly 0.5 or 1.0 (occasionally 0.0), which were suitable to use in a logistic regression where survival rates ≤ 0.5 were coded as 0 and rates > 0.5 as 1.

Five different regression models were constructed. In each model, a fitness measure was used as the dependent variable and territory quality, provisioning rate and group size were used as the independent variables. Modelling was conducted using S-Plus 2000 software (Mathsoft 1999) and diagnostic procedures followed Nicholls (1989). Change in model deviance was used as an indicator of the relationship between the dependent and independent variables.

5.3 RESULTS

5.3.1 Nest-site quality

A total of 48 hollows (30 successful and 18 unsuccessful) were used in the logistic regression analysis. The model with Logit (P) as the predictor of nest success was not significantly different from the constant only model ($\chi_1^2 = 0.021$, $P = 0.88$). Preferentially used nest sites were not associated with higher nest success. To determine if any other measured nest-site characteristics were associated with nest success, I conducted another logistic regression analysis with all variables except relative height, which was highly correlated ($r = 0.80$) with hollow height. The full model was not significantly different from the constant only model ($\chi_9^2 = 9.04$, $P = 0.43$). Comparison of the means between successful and unsuccessful nests suggested small differences in the nest characteristics measured (Table 5.1).

Table 5.1 The nest-site characteristics (mean \pm s.e.) measured at successful (fledging at least one nestling) and unsuccessful nests. Numbers in brackets are sample sizes. Aspect class is not included in the table.

Nest-site characteristic ¹	Successful nests (30)	Unsuccessful nests (18)
DBH (cm)	49.0 \pm 2.79	46.8 \pm 3.75
DWD (%)	38.4 \pm 3.99	26.1 \pm 3.39
TRHE (m)	17.2 \pm 0.63	17.0 \pm 0.93
NHOL	6.9 \pm 0.59	5.2 \pm 0.63
HOHE (m)	9.2 \pm 0.43	7.6 \pm 0.55
REHE (m)	0.5 \pm 0.03	0.5 \pm 0.04
SPNG (°)	70.0 \pm 3.65	64.2 \pm 4.51
SIZE (cm)	7.1 \pm 0.54	7.1 \pm 0.76
CANC (%)	36.1 \pm 4.68	52.2 \pm 7.25

¹See Table 4.12 in Chapter 4 for full variable names.

Territory quality may also influence nest success, but is generally not considered in studies of nest-site selection. I measured nest success in each of my study territories, for the three breeding seasons combined, by dividing the number of successful nests (i.e., those fledging at least one nestling) by the total number of nesting attempts to limit the influence of group size on the likelihood of multiple broods. This measure of nest success was significantly correlated with territory quality (Spearman rank correlation, $r_s = 0.364$, $P = 0.047$, $n = 30$).

5.3.2 Nest fate and hollow fidelity

There was some evidence that nest fate influenced hollow fidelity. A greater proportion of successful hollows were used again within a given breeding season, but this pattern was not repeated in the between year comparison (Table 5.2). This suggests some immediate rather than adaptive response to previous nest fate.

Table 5.2 The proportion of hollows used again for nesting after the initial nest attempt was successful or unsuccessful. Fisher exact tests were used to test the specific (i.e., one-tailed) prediction that a greater proportion of successful hollows would be used again. Numbers in brackets are sample sizes.

Proportion of hollows used again	Previous nest fate		
	Successful	Unsuccessful	<i>P</i>
Within season	59.5 (42)	31.3 (16)	0.05
Between seasons	57.9 (38)	64.3 (14)	0.46

Data on subsequent nest fate, after an unsuccessful nesting attempt, may provide evidence for adaptive behaviour if treecreepers that used a different hollow were more successful than those that remained in the original (failed) hollow. My ability to test this hypothesis is limited owing to small sample size. Within season, five females used the same hollow after initial nest failure, but subsequent nest success (80%) was similar to that of the 11 females that used a different hollow (90%). Also, approximately 40% of females within and between seasons used a different hollow for nesting even though the initial hollow was successful (Table 5.2). This suggests that the use of multiple hollows is not necessarily adaptive.

Based on the data for the three breeding seasons combined, the average probability of a female treecreeper using the same hollow for multiple nesting attempts was 62.5% (this figure is adjusted for years when a territory had a new primary female). This relatively high probability indicates that multiple use of the same hollow may be an adaptive trait. If this is the case, then subsequent nest success for females using the same hollow (regardless of initial nest fate) should be higher than those using a different hollow. Subsequent nest success for females using the same hollow within season (73%, $n = 30$) was not higher than those using a different hollow (82%, $n = 28$, one-tailed Fisher exact test, $P = 0.31$), but between years, hollow fidelity did result in higher subsequent nest success (95%, $n = 21$ for females using the same hollow, 68%, $n = 22$ for females using a different hollow, one-tailed Fisher exact test, $P = 0.03$).

5.3.3 Territory quality

The territory quality, fitness and social measures are summarised in Table 5.3. Mean territory quality varied between study sites; Site A (0.4 ± 0.73), Site B (2.6 ± 1.88) and Site C (3.6 ± 1.26), but this difference was not significant (one-way ANOVA, $F_{2,27} = 1.43$, $P = 0.26$). There were a number of positive correlations between the social and fitness measures and territory quality (Table 5.4). Territory quality was significantly correlated with each fitness measure except female survival rate. Preferential habitat use by the treecreeper, as defined by the structural characteristics of the habitat, was associated with certain measures of individual fitness. Territory quality was also correlated with group size ($r_s = 0.443$, $P = 0.014$)

and provisioning rate ($r_s = 0.433$, $P = 0.017$), but these correlations were not significant at the adjusted level (Table 5.4).

Table 5.3 Quality, fitness and social measures for each of the study territories. Group size values used in analyses of recruitment and primary male and female survival are not included. Refer to Section 5.2.4 for full variable names.

Territory	TQ	GS	TS	PR	GP	FS	RT	MSR	FSR
A1	-1.8	2.0	2.0	29.0	3.0	1.0	1.0	0.5	1.0
A2	0.1	3.0	2.7	24.5	3.0	2.0	0.0	0.5	1.0
A3	-1.5	2.0	2.0	16.0	1.0	1.0	0.0	0.5	0.0
A4	4.6	2.0	2.5	28.0	2.0	2.0	1.0	1.0	0.5
A5	0.9	3.0	1.7	23.0	1.0	1.0	1.0	0.5	1.0
A6	-3.7	2.0	2.2	17.5	1.0	1.0	0.0	0.5	1.0
A7	2.1	2.0	6.0	25.0	1.0	1.0	1.0	0.5	1.0
A8	0.3	3.0	3.5	19.0	2.0	0.0	0.0	0.5	0.5
A9	1.4	2.0	3.1	16.0	1.0	0.0	0.0	0.5	0.5
A10	1.6	3.0	5.1	16.0	1.0	1.0	0.0	1.0	0.5
B1	9.9	4.0	2.6	20.0	4.0	4.0	1.0	1.0	1.0
B2	-0.8	4.0	2.2	16.0	2.0	2.0	2.0	1.0	1.0
B3	5.3	3.0	1.6	17.0	4.0	3.0	1.0	1.0	1.0
B4	-3.7	2.0	2.4	18.5	1.0	0.0	0.0	0.5	0.0
B5	2.2	2.0	2.2	18.0	1.0	1.0	0.0	0.5	1.0
B6	5.6	2.0	2.3	21.0	1.0	1.0	0.0	0.5	0.5
B7	12.8	4.0	2.5	28.0	4.0	4.0	2.0	1.0	1.0
B8	-6.6	2.0	1.8	19.0	2.0	1.0	0.0	0.5	1.0
B9	0.4	5.0	1.9	18.0	2.0	2.0	0.0	0.5	0.5
B10	1.1	4.0	3.3	20.0	2.0	1.0	0.0	0.5	1.0
C1	2.8	3.0	2.7	24.0	3.0	2.0	1.0	1.0	1.0
C2	5.8	5.0	1.9	21.0	3.0	3.0	2.0	1.0	0.5
C3	7.5	5.0	2.9	28.0	4.0	4.0	1.0	1.0	0.5
C4	7.2	3.0	2.4	22.5	2.0	2.0	1.0	1.0	1.0
C5	1.8	3.0	2.2	21.0	2.0	0.0	0.0	1.0	0.5
C6	-3.4	4.0	2.9	22.0	2.0	1.0	0.0	1.0	1.0
C7	-1.2	2.0	1.6	14.5	1.0	1.0	1.0	1.0	1.0
C8	5.2	4.0	2.1	27.0	4.0	4.0	4.0	1.0	1.0
C9	8.8	5.0	3.7	26.0	3.0	2.0	2.0	1.0	0.5
C10	1.5	2.0	2.2	21.0	2.0	1.0	0.0	1.0	0.5

Table 5.4 Spearman rank correlation coefficients between fitness and social measures, and territory quality ($n = 30$). The Bonferroni adjusted significance level for these comparisons is 0.013 (0.1/8). Correlation coefficients marked with an asterisk are significant at this level. Refer to section 5.2.4 for full names of variables.

	TQ	TS	GS	PR	GP	FS	RT	MSR
TS	0.244							
GS	0.443	0.157						
PR	0.433	0.242	0.255					
GP	0.521*	0.007	0.644*	0.546*				
FS	0.634*	-0.093	0.623*	0.408	0.775*			
RT	0.545*	-0.121	0.348	0.456*	0.561*	0.707*		
MSR	0.540*	0.035	0.505*	0.201	0.529*	0.557*	0.569*	
FSR	-0.032	-0.144	0.205	0.165	0.266	0.289	0.314	0.052

Group size was significantly correlated with group productivity and fledgling survival in accordance with the results from Chapter 3. Interestingly, it was also correlated with male survival rate, but not female survival rate (Table 5.4). Provisioning rate was significantly correlated with group productivity and recruitment. There were no significant relationships involving territory size, suggesting that demographic constraints (e.g., the presence of territorial neighbours) may be more influential in defining the space use of treecreepers in Dryandra.

Territory quality, group size and provisioning rate appeared to have a complex interactive influence on fitness measures such as group productivity (Figure 5.1). I used Poisson and logistic regression to examine the relative influence of these factors on each fitness measure. In each model, territory quality was entered first because I was primarily interested in its usefulness as a sole predictor of treecreeper fitness. Provisioning rate was entered next to account for the food availability component of territory quality. This assumes that provisioning rate and food availability are related. Group size was the last variable to be included to determine if it explained a significant proportion of variance in the data once quality and provisioning rate had been considered.

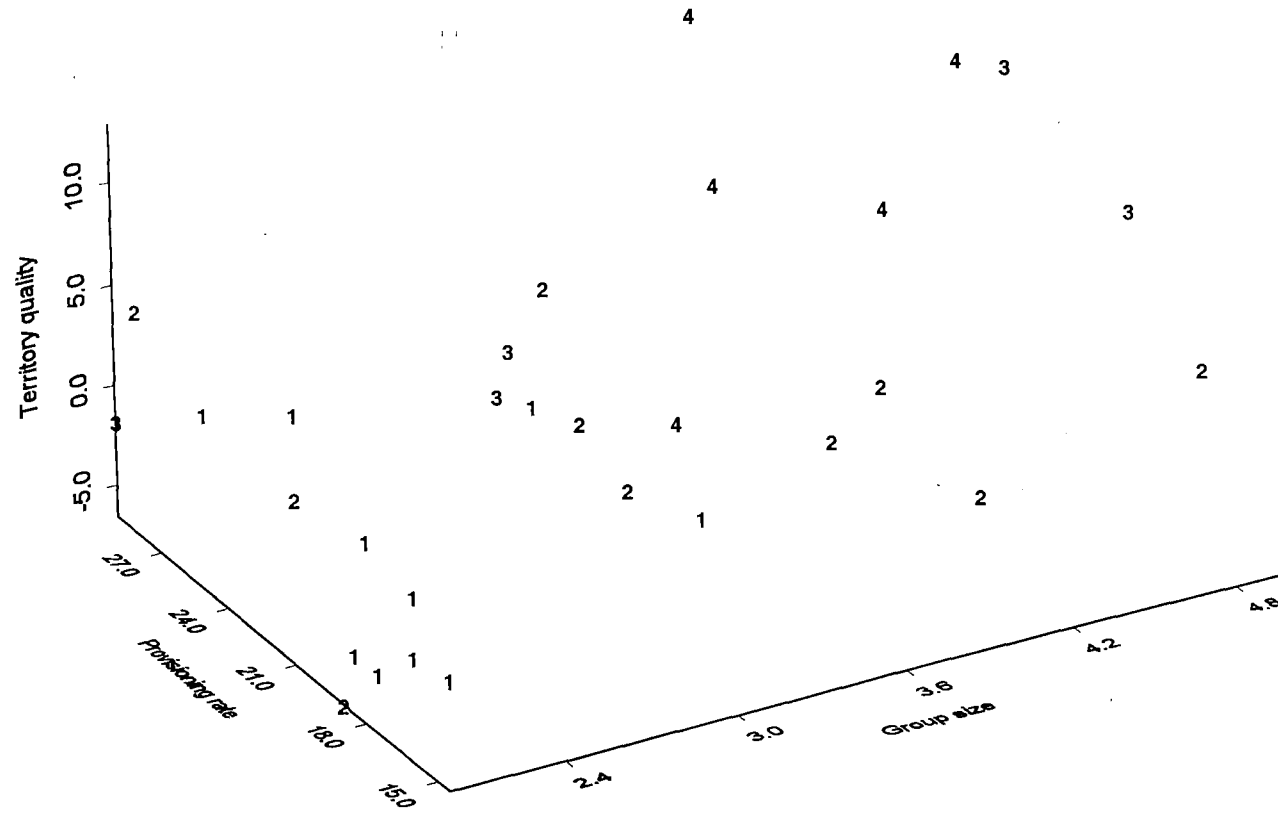


Figure 5.1 The relationship between territory quality, provisioning rate/hr, group size and group productivity. Each data point on the graph shows the number of fledglings produced (group productivity) in each of the study territories ($n = 30$) for a randomly selected, representative year.

There were strong positive correlations between group productivity and fledgling survival, and fledgling survival and recruitment (Table 5.4). Treecreeper groups that produced more fledglings had a higher number reaching independence and subsequently recruited into the breeding population. I initially modelled these relationships by including group productivity as a predictor of fledgling survival, and fledgling survival as a predictor of recruitment in addition to territory quality, provisioning rate and group size. With these fitness measures included as predictors, quality, provisioning rate and group size had no significant influence on fledgling survival or recruitment. Treating each fitness measure independently is not appropriate because initial reproductive output had a significant influence on subsequent success. For comparative purposes, I have included models of the relationship between each fitness measure and territory quality, provisioning rate and group size (i.e., excluding group productivity and fledgling survival as predictors).

There was a significant positive relationship between territory quality and group productivity, which translated into a significant relationship between quality and fledgling survival and recruitment owing largely to the effect of initial reproductive output on subsequent success (Tables 5.5 and 5.6). Territory quality was also significantly related to male survival rate. Additional variance explained by provisioning rate was not significant in any analysis of treecreeper fitness suggesting that vegetation structure alone is a useful measure of habitat quality for treecreepers in *Dryandra*.

With the territory quality measures considered, group size did not contribute significantly to any fitness measure except male survival rate (Table 5.5). The positive relationship with male survival rate suggests a benefit of group living in treecreepers. The surprising result was that territory quality and group size were not related to female survival rate.

Table 5.5 The Poisson and logistic regression analyses examining the relationship between treecreeper fitness and territory quality, provisioning rate and group size ($n = 30$). Table shows change in model deviance (distributed as χ^2) with the addition of each variable. The models of fledgling survival and recruitment are included for comparative purposes only because these fitness measures are not independent of group productivity.

Fitness measure	Territory quality and social measures	df	Change in deviance	Residual df	Residual deviance	<i>P</i>
Group productivity ¹	+Territory quality	1	6.28	28	12.87	< 0.025
	+Provisioning rate	1	1.51	27	11.36	
	+Group size	1	1.97	26	9.39	
Fledgling survival ¹	+Territory quality	1	12.47	28	16.41	< 0.001
	+Provisioning rate	1	0.36	27	16.05	
	+Group size	1	2.35	26	13.70	
Recruitment ¹	+Territory quality	1	8.98	28	26.86	< 0.005
	+Provisioning rate	1	2.18	27	24.68	
	+Group size	1	0.40	26	24.28	
Male survival rate ²	+Territory quality	1	9.87	28	31.58	< 0.025
	+Provisioning rate	1	0.09	27	31.49	
	+Group size	1	4.15	26	27.34	< 0.05
Female survival rate ²	+Territory quality	1	0.21	28	40.84	
	+Provisioning rate	1	0.67	27	40.17	
	+Group size	1	0.12	26	40.05	

¹Poisson regression

²Logistic regression

Table 5.6 The coefficients and standard errors (s.e.) for each of the models examining the relationship between fitness and territory quality, provisioning rate and group size.

Fitness measure	Territory quality and social measures	Coefficients	s.e.
Group productivity	Constant	-0.789	0.813
	Territory quality	0.028	0.035
	Provisioning rate	0.040	0.034
	Group size	0.184	0.130
Fledgling survival	Constant	-0.941	0.931
	Territory quality	0.073	0.041
	Provisioning rate	0.019	0.040
	Group size	0.232	0.150
Recruitment	Constant	-2.843	1.355
	Territory quality	0.090	0.055
	Provisioning rate	0.084	0.061
	Group size	0.095	0.146
Male survival rate	Constant	-2.968	3.124
	Territory quality	0.323	0.169
	Provisioning rate	-0.057	0.126
	Group size	1.276	0.730
Female survival rate	Constant	-1.639	2.302
	Territory quality	-0.089	0.104
	Provisioning rate	0.077	0.105
	Group size	0.162	0.465

To facilitate biological interpretation of the relationships between territory quality and the fitness and territory measures, I determined Spearman rank correlation coefficients between the individual components of Logit (P) (i.e., the original habitat characteristics) and each measure (Table 5.7). This was an exploratory analysis to examine relative measures of association with no statistical significance implied. This analysis showed that the density of hollow bearing logs had relatively strong correlations ($r_s > 0.450$) with group size and each fitness measure except female survival rate. Similarly, the density of Wandoo canopy trees was strongly correlated

with group size ($r_s = 0.659$), provisioning rate ($r_s = 0.450$), and each fitness measure ($r_s > 0.450$) except female survival. This suggests that these two habitat characteristics contributed strongly to the association between territory quality and treecreeper fitness, although simple correlations may not adequately represent the complexity of this relationship.

Table 5.7 Spearman rank correlation coefficients between fitness and territory measures and the individual habitat characteristics that contributed to the measure of territory quality ($n = 30$). Statistical significance is not attributed to these data, which are presented as relative measures only.

	DHOL	WC DEN	TSIZ	DWBM	DHLOG
Territory size	-0.110	0.109	0.129	0.017	0.040
Group size	0.229	0.659	-0.077	-0.111	0.486
Provisioning rate	0.010	0.450	0.052	-0.155	0.269
Group productivity	0.315	0.668	-0.106	-0.220	0.453
Fledgling survival	0.228	0.618	-0.035	-0.068	0.633
Recruitment	0.069	0.454	-0.041	-0.034	0.618
Male survival rate	0.162	0.534	-0.331	-0.131	0.639
Female survival rate	-0.144	0.036	0.009	-0.040	0.107

5.4 DISCUSSION

5.4.1 Nest-site quality

There was no significant relationship between preferential use of hollows with particular structural characteristics and nest success in Rufous Treecreepers. In Chapter 4, the logistic regression analyses on hollow use predicted that 51% of the 90 random (unused) hollows selected for comparison with used hollows were actually suitable for treecreeper nesting based on the structural characteristics I measured. Allowing for the vagaries of statistical modelling and the influence of unmeasured factors (e.g., interspecific competition), this result indicates that the availability of nest sites in Dryandra is not a critical limiting factor, particularly in Wandoo woodland. If potential nest hollows are abundant in any given territory there would be few constraints on nest-site selection. Therefore, variation between used hollows would be small and nest-site characteristics would show no correlation with nest success, as was found in my study.

This result may also be influenced by the relatively small sample size included in my analysis. Confidence in the results of the logistic regression would be strengthened by the inclusion of more unsuccessful hollows, but this was not possible owing to the relatively high nest success of treecreepers in Dryandra.

Nest success did vary and consideration must be given to the possible explanations for this variation. Hollow characteristics that were not measured in my study may have differed between nest sites and affected success. Hooge et al. (1999) found that microclimate characteristics were correlated with higher reproductive success in the cavity-nesting Acorn Woodpecker. Differences in predator activity, nest parasite (e.g., ticks) loads and individual behaviour (e.g., conspicuousness) may also affect success.

Differences in breeder experience and group size are also important factors that may influence nest success. I did not identify any associations between success and breeder experience (Chapter 3), but my sample size was small and the duration of my study limited. However, the percentage of successful nests was significantly higher for groups with greater than three individuals (Chapter 3). Of the 18 failed nest attempts considered here, only one attempt (5.5%) was associated with a group size of > three and nest failure may be a result of small group size rather than nest-site selection. Although, of the 30 successful nest attempts, only six (20%) were associated with group sizes > three, which is not a significantly higher percentage than unsuccessful nests (Fisher exact test, $P = 0.23$). More data are required to test this effect (the power of the above test is only 0.3), but if suitable nest sites are abundant and there are few restrictions on site selection, factors other than nest-site characteristics may have a greater influence on success.

5.4.2 Nest fate and hollow fidelity

Within a given season, treecreepers were more likely to move to a new hollow for re-nesting if they failed to fledge nestlings from the initial nest hollow. This pattern was not consistent for hollow use between years suggesting an immediate rather than adaptive response to nest failure. Factors leading to nest failure such as predation or

nest parasite loads may result in treecreepers abandoning a hollow in the short-term (i.e., within a single breeding season), but may not influence hollow use from one year to the next. The limited data on subsequent nest success also suggested that hollow infidelity was not an adaptive response. This result is similar to Clark and Shutler (1999) who found that, although breeding Mallards *Anas platyrhynchos* dispersed further after a failed nesting attempt, dispersal distance did not influence subsequent nest success.

Multiple use of the same hollow appeared to be an adaptive trait. Between years, subsequent nest success of females using the same hollow was higher than those using a different hollow. Saunders (1982) reported a similar result for the hollow-nesting White-tailed Black Cockatoo *Calyptorhynchus latirostris*. Rufous Treecreepers may construct a platform of bark strips inside a hollow, on which the nest cup is placed (see Figure 3.5 in Chapter 3). Similarly, cockatoos may make structural improvements to hollows (e.g., widening entrances or removing debris from inside). I have no data on the amount of effort required to build a nest platform, but it would appear to be advantageous for treecreepers to re-use a hollow once a platform had been built, especially considering that the primary female does the majority of nest building (Chapter 3). This would reduce the energetic and time requirements of building the nest, allowing the female more time to improve her physical condition prior to egg laying.

Multiple use of the same hollow may also reflect breeder experience and familiarity with a territory, which potentially improve reproductive performance (Russell and Rowley 1988). Multicollinearity may occur between hollow use, breeder experience and nest success, confounding assessments of adaptability in hollow selection. Long-term studies are required to tease apart these potentially interacting factors.

Habitat quality varied between territories and this was positively correlated with nest success (Section 5.3.1). As potential nest hollows appeared to be abundant in my study sites, territory selection rather than nest-site selection may be more critical to reproductive success for treecreepers in Dryandra (see below). Documenting nest success based on nest-site characteristics without data on broader habitat quality (and

vice versa) may lead to erroneous conclusions. Reproductive success should be examined at a number of spatial (and temporal) scales to determine the key factors influencing fecundity.

5.4.3 Territory quality

Territory size

A number of studies have found that territory size has no relationship with food abundance or resource density (Askenmo et al. 1994; Butchart et al. 1999). For Rufous Treecreepers in Dryandra, the relationship between territory size and habitat quality was positive, where an inverse relationship would be expected if quality strongly influenced area of use. Brooker and Rowley (1995) reported a similar result for Splendid Fairy-wrens *Malurus splendens* in habitat that included a Wandoo overstorey. This suggests that factors other than habitat quality may determine territory size in these species.

For the duration of my study, territorial boundaries appeared to remain relatively stable (Chapter 3). Sherman and Eason (1998) argued that changes in territory size resulting from fluctuations in food abundance would only occur in species with flexible territory boundaries. Boundary flexibility is unlikely to be characteristic of well defended, contiguous territories, as there may be costs associated with re-negotiating territorial boundaries with neighbours (Sherman and Eason 1998 and references therein).

Treecreeper territories in Dryandra were contiguous and any given territory could have up to six neighbouring groups (the maximum recorded in my study area). Territorial defence was variable, particularly during the breeding season, but territory contiguity and boundary sharing with multiple neighbours suggests little opportunity for most territory occupants to readily change territory size to reflect resource abundance. That is, demographic factors (e.g., population density) probably have a greater influence on the space use of treecreepers. This highlights the importance of initial territory selection for dispersing individuals and reinforces conclusions about the influence of territory quality on dispersal (Chapter 3). This relationship is complicated by the fact that certain individuals may access the resources of neighbouring territories during the

breeding season (Chapter 3), and access to adjacent territories and relationships with territorial neighbours (genetic or behavioural) may also affect space use by treecreepers.

Habitat structure and quality

The habitat characteristics considered the best predictors of treecreeper territory use (Chapter 4) were also correlated with certain measures of fitness supporting evidence for pattern and process arising from natural selection (Clark and Shutler 1999). A number of studies have demonstrated a positive association between habitat structure and various fitness measures (Conner et al. 1986; Matthysen 1990; Braden et al. 1997; Roberts and Norment 1999). However, structural habitat characteristics are not always the best predictors of fitness and researchers may need to consider other factors such as landscape metrics (Wigley et al. 1999) and interspecific competition (Aho et al. 1999).

Determining associations between food abundance and fitness is important in assessing habitat quality, but direct assessments of abundance may be difficult (see Section 5.1.2). Structural or floristic habitat characteristics may be useful surrogate measures of food abundance if food is correlated with these characteristics (Conner et al. 1986; Smith and Shugart 1987; Huhta et al. 1998). Examination of the individual habitat characteristics that defined territory quality for the Rufous Treecreeper showed that the relationship between quality and fitness appeared to be strongly influenced by the density of Wandoo canopy trees and hollow bearing logs (Table 5.7). Large Wandoo trees were preferentially selected for foraging by treecreepers (Appendix 4.1) and it is possible that territories that contain a higher density of large trees also have greater prey abundance. However, in winter and spring the treecreeper is primarily a ground forager (Appendix 4.1; Recher and Davis 1998) and direct associations between tree and prey abundance may not be important in these seasons.

Logs, or coarse woody debris, are recognised as being important for many Australian bird species (Recher 1993; Barrett 1995; Laven and Mac Nally 1998). Logs harbour a rich diversity of invertebrates (Taylor 1990; New 1995) and an increased density of this substrate would increase prey abundance for treecreepers, but it is

unclear if differences exist between logs with hollows and those without. An important function of hollow bearing logs, relevant to habitat quality, is protecting treecreepers from predators. This is particularly the case for recently fledged young who are weak fliers and spend most of their time near the ground (pers. ob.). The abundance of hollow bearing logs probably has a significant influence on fledgling survival, which is suggested by the relatively strong correlation between these variables (Table 5.7). Hollow logs are also used for protection by adult treecreepers, especially when birds are foraging on the ground (pers. ob.).

Smith and Shugart (1987) found that predicted prey abundance based on vegetation structure was negatively correlated with territory size in Ovenbirds *Seiurus aurocapillus*, but there was no relationship between territory size and actual prey abundance. They invoked the "structural cues hypothesis" to suggest that Ovenbirds assessed territory quality (food abundance) based on the relationship between prey abundance and habitat structure, rather than having direct knowledge of food resources. Using structural cues to assess territory quality may be important for non-breeding adult treecreepers searching for breeding vacancies. Indirect assessment via structural cues would allow rapid evaluation of the quality of surrounding territories, which in most cases would already be occupied. Accurate assessments of territory quality by non-breeders may be particularly important in influencing decisions about whether to disperse or remain on the natal territory (see Chapter 3 regarding other methods treecreepers may use to assess territory quality).

Interrelationships with group size and provisioning rate

In the analyses of territory quality and fitness, I included provisioning rate to nestlings as a surrogate measure of food availability, although provisioning rates may be influenced by a number of other factors including breeder and helper experience, familiarity with territory, and foraging ability. Also, provisioning rate during the breeding season may not represent general food availability in a territory over an entire year. The significant correlations between provisioning rate and group productivity and recruitment (Table 5.4) suggest a relationship with food availability during the breeding

season, and a more general measure of food availability respectively. However, in the regression analyses, provisioning rate did not contribute significantly to any measure of fitness once territory quality (habitat structure) had been considered. This suggests that food availability may not be a limiting factor causing significant variation in territory quality, or that habitat structure may encapsulate differences in food availability.

Group size did not contribute significantly to any of the relationships considered in the regression analyses except primary male survival rate (Table 5.5) suggesting that territory quality may have a greater effect on fitness. However, group size was positively correlated with territory quality ($r_s = 0.443$, $P = 0.014$), which complicates interpretations of its importance. A clue to the relative influence of group size to group productivity may be obtained by examining the number of fledglings produced by the same breeding female in the same territory when group size increased from one year to the next (this assumes that territory quality does not change significantly from one year to the next; sample size was not sufficient to also control for breeding males). Although sample size is small ($n = 10$), an increase in group size only increased group productivity in 20% of cases when breeding female and territory remained constant.

Territory quality and group size were positively related to the survival rate of primary males, but not females. It is unclear why the sexes should differ in this respect, but it raises some important hypotheses requiring further testing. The positive relationship between territory quality and male survival suggests that males would benefit more from remaining philopatric (particularly in good quality territories) and should defend resources from intruders. Males are the more philopatric sex in treecreepers (Chapter 3) and, although all group members assist in territory defence, the primary male generally responded more readily to territory intrusion (pers. ob. based on response to playback tapes).

As group size increases, primary males and females reduce their provisioning effort to nestlings (Chapter 3). Primary males freed from provisioning responsibilities could spend more time foraging for themselves and being vigilant against predators. These benefits are also available to primary females, but females may have to direct a certain proportion of effort into preparing for a second nesting attempt. The likelihood

that a primary female will produce multiple broods increases with group size (Chapter 3). Primary females living in larger groups may reduce provisioning effort to any one brood, but have more broods in a season. Also, the primary female invests more than the primary male in each reproductive effort (e.g., building the nest, incubating and brooding). Assuming this effort is costly in energetic terms (Perrins 1970), and may reduce individual fitness in females, there may be a trade-off between any benefits of group living and the energetic costs of multiple nests. Hence, fitness benefits associated with group living may be more pronounced in males.

In considering relationships between territory quality, provisioning rate and group size, it is important to recognise that increases above a certain level (e.g., larger group sizes or better quality territories) may not offer additional fitness benefits to territory occupants. This is because treecreepers can only produce a restricted number of fledglings in any given season owing to a relatively small clutch size (1.94 ± 0.07) with little variation (Chapter 3). In the 90 group years of my study, no group produced more than four fledglings in a season, and only one group successfully fledged three nestlings from one clutch (indicating it is possible to increase fledgling production above four with multiple nests in a season). Bearing this in mind, only 14.4% of groups (in 90 group years) produced four fledglings in a season (Chapter 3), suggesting that the optimal mix of quality, group size and provisioning rate is rarely achieved.

Part III
THE ECOLOGY OF THE RUFIOUS TREECREEPER
IN A FRAGMENTED LANDSCAPE



My Woodland Home: Part II

*It's gone, my woodland home
A skeleton but remains
And like a misguided angel
White death rises from below
To carry it to the grave*

CHAPTER 6
HABITAT QUALITY, POPULATION DENSITY AND COOPERATIVE
BEHAVIOUR IN A FRAGMENTED LANDSCAPE

SUMMARY

Variation in habitat quality between fragmented and unfragmented landscapes may have significant consequences for population persistence, but fragmentation studies often neglect to assess qualitative differences. Population density may also vary between landscapes, reflecting changes in habitat quality. In this chapter, I compare the structure and quality of habitat, and population density, between Dryandra and Yilliminning. I also examine the social organisation and cooperative behaviour of the Rufous Treecreeper in the fragmented landscape.

Mean habitat quality in each remnant context in Yilliminning was significantly lower than the study sites in Dryandra. This was a result of significant differences in habitat structure between landscapes. Population density was similar between Dryandra and grazed remnants, despite differences in habitat structure, but was extremely low in ungrazed remnants. In Yilliminning, density was highest in the apparently poorer quality remnants. The negative relationship between habitat quality and population density suggests that demographic and social factors have a greater influence on density in the agricultural landscape.

Basic demographic parameters (e.g., sex ratio and group size) of the Yilliminning population were consistent with Dryandra, although the number of nest attendants was generally lower in the fragmented landscape. The influence of helpers on reproductive success was similar between landscapes. A key difference in helping behaviour was the positive correlation between provisioning rate and the number of nest attendants in Yilliminning. This was a result of the primary male and female maintaining their provisioning effort despite an increase in the number of helpers, in contrast to Dryandra where there was a significant reduction in provisioning effort (Chapter 3). Under constrained environmental conditions (e.g., low food availability), primary males and females may not be able to reduce their provisioning effort despite the assistance of helpers.

6.1 INTRODUCTION

6.1.1 Overview

In the following three chapters, I examine the ecological characteristics and population dynamics of the Rufous Treecreeper in the agricultural landscape of Yilliminning, and compare these with the population in Dryandra. In Chapters 6 and 7, comparisons are made between seven "habitat contexts" for data collected in 1998 and 1999. The habitat contexts are the three sites in Dryandra (Site A, B and C – each containing 10 territories) and large ungrazed (LU – nine territories), large grazed (LG – eight territories), small ungrazed (SU – six territories) and small grazed (SG – seven territories) remnants in Yilliminning (see Chapter 2 for more details).

In this chapter, I compare the structure and quality of the habitat used by the treecreeper in Yilliminning with that used in Dryandra. I also assess differences in population density between landscapes and the relationship between density and habitat quality, and compare basic population demography (differences in reproductive success are analysed in Chapter 7). Finally, I examine the role of helping behaviour in the agricultural landscape and differences in parental response to the presence of helpers. The aims of this chapter are to compare:

- a) the structural characteristics and habitat quality of territories in Dryandra and Yilliminning;
- b) territory size and population density in each habitat context;
- c) basic population demography (e.g., population sex ratio and group size);
and
- d) landscape differences in helping behaviour.

6.1.2 Habitat structure and quality

Habitat fragmentation research has largely focussed on the consequences of changes to the spatial characteristics of remnant vegetation (Dunning et al. 1992; Andrén 1994; Collinge 1996). These include differences in remnant size, shape, isolation and connectedness. These characteristics often differ dramatically between areas with varying levels of fragmentation and are an obvious focus for study. This approach has been strongly influenced by the theoretical frameworks of island biogeography (MacArthur and Wilson 1967) and metapopulation biology (Levins

1969; Hanski and Simberloff 1997), where remnant size and isolation are considered important influential factors in community and population dynamics.

In addition to variability in the spatial characteristics of remnants, habitat structure and function within remnants may differ dramatically between fragmented and relatively unfragmented landscapes. The preferred habitat of the Rufous Treecreeper, Wandoo *Eucalyptus wandoo* woodland, has been reduced to just 6% of its original cover (Hobbs and Mooney 1998). Therefore, the habitat used by the species in highly fragmented regions may differ substantially in structure and quality from habitat used in unfragmented and relatively undisturbed areas. It is extremely important to document these differences to provide a more complete picture of the threats to population persistence and the potential management actions that may be implemented to alleviate these threats.

6.1.3 Population density

The population density of a species often differs between habitats and density variation may be used to infer habitat quality (i.e., higher quality habitats may support higher densities; Van Horne 1983; Vickery et al. 1992). A number of studies have found higher population densities of particular bird species in large compared to small remnants or continuous versus fragmented habitat, supporting the assertion that highly fragmented habitat is of lower quality (Gibbs and Faaborg 1990; Villard et al. 1993; Wenny et al. 1993; Huhta et al. 1998). However, these patterns may not be consistent for different species studied in the same landscape (Gibbs and Faaborg 1990; Wenny et al. 1993), or for the same species studied in different landscapes (Sabine et al. 1996).

The relationship between population density and habitat quality can be misleading if other factors influence density. For example, dominance hierarchies and territorial behaviour may force subordinate individuals from high quality habitat, increasing densities in suboptimal areas (Van Horne 1983). It is imperative that data on reproductive success are collected from populations that differ in density to provide a clearer picture of habitat quality relationships (see Chapter 7). In some cases, reproductive success may indeed be correlated with population density, but there are examples where success is greatest at lower densities (Vickery et al. 1992; Purcell and Verner 1998; Chapter 7). An independent measure of habitat

quality (e.g., habitat structure or food availability) would contribute to our understanding of this relationship.

6.1.4 Demography and helping behaviour

Determining differences in basic demographic characteristics between fragmented and unfragmented landscapes contributes to our understanding of the consequences of fragmentation. A number of studies in North America have recorded the presence of a greater number of unpaired Ovenbird *Seiurus aurocapillus* males in fragmented compared to continuous forest (Gibbs and Faaborg 1990; Van Horn et al. 1995). This suggests that female dispersal or settling behaviour may be disrupted by fragmentation (also see Walters et al 1999). Documenting population sex ratio and site fidelity may assist in understanding these relationships.

For cooperative breeders, landscape differences in helping behaviour may have significant consequences for population persistence. In Chapter 3, I found that group size was positively related to nest success, multibroodedness and fledgling production (although this was not independent of habitat quality – see Chapter 5). There was also a positive correlation between territory quality and group size (Chapter 5). If habitat quality is reduced in fragmented landscapes, territories may not be able to support large groups and any benefits from group living may not be realised. Conversely, offspring may remain philopatric regardless of territory quality, potentially leading to large group sizes being a disadvantage if resources are not sufficient to support multiple individuals. The paradox in this situation is that the assistance of helpers may be more critical for reproductive success in habitats of low quality.

6.2 METHODS

6.2.1 Habitat structure and quality

Habitat structural characteristics were measured in each territory in Yilliminning following the methods described in Chapter 4. I took measurements in each of the original 30 territories, including four territories that were unoccupied in 1999 (see Chapter 7). These territories were divided between the habitat contexts described in Section 6.1.1. I used multidimensional scaling (MDS) to examine

overall differences in vegetation structure between habitat contexts. This was as an exploratory analysis only, used to plot the location of a territory in multidimensional space relative to other territories in the same or different habitat context. I used changes in the measure of stress to determine the number of dimensions suitable for analysis (see Hair et al. 1995 p. 505).

A habitat quality index was calculated for each territory in Yilliminning using the regression equation from Chapter 4 and the values for hollow log density (DHLOG), deadwood biomass (DWBM), tree size (TSIZ), tree hollow density (DHOL) and Wandoo canopy tree density (WC DEN). To create the composite variables of tree age (TAGE = DWBM + TSIZ) and nest sites (NSITE = DHOL + WC DEN), which were required for the regression equation (see Chapter 4), measures for all territories (Dryandra and Yilliminning) were included in a principal component analysis so that factor scores represented a relative measure between territories (DWBM was \log_{10} transformed before analysis). Factor loadings between the original habitat measures and the first two principal components were 0.93, 0.94, 0.84 and 0.89 respectively, after factors were subject to a varimax rotation.

As a result of the above analysis, the habitat quality indices for the Dryandra territories were re-calculated to reflect their relative value in relation to the Yilliminning territories. I calculated a mean quality value for each habitat context and examined differences between these values using one-way analysis of variance (ANOVA) and Tukey's honestly significant difference (HSD) for unequal sample sizes. I also compared the values of the original habitat measures that comprised the quality index (i.e., DHLOG, DWBM – \log_{10} transformed, TSIZ, DHOL and WC DEN) between Dryandra and Yilliminning using multiple analysis of variance (MANOVA) and Tukey's HSD. Differences in ground and shrub cover are analysed in Appendix 4.1.

6.2.2 Territory size and population density

Population density was determined by dividing breeding group size with territory size and calculating a mean value per habitat context. I calculated the size of each territory in Yilliminning using the methods described in Chapter 3. Treecreepers occasionally foraged at woodland-paddock edges, but generally avoided using agricultural land. Therefore, calculations of territory size were

constrained by remnant boundaries and excluded any agricultural land that was encompassed by the outer points of the minimum convex polygon. Some groups regularly crossed, but did not use, cleared land to incorporate more than one woodland remnant in their territory. In these cases, territory size was considered the combined area of the woodland remnants used, disregarding the area of cleared land that was crossed. I recorded a minimum of 40 locational fixes per territory, except the four territories that were only occupied for one breeding season, where I recorded a minimum of 20 locational fixes (the size of these territories may be underestimated). I compared territory size between landscapes using the Mann-Whitney test, and between habitat contexts in Yilliminning using one-way ANOVA and Tukey's HSD after data were \log_{10} transformed.

Population density estimates based on territory size fail to consider suitable, unoccupied habitat, and overestimate the total population density in each habitat context and the entire landscape. This was not a problem for grazed remnants because tree-creeper territories covered the entire remnant area, but my density calculations for ungrazed remnants are an overestimate because suitable habitat was unoccupied. However, density calculations based on group size and territory area were the most appropriate to compare between Dryandra and Yilliminning, because it was impossible to determine the percentage of suitable habitat in Dryandra that was unoccupied. For comparative purposes, I calculated a total population density for Yilliminning based on the area of Wandoo woodland (occupied and unoccupied) and estimated population size (including irregularly monitored territories that were assigned average group and territory sizes). Assuming that the majority of Wandoo woodland in Dryandra is occupied, population density in this woodland type would probably be similar to the combined value calculated for the three study sites.

Trends in density were consistent for each habitat context in 1998 and 1999, so I combined the data from both years to examine differences in mean population density between contexts using one-way ANOVA and Tukey's HSD (data were square root transformed before analysis). I used Spearman rank correlations to examine relationships between habitat quality, population density, group size and territory size in Yilliminning.

6.2.3 Demography and helping behaviour

I recorded the following demographic traits for the treecreeper population in Yilliminning: population size, sex ratio of adults and fledglings, group size, number of nest attendants, number of nest attempts per female, the percentage of breeding groups re-nesting after a successful nest attempt, the percentage of groups successfully raising two broods in a season, and the percentage of groups receiving help from neighbours in provisioning nestlings. The details of how these data were collected are in Chapter 3.

I compared group sizes and the number of nest attendants between habitat contexts using the Kruskal-Wallis test and a non-parametric multiple comparisons test (Zar 1996). I also compared differences in the nest success and number of fledglings produced by primary females in Yilliminning with at least 1 years' breeding experience, to those assumed to have no prior experience (see Chapter 3). The relationship between group size and nesting success and group productivity was also analysed.

In Dryandra, provisioning rate to nestlings was correlated with certain environmental and demographic variables, but had no relationship with the number of nest attendants (Appendix 3.1). Moreover, there was a significant negative relationship between the number of nest attendants and the provisioning rate of the primary male and female (Chapter 3). Using the methods described in Chapter 3 and Appendix 3.1, I collected data on the provisioning behaviour of treecreepers in Yilliminning to assess the importance of environmental and demographic variables on provisioning rate (these variables are detailed in Appendix 3.1), and changes in the provisioning effort of the primary male and female with differing levels of help.

Relationships between provisioning rate/hr and environmental and demographic variables, and the number of nest attendants, were modelled using Poisson regression (S-Plus 2000; Mathsoft 1999) following the methods of Nicholls (1989). The relationships between the provisioning rate of the primary male and female and the number of helpers were analysed using simple linear regression after data were square root transformed. In these analyses, scatterplots of residuals were examined for violations of regression assumptions.

6.3 RESULTS

6.3.1 Habitat structure and quality

The MDS identified reasonably clear differences in vegetation structure between territories. To assist in interpretation, I have only included data from Site B in Dryandra (previous analyses showed consistent patterns between sites), which were compared with each habitat context in Yilliminning. The majority of territories in the ungrazed remnants (67.7%, $n = 15$) clustered together in multidimensional space, separate from the Dryandra territories (Figure 6.1a). Those most similar to the Dryandra territories were generally from the large ungrazed habitat context. Most of the territories in the small grazed remnants also clustered away from the Dryandra territories, but the majority of territories in the large grazed habitat context (75%, $n = 8$) were positioned relatively close to a number of the Dryandra territories (Figure 6.1b). This suggests some structural similarity between these territories, which is interesting considering similar trends in population density were also identified (see below).

There were significant differences in quality between the habitat contexts (ANOVA, $F_{6,53} = 17.04$, $P < 0.001$; Figure 6.2). The mean quality of territories in Sites B and C in Dryandra was significantly higher than the mean quality of territories in each habitat context in Yilliminning (Tukey's HSD, $P < 0.05$). The mean quality of territories in Site A was significantly higher than the territories in the small ($P < 0.001$) and large ($P < 0.01$) grazed remnants, but there was no significant difference in quality between the habitat contexts in Yilliminning (Figure 6.2). Values of the original habitat measures that comprised the quality index also differed significantly between Dryandra and Yilliminning (MANOVA, $F_{5,54} = 23.52$, $P < 0.001$). All values were significantly lower in Yilliminning (Table 6.1).

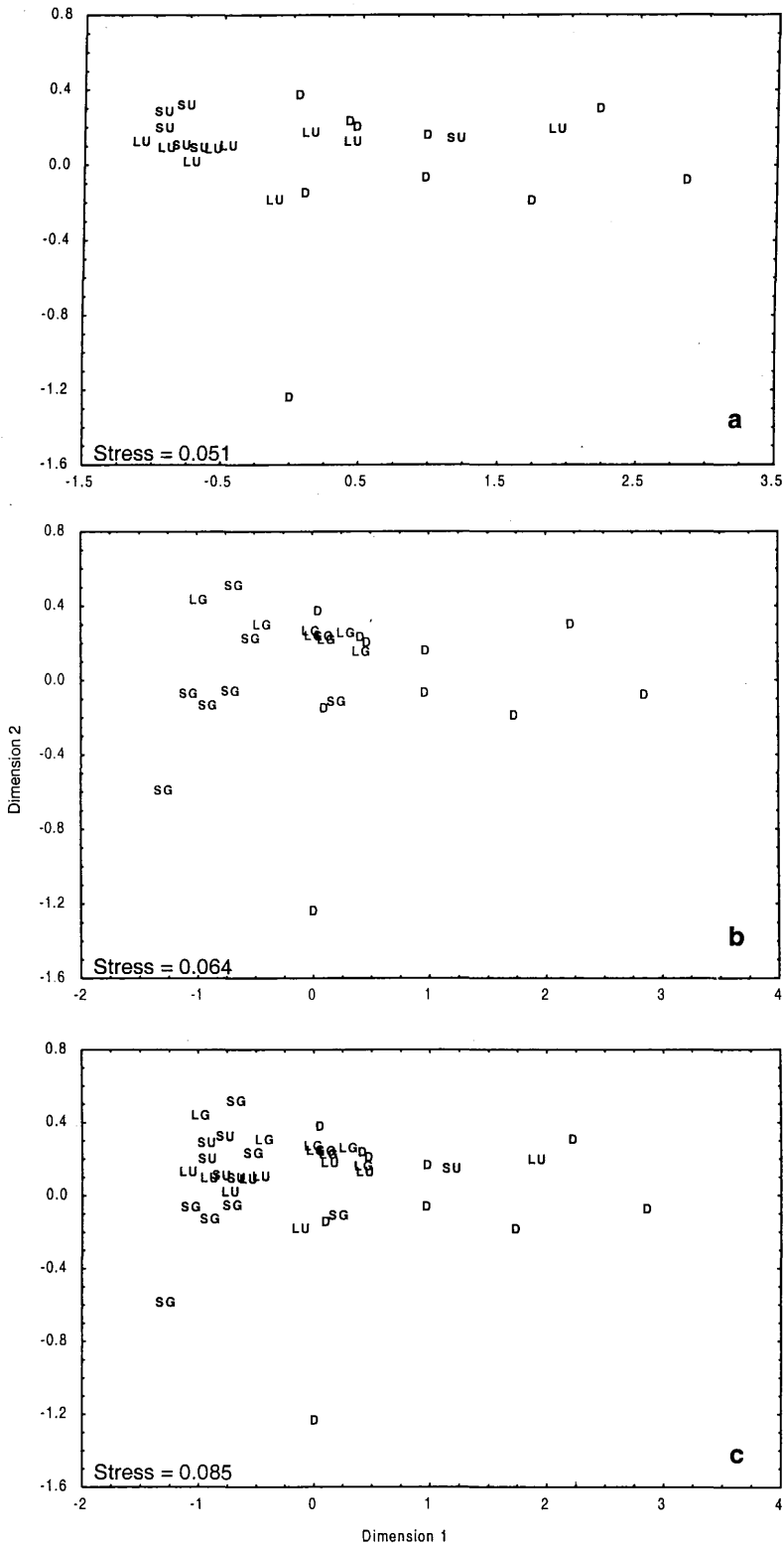


Figure 6.1 The multidimensional scaling analysis of the habitat structure of treecreeper territories in Dryandra (D) and the large and small ungrazed (LU and SU) and large and small grazed (LG and SG) remnants in Yilliminning. To aid interpretation, only data from Site B in Dryandra were used. Plots 'a' and 'b' show the position of territories in ungrazed and grazed remnants respectively, and plot 'c' shows all territories (the position of territories does not differ between plots).

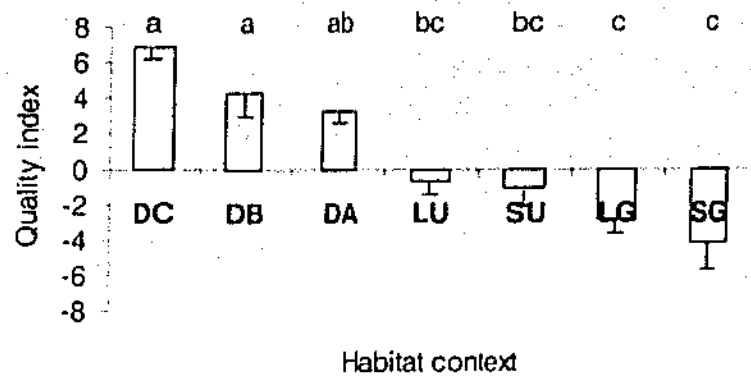


Figure 6.2 The mean quality index (in decreasing order) of territories in each site in Dryandra (DA – DC) and the four habitat contexts in Yilliminning (LU – SG, $n = 60$). Values with the same letter (above columns) are not significantly different.

Table 6.1 Mean (\pm s.e.) value of each habitat characteristic that comprised the habitat quality index, averaged across all territories in Dryandra and Yilliminning. Numbers in brackets are sample sizes. All differences are significant (Tukey's HSD); significance levels correspond to: * $P < 0.05$ and ** $P < 0.001$.

Habitat characteristic	Dryandra (30)	Yilliminning (30)	<i>P</i>
Deadwood biomass	19.4 \pm 1.58	15.2 \pm 1.49	*
Tree size (cm)	65.5 \pm 3.19	55.5 \pm 2.78	*
Density of hollows ha ⁻¹	110.7 \pm 7.37	62.3 \pm 6.49	**
Density of hollow bearing logs ha ⁻¹	22.7 \pm 1.62	12.9 \pm 1.31	**
Wandoo canopy tree density ha ⁻¹	70.4 \pm 4.35	21.0 \pm 1.86	**

6.3.2 Territory size and population density

Territory size in Yilliminning (3.5 ha \pm 0.34, $n = 30$) was significantly larger than Dryandra (2.6 ha \pm 0.18, $n = 30$, Mann-Whitney test, $Z = 1.99$, $P = 0.047$), but territory size differed significantly between habitat contexts in Yilliminning (ANOVA, $F_{3,26} = 10.47$, $P < 0.001$). Territories in ungrazed remnants were significantly larger than territories in grazed remnants (Tukey's HSD, $P < 0.05$; Table 6.2).

Population density did not differ significantly between Dryandra (1.36 \pm 0.12 individuals ha⁻¹) and Yilliminning (1.14 \pm 0.12 individuals ha⁻¹) in 1998 (t -test, $t_{58} = 1.20$, $P = 0.24$), but was significantly higher in Dryandra (1.29 \pm 0.12 individuals ha⁻¹) in 1999 (Yilliminning: 0.86 \pm 0.12 individuals ha⁻¹, $t_{54} = 3.14$, $P = 0.003$). If

unoccupied, apparently suitable habitat is considered, total population density for Yilliminning (averaged over 1998 and 1999) is reduced to just 0.21 individuals ha^{-1} . This is substantially less than the average population density for the three study sites in Dryandra (1.33 individuals ha^{-1} ; averaged over 1998 and 1999), which may be representative of total population density in Wandoo woodland in this landscape.

Table 6.2 Territory size (mean \pm s.e.) in each habitat context in Yilliminning. Means with the same letter are not significantly different. Numbers in brackets are sample sizes.

Habitat context	Territory size (ha)
Large ungrazed (9)	4.9 \pm 0.73 ^a
Large grazed (8)	2.2 \pm 0.25 ^b
Small ungrazed (6)	4.6 \pm 0.61 ^a
Small grazed (7)	2.5 \pm 0.32 ^b

I compared population density between grazed and ungrazed remnants, and Dryandra, for both years combined because trends were consistent within each of these contexts (Table 6.3). Mean density differed significantly in this comparison (ANOVA, $F_{2,57} = 11.96$, $P < 0.001$). Ungrazed remnants had significantly lower density than grazed remnants and Dryandra (Tukey's HSD, $P < 0.001$).

Table 6.3 Population density (mean \pm s.e.) in each habitat context. Means with the same letter are not significantly different (comparing combined ungrazed, combined grazed and Dryandra). Numbers in brackets are sample sizes.

Habitat context	Population density (individuals ha^{-1})		
	1998 (60)	1999 (59)	Overall
Large ungrazed	0.71 \pm 0.12	0.69 \pm 0.09	0.70
Large grazed	1.70 \pm 0.27	1.06 \pm 0.13	1.38
Small ungrazed	0.60 \pm 0.11	0.55 \pm 0.17	0.58
Small grazed	1.51 \pm 0.35	1.10 \pm 0.17	1.31
Combined ungrazed	0.67 \pm 0.08	0.63 \pm 0.08	0.65 ^a
Combined grazed	1.61 \pm 0.21	1.08 \pm 0.10	1.35 ^b
Dryandra	1.36 \pm 0.12	1.29 \pm 0.12	1.33 ^b

In Yilliminning, larger territories did not support larger groups ($r_s = -0.218$, $P = 0.245$) and territory size was positively correlated with habitat quality ($r_s = 0.432$, $P = 0.017$), where a negative correlation would be expected if space use by

treecreepers was mediated by the quality of the habitat. Mean population density for both years combined was negatively rather than positively correlated with habitat quality ($r_s = -0.308$, $P = 0.098$, $n = 30$).

6.3.3 Demography and helping behaviour

Demography

The size of the study population in Yilliminning was 93 in 1998 and 72 in 1999. There was a trend for the sex ratio to be biased towards males in 1998 ($\delta:\text{♀} = 55:38$, Binomial test, $Z = 1.76$, $P < 0.10$), but there was no difference in 1999, although the trend was in the same direction ($\delta:\text{♀} = 42:30$, $Z = 1.41$, $P > 0.10$). Similarly, there was no difference in the sex ratio of fledglings born in 1998 ($\delta:\text{♀} = 14:18$) and 1999 ($\delta:\text{♀} = 15:13$), but sample sizes were small.

Group size ranged from one to six individuals (2.8 ± 0.13 , $n = 59$ group years), and the number of nest attendants from two to six (2.9 ± 0.11 , $n = 82$ nest watches). Group size did not differ between habitat contexts in 1998 or 1999, but the number of nest attendants differed significantly in both years (Table 6.4). This was primarily a result of the high number of nest attendants at Site C in Dryandra. The number of nest attempts per female was similar between landscapes (Table 6.5). The percentage of breeding groups receiving assistance from neighbours in provisioning nestlings was slightly higher in Dryandra for both years, but the differences were not significant. In 1999, significantly more groups in Dryandra re-nested after a successful nesting attempt and raised two broods to fledging (Table 6.5).

Primary female experience

In contrast to the results obtained in Dryandra, there were significant differences in productivity between primary females with at least 1 years' breeding experience (2nd year females) and those assumed to have no prior experience. Nest success was significantly higher for 2nd year females (62.5%, $n = 24$ vs 28.3%, $n = 14$, Fisher exact test, $P = 0.04$), as was the number of fledglings produced in a season (1.4 ± 0.29 vs 0.5 ± 0.22 , Mann-Whitney test, $Z = 2.05$, $P = 0.04$).

Table 6.4 Group size and number of nest attendants (mean \pm s.e.) in each habitat context in 1998 and 1999. Non-parametric multiple comparisons test indicated that Site C had significantly more nest attendants than all other contexts except Site B in 1998 (the test failed to identify which contexts differed in 1999, despite there being an overall difference). Numbers in brackets are sample sizes (number of territories for habitat context and number of nest watches for nest attendants).

<i>Habitat context</i>	Group size		Nest attendants	
	<i>1998</i>	<i>1999</i>	<i>1998</i>	<i>1999</i>
<i>Dryandra</i>				
Site A (10)	2.4 \pm 0.16	2.7 \pm 0.21	2.5 \pm 0.16 ^a (16)	3.1 \pm 0.19 (11)
Site B (10)	3.3 \pm 0.33	2.8 \pm 0.36	3.7 \pm 0.31 ^{ab} (14)	3.2 \pm 0.30 (19)
Site C (10)	4.0 \pm 0.56	3.7 \pm 0.54	5.4 \pm 0.34 ^b (17)	4.4 \pm 0.39 (20)
Overall	3.2 \pm 0.25	3.1 \pm 0.23	3.9 \pm 0.24	3.6 \pm 0.19
<i>Yilliminning</i>				
LU (9)	3.0 \pm 0.24	3.0 \pm 0.29	3.4 \pm 0.37 ^a (13)	2.7 \pm 0.26 (10)
LG (8)	3.4 \pm 0.42	2.4 \pm 0.26	2.7 \pm 0.22 ^a (14)	2.8 \pm 0.40 (9)
SU (6/5)	2.5 \pm 0.34	2.0 \pm 0.45	2.9 \pm 0.35 ^a (8)	2.8 \pm 0.37 (5)
SG (7)	3.4 \pm 0.61	2.6 \pm 0.30	3.3 \pm 0.22 ^a (14)	2.8 \pm 0.28 (9)
Overall	3.1 \pm 0.21	2.5 \pm 0.16	3.1 \pm 0.15	2.8 \pm 0.16
<i>Context comparison</i>	$H_{5,60} = 9.72$ $P = 0.14$	$H_{6,59} = 8.04$ $P = 0.24$	$H_{6,95} = 38.58$ $P < 0.001$	$H_{6,89} = 14.51$ $P = 0.02$

Table 6.5 The number of nest attempts per female, percentage of breeding groups receiving provisioning assistance from neighbours (cross-territorial), and percentage of females re-nesting after a successful nest attempt or raising two broods to fledging in a season. Values marked with an asterisk are significantly different (Dryandra vs Yilliminning, Fisher exact test, $P < 0.03$). Numbers in brackets are sample sizes.

	Dryandra		Yilliminning	
	<i>1998 (30)</i>	<i>1999 (30)</i>	<i>1998 (30)</i>	<i>1999 (28)</i>
Nest attempts/female	1.6	1.9	1.6	1.6
% cross-territorial	30.0	10.0	16.7	4.2
% re-nesting	40.0	70.0*	30.0	35.7*
% two broods	26.7	46.7*	13.0	17.9*

Helping behaviour

In Yilliminning, there were positive relationships between reproductive success and group size, similar to the results obtained in Dryandra (Chapter 3). Groups of \geq three individuals raised a significantly higher percentage of multiple broods to fledging (within a season), and had a lower percentage of failed nests (weakly significant; Table 6.6). Groups $>$ three also raised almost twice as many fledglings (1.64 ± 0.32 , $n = 14$) as groups of two (0.88 ± 0.19 , $n = 26$) or three (0.89 ± 0.23 , $n = 18$), but the difference was only weakly significant (Kruskal-Wallis test, $H_{2,58} = 4.71$, $P = 0.095$). Group size was not significantly related to productivity once other factors had been considered (Chapter 7).

Table 6.6 The percentage of failed nests, groups re-nesting after raising a brood to fledging, and groups successfully raising two broods in a season for groups of $<$ three and \geq three individuals. Data were analysed using the Fisher exact test. Numbers in brackets are sample sizes.

	Group size		<i>P</i>
	< 3	≥ 3	
Failed nests (91)	64.0	44.0	0.09
Re-nesting (58)	22.7	42.8	0.18
Two broods (58)	3.8	28.1	0.02

Data from 46 nest watches in Yilliminning were included in the analyses of relationships between provisioning rate per hour and environmental and demographic variables, and the number of nest attendants. The Poisson modelling procedure identified correlative relationships between provisioning rate and the number of nestlings, nest stage and time of day, in accord with the results from Dryandra (Appendix 3.1). In contrast to Dryandra though, there was a significant positive relationship between the number of nest attendants and provisioning rate (Tables 6.7 and 6.8). In fact, the number of nest attendants was associated with the largest change in model deviance.

Table 6.7 Change in model deviance (distributed as χ^2) with the addition of the independent variables listed ($n = 46$).

Model	df	Change in deviance	Residual df	Residual deviance	<i>P</i>
Null			45	139.4	
No. of nest attendants	1	33.8	44	105.6	< 0.001
No. of nestlings	1	17.4	43	88.2	< 0.001
Nest stage	2	10.0	41	78.2	< 0.01
Time of day	1	6.1	40	72.1	< 0.025

Table 6.8 The coefficients and standard errors (s.e.) of each variable included in the final Poisson model.

Variable	Coefficient	s.e.
Constant	0.697	0.285
No. of nest attendants	0.172	0.039
No. of nestlings	0.359	0.117
Nest stage 1	0.256	0.101
Nest stage 2	0.124	0.039
Time of day	-0.043	0.017

The positive relationship between provisioning rate and the number of nest attendants in Yilliminning suggests care was additive rather than compensatory in this landscape (see Appendix 3.1). Therefore, the provisioning rate of primary males and females is likely to remain relatively constant regardless of the number of helpers. I controlled for number of nestlings, nest stage and time of day, and examined the relationship between the provisioning rate of the primary male and female and the number of helpers at the nest using linear regression. The slope of the regression was negative for both sexes (Figure 6.3a and b), but there was no significant relationship between the provisioning rate of the primary male ($F_{1,32} = 0.69$, $P = 0.41$, Adjusted $R^2 = -0.009$) or primary female ($F_{1,32} = 0.22$, $P = 0.64$, Adjusted $R^2 = -0.024$) and the number of helpers. Both sexes provisioned at a relatively constant rate. The decline in provisioning rate was slightly greater in males (slope of regression -0.146 ± 0.18) than females (-0.082 ± 0.18), consistent with the results from Dryandra, but the difference between the sexes was not significant ($t_{64} = 0.86$, $P > 0.10$).

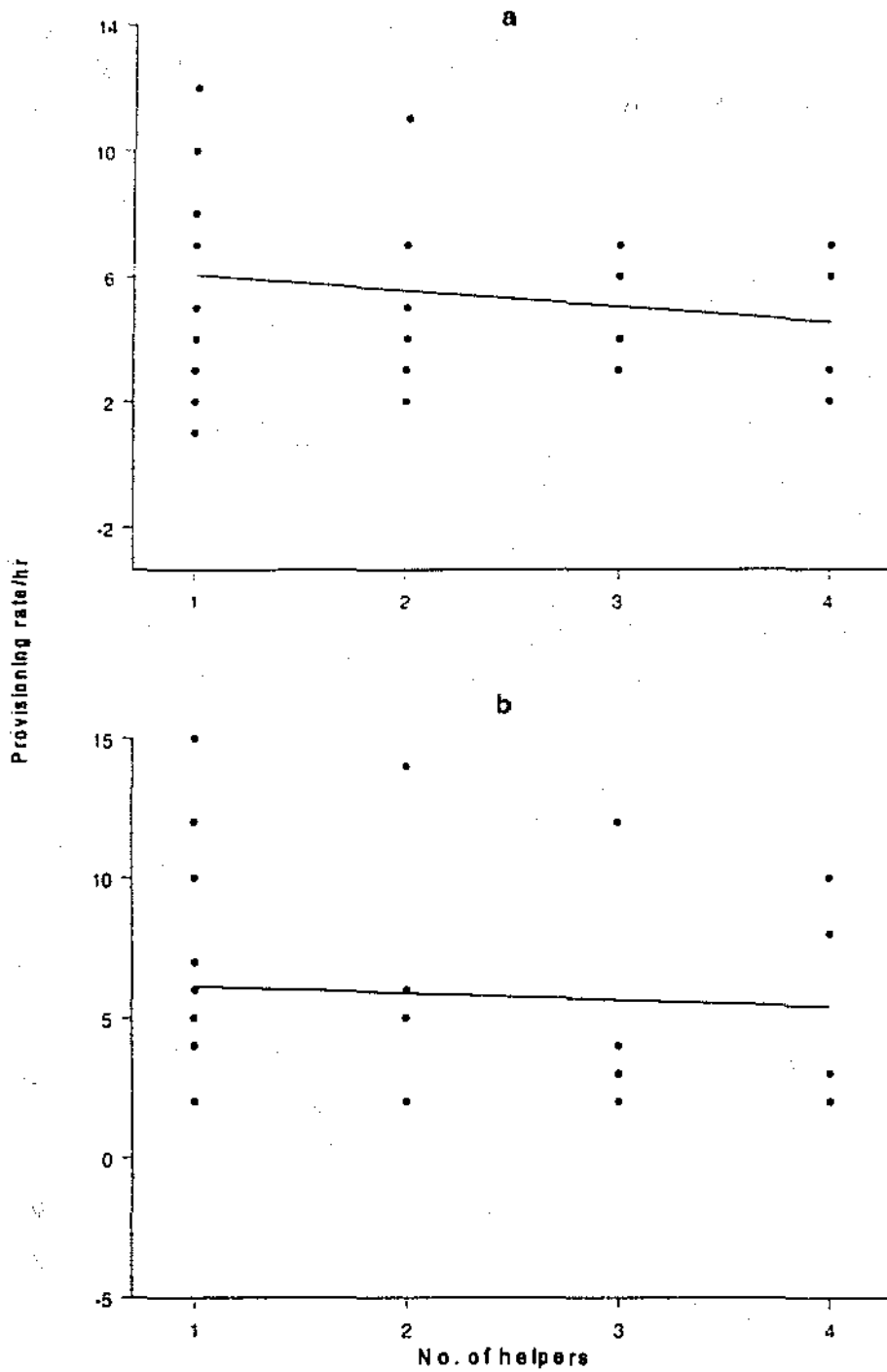


Figure 6.3 The provisioning rate/hr of the: a) primary male, and b) primary female with an increase in the number of helpers at the nest. Not every datum is shown ($n = 34$), as cases with the same value are represented by a single point. The solid line is the line of best fit; dotted lines are 95% confidence intervals.

6.4 DISCUSSION

6.4.1 Habitat structure and quality

The structure of the habitat used by treecreepers in Yilliminning differed significantly from Dryandra, particularly in the characteristics that comprised the habitat quality index (Table 6.1; see Appendix 4.1 for differences in ground and shrub cover). Consequently, habitat quality differed significantly between landscapes, but there were no significant differences between habitat contexts in Yilliminning (Figure 6.2). Differences in habitat structure between landscapes was influenced to a degree by treecreeper use of different woodland types in Yilliminning, but most of the original 30 territories (76.7%) were in predominantly Wandoo woodland. These woodlands have been altered by a number of processes mostly emanating from the surrounding landscape. Although much of the fragmentation literature has focussed on remnant spatial characteristics, within-remnant disturbances also represent substantial threats to population viability.

In the territories occupied by treecreepers in Yilliminning, the mean density of tree hollows and hollow bearing logs was almost half that of Dryandra, and the density of Wandoo canopy trees was less than half (Table 6.1). The density of these important habitat characteristics may not be critically low at the moment, but they will continue to decline if habitat degradation persists. Current degrading processes include grazing (which limits seedling recruitment), selective logging, removal of deadwood for fires or to “clean-up” woodland patches, salinity and altered fire regimes. A major effort is required to ensure that important habitat characteristics are maintained in woodland remnants in agricultural landscapes.

As habitat structure differed between Dryandra and Yilliminning, it would be necessary to control for the confounding influence of these differences to determine the independent effects of remnant and landscape spatial characteristics on population viability. However, in highly disturbed landscapes like the Western Australian wheatbelt, there is always likely to be habitat structural differences between fragmented and unfragmented areas. It is important to document these differences to avoid potentially erroneous conclusions about the influence of remnant spatial characteristics on the ecological traits of species. If differences in habitat structure are a significant threat to population viability, habitat manipulation (e.g., scouring the soil to encourage seedling recruitment) may confer a greater

benefit than increasing the size or connectivity of remnants (Tellería and Santos 1995).

6.4.2 Population density

Total population density was significantly higher in Dryandra compared to Yilliminning in 1999, but not 1998. This comparison includes an inflated density estimate for Yilliminning, and when suitable, unoccupied habitat was also considered, population density in the agricultural landscape was substantial less than Dryandra. Lower population density may occur in small habitat remnants compared to larger areas (Gibbs and Faaborg 1990; Villard et al. 1993; Wenny et al. 1993; Matthysen 1999). Lower density may also be a result of poor habitat quality (Burke and Nol 1998), but density can still vary in cases where habitat structure is similar between fragmented and unfragmented areas (Wenny et al. 1993).

Significant variability in population density occurred between habitat contexts in Yilliminning. Density was extremely low in ungrazed remnants, with density in grazed remnants similar to that recorded in Dryandra (Table 6.3). Differences in density did not appear to be related to changes in habitat quality because grazed remnants were of a lower quality than ungrazed remnants (Figure 6.2). Also, territory size was positively correlated with habitat quality similar to the findings of Brooker and Rowley (1995) in their study of the Splendid Fairy-wren *Malurus splendens*.

Habitat selection theory generally assumes that species preferentially select habitat where fitness is maximised (Fretwell and Lucas 1970; Rosenzweig 1991). This could result in population density being highest in preferred habitat. However, the distribution of individuals among habitats may be influenced by density-dependent effects (ideal-free distribution) or territorial aggression by established breeders (ideal-despotic distribution; Fretwell and Lucas 1970). In the ideal-free model, density-dependent effects that reduce fitness in preferred habitats may result in individuals using less preferred habitat with no adverse consequences for fitness (e.g., reproductive output would be similar across habitats). In the ideal-despotic model, competitively superior individuals may exclude others from high quality habitat, possibly resulting in low densities, but increased fitness in these habitats

(Fretwell and Lucas 1970; Van Horne 1983; Rodway and Regher 1999). In this situation, population density may be highest in low quality habitat.

The distribution of Rufous Treecreepers in Yilliminning appears to be closer to the ideal-despotic model (which may be expected for territorial species), particularly considering the negative relationship between density and reproductive success (Chapter 7). However, patterns in distribution and density could be complicated by fragmentation effects and the social organisation of the species. Grazed remnants had the highest population densities, but also had a low percentage of surrounding native vegetation (Chapter 7). Treecreepers in these remnants had fewer close dispersal options, which may lead to a crowding effect whereby individuals choose to remain in a remnant rather than undertake long and potentially dangerous dispersals.

The social organisation of the Rufous Treecreeper suggests that population density may be mediated by factors other than, or in addition to, habitat quality. In Chapter 5, I found that territory size was not correlated with habitat quality, and argued that territory contiguity and interactions between territorial neighbours had a greater influence on space use by treecreepers. This could be disadvantageous in habitat of poorer quality where individuals may need to maintain larger territories to ensure access to sufficient resources (Wiens et al. 1985). In Dryandra, breeding groups formed interactive, ecological neighbourhoods, and sociality may be an important ecological trait in the treecreeper (Chapter 3). The theory of conspecific attraction suggests that individuals preferentially select to settle in sites that already contain conspecifics (Smith and Peacock 1990; Muller et al. 1997). Hence, the presence of conspecifics is used as a cue to identify suitable habitat.

There is no clear reason why social processes that potentially influence density should differ between grazed and ungrazed remnants, but it may reflect differences in group stability. In Yilliminning, 16 breeding groups disappeared during the 2 years of the study (Chapter 8). Eleven of these were from grazed remnants where group turnover appeared to be common. Group stability in ungrazed remnants may be higher and territory occupants would be more experienced and familiar with their surroundings, which may confer a competitive advantage. That is, stable groups may be competitively superior at excluding new immigrants.

Regardless of the potential reasons for differences in population density, an important conclusion from these results is that density is an inappropriate indicator of habitat quality in Yilliminning, supporting the assertions of Van Horne (1983). However, on examining the relationship between density, habitat quality and group productivity in Dryandra, I found a consistent pattern across the three study sites whereby density was positively related with quality and group productivity (Figure 6.4). In relatively undisturbed landscapes like Dryandra, population density may well be a reasonable surrogate for habitat quality, but the density-quality relationship may be disrupted with habitat fragmentation.

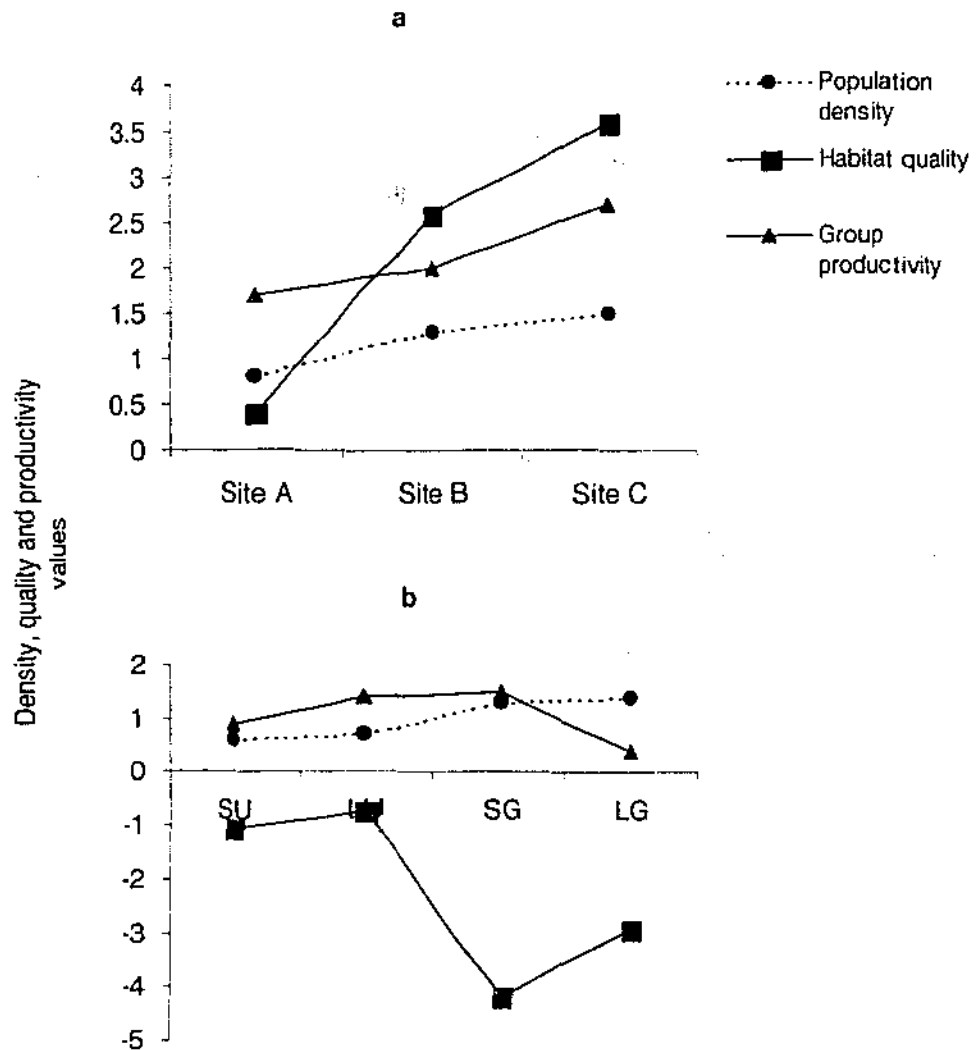


Figure 6.4 The average population density, habitat quality and group productivity values for: a) each site in Dryandra, and b) each habitat context in Yilliminning for the duration of the study. The trend in Dryandra is for increasing density values to correspond with increasing quality and productivity values. A similar trend was not observed in Yilliminning.

6.4.3 Demography and helping behaviour

Demography, helping behaviour and breeder experience

There was no significant bias in population sex ratio for treecreepers in Yilliminning, although the trend was towards a greater number of males (Section 6.3.3). This is consistent with the results in Dryandra and is most likely a consequence of female-biased dispersal (Chapter 3). Importantly, I did not find a large number of unpaired males occupying territories in the fragmented landscape, as has been found for the Ovenbird in the United States (Gibbs and Faaborg 1990; Van Horn et al. 1995; Burke and Nol 1998) and the Brown Treecreeper *Climacteris picumnus* in New South Wales (Walters et al. 1999). This includes all territories that were surveyed in the study area ($n = 41$). In 1999, four individuals (two males and two females) remained unpaired for at least 6 months, but three were eventually paired by the beginning of the breeding season. These results suggest that the level of habitat fragmentation in Yilliminning does not significantly impair the movement of the Rufous Treecreeper between remnants, although it may impact on their ability to locate potential breeding vacancies (Chapter 9).

There was no significant difference in breeding group size between habitat contexts, but there was a significant difference in the number of nest attendants in both years. This result was influenced by the high number of nest attendants at Site C in Dryandra (Table 6.4), and the slightly smaller group sizes and low percentage of cross-territorial provisioning recorded in Yilliminning. The percentage of cross-territorial provisioning of nestlings did not differ significantly in either year of my study (Table 6.5), but the difference was significant with both years combined (Dryandra 23.3%, $n = 60$ vs Yilliminning 7.4%, $n = 54$, Fisher exact test, $P = 0.02$).

The lower percentage of cross-territorial provisioning in Yilliminning may result from the greater distance between territories, barriers to movement (e.g., roads) and a lower number of territorial neighbours owing to the size and shape of habitat remnants. The average number of territorial neighbours for a given territory in Dryandra (3.9 ± 0.21 , $n = 30$) was significantly higher than Yilliminning (2.2 ± 0.21 , $n = 30$, Mann-Whitney test, $Z = 4.41$, $P < 0.001$). If cross-territorial provisioning is driven by relatedness between territory owners (Chapter 3), a lower occurrence in Yilliminning may also be a result of a relatively high turnover of

territory ownership (Chapter 8), limiting the opportunities for the establishment of interrelated, interactive neighbourhoods.

In contrast to the results from Dryandra (Chapter 3), primary females in Yilliminning with at least 1 years' breeding experience had significantly higher nest success and produced more fledglings than those assumed to have no prior experience (at least in their adopted territory). I propose three possible reasons for the greater influence of breeder experience on reproductive success in Yilliminning. First, environmental conditions were more constrained (e.g., lower habitat quality and possibly reduced food availability) and territory familiarity may offer a greater reproductive advantage to experienced females. Second, the dispersal distance travelled by females settling into new territories may be greater in fragmented landscapes (Matthysen et al. 1995; Breininger 1999) and this could reduce female condition. Third, most new females in Yilliminning (78.6%, $n = 14$) began their reproductive life in pairs, and pairs had a lower reproductive output than larger groups (Section 6.3.3).

High turnover of territory ownership in Yilliminning meant that inexperienced breeders were relatively common. Disappearance from a territory (i.e., death or dispersal) was also more likely after reproductive failure (Chapter 8). This scenario represents a concerning cycle for treecreepers in the agricultural landscape. New females have greater reproductive failure, which may lead to them vacating a territory, which in turn is occupied by a new female. Therefore, few territories would have experienced, established breeders, which are often the high producers of the breeding population (Rowley and Russell 1991).

Compensatory vs additive care

An important result from my study was the landscape differences in provisioning effort recorded for primary males and females. In Dryandra, there was a significant negative relationship between provisioning rate and the number of helpers for both primary sexes (Chapter 3). As the number of helpers increased, primary males and females exhibited compensatory behaviour by reducing their provisioning effort. Consequently, total provisioning rate to nestlings was not related to changes in the number of helpers. In contrast, primary males and females in Yilliminning did not significantly reduce their provisioning effort in the presence of

helpers and there was a strong positive correlation between the number of helpers and provisioning rate to nestlings (Table 6.7). In this instance, care was additive.

A number of cooperatively breeding birds exhibit compensatory care whereby one or both of the breeding pair reduce their provisioning contribution in the presence of helpers (Brown et al. 1978; Lewis 1981; Curry 1988; Russell and Rowley 1988; Wright and Dingemanse 1999). Other species exhibit additive care (Mumme et al. 1990; Walters 1990; Emlen and Wrege 1991), and in one species (Long-tailed Tit *Aegithalos caudatus*) both "investment strategies" have been recorded owing to differences in the number of helpers (Hatchwell 1999).

Hatchwell (1999) reviewed the incidence of compensatory and additive care in cooperative breeders. The main conclusion from this work was that care was additive when nestling starvation (resulting in brood reduction) was frequent, and compensatory when starvation (and brood reduction) was rare. This conclusion was supported from an analysis of 27 species of cooperative breeders. The incidence of nestling starvation in the two treecreeper populations examined in my study is difficult to determine owing to limited access to nests, but inferential evidence suggests that nestling starvation could have been more common in Yilliminning.

Total provisioning rates and food biomass delivered to nestlings was significantly lower in Yilliminning suggesting that food availability was reduced in this landscape (Chapter 7). This may increase the chances of nestling starvation, but evidence of this was not found when comparing fledgling weights between landscapes (Chapter 7). If nestling starvation is more frequent in Yilliminning, nest success (the probability of fledging at least one nestling) should be lower than Dryandra and there should be a positive relationship between success and the number of helpers at the nest. Data from my study support these assertions, with nest success being significantly higher in Dryandra (Chapter 7), and a positive relationship between success and group size in Yilliminning (Table 6.6). However, this positive relationship was also evident in Dryandra (Chapter 3) where nest failure (and presumably nestling starvation) was low. Importantly though, the level of nest failure for unassisted pairs in Yilliminning (64%, $n = 41$) was significantly higher than Dryandra (36%, $n = 25$, Fisher exact test, $P = 0.04$).

Further inferential support for nestling starvation as a primary factor contributing to the difference in nest success between landscapes is that nest

predation did not appear to be an important determinant of success for Rufous Treecreepers, and relative predation rates did not differ between Dryandra and Yilliminning (Chapter 7). My assertion is largely based on results from artificial nest experiments and further research on the influence of nest predators on the success of hollow-nesters is required.

Nestling starvation would result in brood reduction (Hatchwell 1999) and the incidence of smaller broods should be greater in Yilliminning, but small broods appear to be characteristic of the Rufous Treecreeper (a brood size of two is common – Chapter 3) and any reduction in size could result in complete nest failure. This raises difficulties when attempting to determine the cause of nest failure for inaccessible nests because complete nest failure may be a result of predation, as opposed to brood reduction through nestling starvation. Determining differences in the number of breeding groups with a brood size of one may give some indication of the incidence of nestling starvation. In this case, brood reduction is unlikely to be a result of predation because it would be reasonable to expect predators to cause complete nest failure (this comparison does not account for landscape differences in clutch size).

If nestling starvation was greater in Yilliminning, a reasonable prediction would be that brood sizes of one should be more common in this landscape than Dryandra. Out of the total number of nests that produced fledglings in each landscape, I determined the percentage of nests producing only one fledgling. The difference between landscapes was in the predicted direction with a slightly higher percentage of nests in Yilliminning (51.2%, $n = 41$) producing one fledgling (Dryandra; 38.7%, $n = 80$), but this difference was not significant (one-tailed Fisher exact test, $P = 0.13$).

Although data on the incidence of nestling starvation in each landscape are equivocal, it is clear that parental response to helpers may vary in the same species under different environmental conditions, and generalisations for a given species may not be appropriate. In Yilliminning, habitat quality (and apparently food availability) was significantly lower than Dryandra. I predict that in poor quality habitats where food availability is limited, the investment strategy in nestling care will be additive rather than compensatory for cooperative breeders. In addition, the costs to helpers in providing care may be greatly increased under constrained

environmental conditions. For example, Boland et al. (1997) found that White-winged Chough *Corcorax melanorhamphos* helpers engaged in deceptive “non-feeding” of nestlings (i.e., carrying food to nestlings and appearing to feed them, but consuming the food themselves) probably as a result of a difficult foraging niche (Heinsohn and Legge 1999). This behaviour was reduced with the supplementation of food.

I have no evidence that helping was more costly in Yilliminning compared to Dryandra. A food supplementation experiment in Yilliminning would help determine if lower food availability is a possible reason for the prevalence of additive care. It would also be useful to examine correlations between seasonal and annual differences in food availability, and parental response to the presence of helpers. With food supplementation, I predict that parental responses in Yilliminning would be compensatory rather than additive.

Restrictions on the amount of food delivered to nestlings may have adverse consequences for nestling fitness (e.g., growth rate, weight and survival) and breeder productivity (Seki and Takano 1998; Siikamäki 1998; Naef-Daenzer and Keller 1999). For cooperative breeders, the role of helpers in constrained environmental conditions may be even more critical to reproductive output. However, a trade-off could exist between habitat quality, group size and reproductive success. More helpers means additional food brought to nestlings, but it would also increase the demands placed on the habitat. In this case, if territory size and resource availability are correlated, groups occupying larger territories may be at a reproductive advantage, as found in my study (Chapter 7). Under constrained environmental conditions, cross-territorial provisioning could also be extremely important, as non-resident helpers may bring food from their own territory to provision nestlings (Chapter 3). Conversely, if non-residents use helping as a means of accessing resources in adjacent territories, their presence may have adverse consequences by increasing the demand placed on a given territory.

The complexity of these relationships and the potential consequences of habitat fragmentation means that assessing the threats to population persistence for Rufous Treecreepers is extremely difficult. An observational study such as mine can only suggest possible causal relationships, but it establishes the platform on which carefully directed, experimental studies can be based. I join with Zanette et al. (2000)

in calling for more work to be focussed on the relationships between habitat fragmentation, food availability, species behaviour, reproductive success and survival.

CHAPTER 7
LANDSCAPE DIFFERENCES IN REPRODUCTIVE SUCCESS
AND SURVIVAL

SUMMARY

Lower reproductive success and survival in fragmented landscapes may adversely affect the population viability of woodland dependent birds. This is one possible reason for the decline of these species in the agricultural regions of southern Australia. I compared the reproductive success and offspring survival of the Rufous Treecreeper between the three sites in Dryandra and the four habitat contexts in Yilliminning.

Nest success and annual group productivity were significantly higher in Dryandra, but varied between sites and contexts within landscapes. In Yilliminning, nest success was lowest in grazed remnants and was also influenced by nest-site selection. Group productivity was positively associated with territory size. However, grazing and territory size were related because grazed remnants contained smaller territories. Fledgling survival rate did not differ between landscapes, but there was a trend for juvenile survival rate to be higher in Dryandra.

I used artificial nests to compare relative predation rates between Dryandra and Yilliminning. Overall predation rate was relatively low (33.1%) and did not differ significantly between landscapes. I also recorded provisioning rates and prey biomass brought to nestlings to examine inferential evidence for differences in food availability. Provisioning rates to nestlings and total prey biomass were significantly lower in Yilliminning suggesting that food availability may be reduced in this landscape.

Lower reproductive success, juvenile survival and food availability may threaten the persistence of the Rufous Treecreeper population living in Yilliminning. Improvements in habitat quality may be required to ensure the future viability of the species.

7.1 INTRODUCTION

7.1.1 Overview

In the first part of this chapter, I examine patterns in nest success, group productivity and offspring survival between the seven habitat contexts described in Chapter 6 (Section 6.1.1). I then assess correlative relationships between reproductive success and a number of social, habitat, remnant and landscape measures. This is a first step to examining some of the processes (e.g., grazing) that may underlie the identified patterns. In the final section of this chapter, I analyse selected threatening processes more directly. These processes are nest predation, nest-site selection and food availability. The aims of this chapter are to:

- a) compare reproductive success and offspring survival between the three sites in Dryandra and the four habitat contexts in Yilliminning;
- b) examine correlative relationships between nest success and group productivity, and a range of social, habitat, remnant and landscape measures; and
- c) directly assess selected threatening processes.

7.1.2 Patterns in reproductive success

In North America, patterns of decline have been recorded for certain Neotropical migrant bird species in highly fragmented forests (Askins et al. 1990; Wilcove and Robinson 1990). One of the main reasons for this decline appears to be lower reproductive output in disturbed, fragmented habitat compared to more continuous forest (Wilcove and Robinson 1990; Robinson et al. 1995). Reduced reproductive output may be a result of lower population density or lower pairing and reproductive success in fragmented habitat.

The results of studies that have compared the reproductive success of selected Neotropical migrants between continuous and fragmented forest (or large and small forest remnants) have been equivocal. For example, the reproductive success of the Ovenbird *Seiurus aurocapillus* may be reduced in small forest remnants (Pomeluzi and Faaborg 1999), but these patterns are not always consistent (Donovan et al. 1995). Lower success in small remnants has also been recorded for the Wood Thrush *Hylocichla mustelina* (Hoover et al. 1995; Weinberg and Roth 1998), but not the Worm-eating Warbler *Helmitheros vermivorus* (Gale et al. 1997).

Studies in Europe have also yielded varying results. Open-nesting species may suffer lower reproductive success in small forest remnants (Kurki and Lindén 1995), but studies of hollow-nesting species have found no relationship between fragmentation and success (Tjernberg et al. 1993; Matthysen and Adriaensen 1998; Nour et al. 1998).

In Australia, only a handful of studies have compared the reproductive success of birds between areas with differing levels of habitat fragmentation. Saunders (1977) found that the average number of fledglings produced by the White-tailed Black Cockatoo *Calyptorhynchus latirostris* was twice as high in an area with large tracts of indigenous vegetation compared to a landscape that was extensively cleared. A study of the Brown Treecreeper *Climacteris picumnus* found no difference in reproductive success between "more" and "less" fragmented habitat (Walters et al. 1999). The average nest success and fledgling production of the Eastern Yellow Robin *Eopsaltria australis* was higher in small (55 ha) compared to large (> 500 ha) habitat remnants, although the trends were not consistent between replicated remnants of the same size class (Zanette 2000).

It is difficult to interpret general patterns from these studies owing to differences in land-use history, levels of fragmentation, habitat type and the ecological characteristics of species. The size of remnant vegetation patches may also differ dramatically between studies. In their study of the Wood Thrush, Weinberg and Roth (1998) compared reproductive success between a 15 ha "large" remnant and "small" remnants ≤ 2.1 ha, whereas in a study of the same species, Hoover et al. (1995) considered remnants < 80 ha as small. These differences may not be important if there is a linear relationship between reproductive success and remnant area or level of fragmentation (Robinson et al. 1995), but if the relationship is nonlinear, or species exhibit threshold effects, careful consideration must be given to the choice of comparative sites. With little prior knowledge of a species' reproductive capacity under different conditions, it would be prudent to maximise the difference between sites in order to ascertain any relationships with fragmentation.

Comparative fragmentation studies often use individual nest success as a measure of reproductive output (Donovan et al. 1995; Hoover et al. 1995), but this

does not account for levels of re-nesting (and subsequent success). More direct measures of population viability are annual productivity of marked individuals and survival of juveniles (Murray 2000). Few studies have compared differences in annual productivity between remnants of differing size (Weinberg and Roth 1998; Porneluzi and Faaborg 1999) and even fewer have measured juvenile survival (Zanette 2000).

7.1.3 Potential threatening processes

Processes that may cause lower reproductive success in fragmented landscapes include reduced habitat quality, an increase in nest predation or parasitism, lower food availability, disrupted dispersal, or changes in species behaviour. For Neotropical migrants, there is reasonably strong evidence indicating that increased nest predation (Paton 1994; Hoover et al. 1995) and brood parasitism by the Brown-headed Cowbird *Molothrus ater* (Brittingham and Temple 1983; Robinson et al. 1995) in fragmented forests are two primary mechanisms leading to lower reproductive success. However, a study by Burke and Nol (1998) found that prey biomass (invertebrates) for Ovenbirds was significantly lower in small compared to large forest remnants.

Matthysen and Adriaensen (1998) suggested that, although important for open-nesters, nest predation and brood parasitism may not be the primary processes leading to the decline of hollow-nesting species in fragmented landscapes. Their conclusion is supported by the few studies of hollow-nesting birds in habitat remnants (Kuitunen and Helle 1988; Tjemberg et al. 1993; Nour et al. 1998; Walters et al. 1999). In the Western Australian wheatbelt, Saunders (1977) suggested that the lower fledging success of the hollow-nesting White-tailed Black Cockatoo in the more fragmented landscape was a result of disrupted foraging and nesting behaviour owing to a lack of suitable food near the nest site and reduced connectivity between foraging and nesting areas. His conclusions were supported by significantly lower fledging weights for nestlings in the more fragmented site.

Other studies that have examined differences in food availability (Nour et al. 1998) or foraging behaviour (Huhta et al. 1999; Walters et al. 1999) have generally failed to document any negative effects of fragmentation on prey availability or

foraging and subsequent reproductive success. Burke and Nol (1998) found that lower food abundance was associated with lower densities of Ovenbirds and lower pairing success for territorial males, but did not examine relationships with reproductive success.

There are a number of processes that may influence the reproductive success of birds living in fragmented landscapes. Researchers must examine as many of these as possible to adequately assess the relationships between fragmentation and population persistence. These relationships are likely to be complex and interacting, and may vary between regions and species.

7.2 METHODS

7.2.1 Comparisons between habitat contexts

I compared the reproductive success of the Rufous Treecreeper between the seven habitat contexts during the 1998 and 1999 breeding seasons. The sites in Dryandra were split because reproductive output varied between sites (Chapter 3). The data presented in this chapter for Dryandra are a summary of the more extensive data presented in Chapter 3.

I compared the following reproductive measures between contexts (details of how these data were collected are presented in Chapter 3):

- a) nest success – a nest was considered successful if it produced at least one fledgling;
- b) group productivity – the total number of fledglings produced per breeding group per season (i.e., annual productivity);
- c) fledgling survival – the total number of fledglings surviving to independence (30 days post-fledging);
- d) fledgling survival rate – the probability of a fledgling surviving to independence;
- e) juvenile survival – the total number of juveniles surviving to the beginning of the next breeding season; and
- f) juvenile survival rate – the probability of a juvenile surviving to the beginning of the next breeding season.

Data were examined for departures from normality and were transformed if possible or analysed using non-parametric methods. Percent nest success was analysed using a chi-square equivalent test for multiple proportions and a Tukey-type multiple comparisons test (Zar 1996 p. 559). Group productivity was analysed using a one-way analysis of variance (ANOVA) and Tukey's honestly significant difference (HSD) for unequal sample sizes after data were square root transformed. Homogeneity of variances was examined using Levene's test. I did not test for differences in the number of fledglings and juveniles surviving because these data are not independent of group productivity (see Chapter 5).

Landscape differences in fledgling and juvenile survival rates were tested using the computer program CONTRAST (Sauer and Williamis 1989). I did not test for differences between each habitat context owing to low sample sizes and large standard errors. The survival rate measures assume that all disappearing birds died. This is unlikely to be the case, but the level of error should be comparable between the two landscapes. In all analyses, I combined the data for 1998 and 1999 owing to small differences between years.

7.2.2 Correlative relationships with reproductive success

I examined correlations between reproductive success (dependent variable) and a number of social, habitat, remnant and landscape measures (Table 7.1). These relationships were only examined in Yilliminning (data for Dryandra are analysed in Chapter 5), and only for nest success and group productivity (survival data were not sufficient to analyse). Nest success was analysed using logistic regression models and group productivity was analysed using Poisson regression with the S-Plus 2000 statistical package (MathSoft 1999). Correlations between independent variables were examined using Spearman rank correlation. Highly correlated ($r_s \geq 0.7$) variables were not included in the same model. Modelling and diagnostic procedures followed Nicholls (1989).

Table 7.1 The social, habitat, remnant and landscape measures (independent variables) used in the regression models examining relationships with reproductive success.

Measurements (variable type)	Methods of data collection
<i>Social measures</i>	
Group size (continuous)	Measured per Chapter 3.
Territory density (continuous)	The number of territories within a 500 m radius of the centre of the focal territory. Measured directly in the field.
Territory size (continuous)	Measured per Chapter 6
<i>Habitat measures</i>	
Habitat quality (continuous)	Measured per Chapter 6
Woodland type (categorical)	Woodland type was determined by the predominant overstorey species and categorised as Wandoo <i>Eucalyptus wandoo</i> , Morrell <i>E. forficornis</i> or Mallett <i>E. astringens</i> .
<i>Remnant measures</i>	
Remnant size (categorical)	Remnants were arbitrarily categorised as small (≤ 30 ha) or large (≥ 60 ha).
Remnant shape (continuous)	Determined for each remnant using the equation of Patton (1975): $\text{Shape} = \frac{P}{2\sqrt{A \cdot \pi}}$ where P is the perimeter length of a remnant and A is the area. Perimeter and area values were calculated using ARCVIEW.
Grazing (categorical)	Grazed remnants were in paddocks subject to annual or biannual grazing by sheep, ungrazed remnants had been free from grazing for at least 15 years.
Distance to edge (continuous)	For nest success, distance was from the nest site to the nearest edge abutting agricultural land. For group productivity, it was from the centre of the focal territory to the nearest agricultural edge. Distances were measured directly in the field using a 100 m tape.
<i>Landscape measures</i>	
Percent cover of native vegetation (remnants ≥ 3 ha) in a 500 m, 1 km and 2 km radius from the centre of the focal territory (continuous).	Calculated using ARCVIEW from the GIS database of Yilliminning vegetation cover (see Chapter 2).
Percent cover of Wandoo woodland (≥ 3 ha) in the areas listed above (continuous).	As above.

In the nest success model, I used only the first nest attempt of the season and one attempt per female (i.e., one attempt for the 2 years) to avoid pseudoreplication. Nesting attempts by new primary females were included if the new female used a different hollow to the female she replaced. For group productivity, I used the number of fledglings produced in one year only (chosen at random) if the same group occupied a territory in both years. If the breeding group or primary female changed from one year to the next, I used both years' data. Four territories that were occupied in 1998 were unoccupied by a breeding group in 1999. I located replacement territories for three of these (in the same habitat context), which were used in the analyses. The remaining territory and another containing only a primary female (both in small ungrazed remnants) were not used. I also excluded data where a breeding group received help from neighbouring birds in provisioning nestlings.

In all analyses, I assumed that success in one territory was independent of success in another territory in the same patch, but there appeared to be a level of spatial dependence in the data (see Discussion). Also, these data are pseudoreplicated in the sense that multiple territories occupied a single remnant, but were considered replicates. This was unavoidable owing to the low number of remnants available for use, and the need to assess the social organisation of the species, which is strongly influenced by territory contiguity (Chapter 3). Also, this experimental design has the advantage of providing productivity data for entire remnants, which is useful for source-sink analysis and identifying highly productive remnants in the landscape (Chapter 8).

7.2.3 Potential threatening processes

Nest predation

I examined a number of potential processes that may have contributed to landscape differences in the reproductive success of the treecreeper. Nest predation was difficult to measure directly because nests were generally inaccessible. Therefore, I used artificial nests to measure relative predation rate between landscapes and habitat contexts. Artificial nests were placed in natural hollows, 1.5 – 3 m above the ground, in eucalypt trees. There was no significant difference in the

microhabitat characteristics of the artificial nest sites used in Dryandra and Yilliminning (Appendix 7.1).

If the hollow had no base, a cardboard disk was placed inside the hollow at arms length. On top of the disk or natural hollow base, I placed a handful of nesting material (e.g., grass, leaves, bark, feathers and fur) obtained from accessible treecreeper nests. In each artificial nest, I placed a fresh, commercially produced quail egg (approximately 20 mm × 30 mm, cream coloured with brown and black speckling) and a smaller plasticine egg (approximately 15 mm × 20 mm, cream coloured and unmarked). Rubber gloves were used when handling eggs. Metal tongs were used to place artificial nests and eggs in hollows with narrow internal dimensions. The real egg provided an olfactory cue to potential predators and the plasticine egg was used to record visits by smaller predators, which may not have been able to break the shell of the quail egg (Haskell 1995; Maier and DeGraaf 2000), but could leave indentations in the soft plasticine.

I conducted two nest predation experiments during the 1999 breeding season; one between October 4 – 20 and one between December 1 – 17. In each experiment, I placed 40 nests in each landscape over a period of 2 consecutive days (1 day per landscape). The nests were divided evenly among the three sites in Dryandra (13 – 14 nests at each site) and the four habitat contexts in Yilliminning (10 nests in each context). One nest was placed in each of the monitored treecreeper territories, and additional nests were placed in adjacent territories or nearby areas. If possible, a different hollow (in the same territory) was used in the second experiment. Nest location was marked using flagging tape placed around a tree 10 – 20 m away from the nest tree at a recorded compass direction.

Nests were exposed for 17 days, equivalent to the incubation period of the Rufous Treecreeper (Rose 1996), and were not re-visited during this period. A nest was considered preyed upon if one or both of the eggs were removed from the nest, broken (quail egg) or had clear indentations (e.g., bill or teeth) in the surface (plasticine egg). At the end of each experiment, nest contents and cardboard base were removed from the hollow.

Nest-site selection

To determine if nest-site selection differed between landscapes, I measured the structural characteristics of hollows and nest trees used by treecreepers in Yilliminning and compared these with the results from Dryandra (Chapter 4). The characteristics measured and the methods of data collection are detailed in Chapter 4. Landscape differences in nest-site selection were analysed using multiple analysis of variance (MANOVA) with post hoc multiple comparisons (Tukey's HSD for unequal sample sizes) after data were transformed (see Table 7.5). Normal probability plots of residuals were examined for linearity.

Nest-site selection differed significantly between landscapes (see Section 7.3.3). To determine if any nest-site characteristic correlated with nest success for treecreepers in Yilliminning, I used the modelling procedures (logistic regression) described in Section 7.2.2. One characteristic, hollow height, was significantly associated with nest success. Therefore, hollow height was included in subsequent models that examined the relationship between this characteristic and the measures detailed in Table 7.1, and nest success.

Food availability (provisioning rates)

Food availability was measured indirectly by recording provisioning rates to nestlings by adult birds. Nest watches were conducted in Dryandra and Yilliminning following the methods described in Appendix 3.1. When comparing provisioning rates between habitat contexts, I used only the first nest attempt of the season and controlled for brood size (= two), time of day (later than 0900 hrs), nest stage (mid – late) and maximum daytime temperature (< 30° Celsius) because these may influence nestling provisioning (see Appendix 3.1 and Chapter 6). Differences in provisioning rate were analysed using two-way ANOVA with year and habitat context as the independent, fixed factors. Post hoc comparisons were conducted using Tukey's HSD for unequal sample sizes. In this analysis, the sites in Dryandra were combined and treated as one habitat context (there were no significant differences between sites – see Appendix 3.1) and territories in the small grazed and ungrazed remnants were also combined owing to small sample sizes.

To further assess differences in food availability, adults provisioning nestlings were video-taped at 10 nests in each landscape during 1999. In these nest watches, I controlled for brood size, maximum daytime temperature and nest stage. All nests were taped for 4 hours between 0730 and 1230 hrs using a video camera mounted on a tripod.

The purpose of the video taping was to assess differences in food biomass being bought to nestlings. Provisioning rates may differ between landscapes, but lower rates may simply mean adults are provisioning their nestlings with larger food items. Treecreepers generally carry food items in their bill before feeding nestlings. Therefore, the size of food parcels for each visit was classified relative to the size of a treecreepers bill (i.e., small – smaller than bill; medium – same size as bill; and large – larger than bill). These size categories were given a weighting (i.e., small = 1, medium = 3, large = 9) to represent the relationship between prey length and biomass (following Cale 1999). Provisioning rate and prey biomass were determined during playback of video tapes. Visits where prey size could not be identified were allocated to each size category in proportion to the known contribution made in each category. Differences in total prey biomass between Dryandra and Yilliminning were analysed using a *t*-test for independent samples.

7.3 RESULTS

7.3.1 Comparisons between habitat contexts

Nest success

Overall nest success was significantly higher in Dryandra (77.4%, $n = 103$) than Yilliminning (46.0%, $n = 91$, Fisher exact test, $P < 0.001$). Nest success was similar between sites in Dryandra (Chapter 3), so I combined these data and compared average nest success in Dryandra with each habitat context in Yilliminning. There was a significant difference between these contexts ($\chi^2_4 = 28.25$, $P < 0.001$; Table 7.2). Breeding groups in Dryandra had higher nest success than groups in the large ($q = 7.35$, $P < 0.001$) and small grazed remnants ($q = 4.30$, $P < 0.025$), and groups in the large ungrazed remnants had higher nest success than groups in the large grazed remnant ($q = 4.27$, $P < 0.025$; Table 7.2).

Group productivity

Annual group productivity was twice as high in Dryandra (2.2 ± 0.14 , $n = 60$) compared to Yilliminning (1.1 ± 0.14 , $n = 58$, Mann-Whitney test, $Z = 3.82$, $P < 0.001$), but productivity varied depending on habitat context. I have already established that group productivity differed between the three sites in Dryandra (Chapter 3), so I examined differences between the Dryandra sites and the habitat contexts in Yilliminning. I combined the data for small remnants owing to small sample sizes (i.e., two territories in small ungrazed remnants were not occupied in 1999 reducing the sample size to four). There was a significant difference in group productivity between habitat contexts ($F_{5,52} = 7.91$, $P < 0.001$). All sites in Dryandra produced more fledglings per year than groups in the large grazed remnant (Tukey's HSD, $P < 0.01$; Table 7.2). Groups in Site C also produced more fledglings than groups in the small remnants ($P < 0.05$), with a trend for productivity to be higher than groups in the large ungrazed remnants ($P = 0.07$). There were also trends for group productivity to be higher in the large ungrazed ($P = 0.06$) and small remnants ($P = 0.07$) compared to the large grazed remnant.

Fledgling and juvenile survival rates

Fledgling survival rate did not differ between landscapes (Dryandra 0.76 ± 0.06 vs Yilliminning 0.66 ± 0.11 , CONTRAST, $\chi^2_1 = 0.64$, $P = 0.42$), but there was a trend for juvenile survival rate to be higher in Dryandra (0.41 ± 0.07) than Yilliminning (0.22 ± 0.08 , CONTRAST, $\chi^2_1 = 3.19$, $P = 0.07$). Fledgling survival rate was very low in the large grazed remnant (sample size was small, as only six fledglings were produced), but was comparable between the other habitat contexts (Table 7.2). No juvenile survived to the following breeding season in the large grazed remnant (only two fledglings were produced in 1998) and survival rate was also low in the small grazed remnants.

Table 7.2 Measures of reproductive success and survival in each habitat context (mean \pm s.e.). Numbers in brackets are sample sizes (i.e., number of breeding groups for habitat context and number of nesting attempts for nest success).

	Year	Dryandra			Yilliminning			
		Site A (10)	Site B (10)	Site C (10)	LU (9)	LG (8)	SU (4-6)	SG (7)
% nest success	1998	81.3 (16)	71.4 (14)	76.5 (17)	61.5 (13)	14.3 (14)	50.0 (8)	50.0 (14)
	1999	76.5 (17)	73.7 (19)	85.0 (20)	66.7 (12)	33.3 (12)	50.0 (6)	41.7 (12)
	98/99	78.9	72.6	80.8	64.1	23.8	50.0	45.9
Group productivity	1998	1.6 \pm 0.27	1.8 \pm 0.39	2.4 \pm 0.31	1.4 \pm 0.44	0.3 \pm 0.16	1.0 \pm 0.36	1.7 \pm 0.36
	1999	1.9 \pm 0.28	2.4 \pm 0.40	2.9 \pm 0.31	1.4 \pm 0.34	0.5 \pm 0.19	0.8 \pm 0.48	1.3 \pm 0.56
	98/99	1.8 \pm 0.19	2.1 \pm 0.28	2.7 \pm 0.22	1.4 \pm 0.27	0.4 \pm 0.13	0.9 \pm 0.28	1.5 \pm 0.33
Fledgling survival	1998	1.1 \pm 0.18	1.5 \pm 0.34	2.0 \pm 0.36	1.2 \pm 0.43	0.1 \pm 0.13	0.5 \pm 0.34	1.4 \pm 0.30
	1999	1.3 \pm 0.30	1.8 \pm 0.42	2.2 \pm 0.39	1.2 \pm 0.28	0.1 \pm 0.13	0.8 \pm 0.48	0.6 \pm 0.43
	98/99	1.2 \pm 0.17	1.7 \pm 0.21	2.1 \pm 0.26	1.2 \pm 0.25	0.1 \pm 0.08	0.6 \pm 0.27	1.0 \pm 0.28
Fledgling survival rate	1998	0.69 \pm 0.11	0.83 \pm 0.13	0.83 \pm 0.08	0.85 \pm 0.11	0.50 -	0.50 \pm 0.29	0.82 \pm 0.09
	1999	0.68 \pm 0.13	0.75 \pm 0.12	0.76 \pm 0.09	0.85 \pm 0.08	0.25 \pm 0.25	1.00 -	0.46 \pm 0.19
	98/99	0.69 \pm 0.08	0.79 \pm 0.10	0.79 \pm 0.07	0.85 \pm 0.06	0.38 \pm 0.21	0.75 \pm 0.21	0.64 \pm 0.12
Juvenile survival	1998-99	0.7 \pm 0.16	0.6 \pm 0.22	1.1 \pm 0.41	0.6 \pm 0.18	0.0	0.3 \pm 0.21	0.3 \pm 0.18
Juvenile survival rate	1998-99	0.44 \pm 0.08	0.33 \pm 0.10	0.46 \pm 0.12	0.38 \pm 0.14	0.0	0.33 \pm 0.17	0.17 \pm 0.09

7.3.2 Correlative relationships with reproductive success

Nest success

There was a high degree of intercorrelation ($r_s \geq 0.7$) between the social, habitat, remnant and landscape variables. A number of variables were also related to nest success. Grazing resulted in the largest change in deviance when entered into the model separate from all other variables. With grazing in the model, there were no significant changes in deviance with the addition of other variables. I also examined all two-way interactions, but none were significant.

The final model included grazing as the single best predictor of nest success (Table 7.3); treecreeper groups in grazed remnants had lower success. This result was strongly influenced by the low nest success of groups occupying the large grazed remnant. Importantly though, grazing was negatively correlated ($r_s = -0.80$) with the percent cover of native vegetation within a 2 km radius of the focal territory, and positively correlated ($r_s = 0.71$) with territory density. The first correlation suggests that treecreepers in grazed remnants had fewer close dispersal options (i.e., little surrounding vegetation) and the second indicates that territories in grazed remnants were more tightly packed. This second relationship is intriguing because it suggests a possible density dependent association with nest success (see Discussion).

Table 7.3 The nest success model including grazing as the best predictor of nest success in Yilliminning ($n = 34$). Territories in ungrazed remnants had higher success than those in grazed remnants.

	df	Change in deviance	Residual df	Residual deviance	P
Null model			33	47.13	
+ Grazing	1	10.22	32	36.91	< 0.005
		Coefficients	s.e.		
Constant		0.178	0.414		
Grazing		1.208	0.414		

Group productivity

The modelling procedure for group productivity followed that of nest success. The only variable to be significantly associated with group productivity was territory size (\log_{10} transformed; Table 7.4). Groups occupying larger territories had higher annual productivity. Territory size was also negatively correlated with grazing ($r_s = -0.78$) reflecting the positive relationship between grazing and territory density (see above). Importantly, territory quality, which was significantly related to group productivity in Dryandra (Chapter 5), had no relationship with productivity in Yilliminning. I also examined bivariate correlations between productivity and each habitat characteristic measured, but none were significant.

Table 7.4 The group productivity model including (\log_{10}) territory size as the best predictor of group productivity ($n = 43$). Groups occupying larger territories had higher productivity.

	df	Change in deviance	Residual df	Residual deviance	P
Null model			42	59.30	
+ (log) Territory size	1	5.61	41	53.69	< 0.025
		Coefficients	s.e.		
Constant		-1.104	0.462		
(log) Territory size		1.813	0.762		

7.3.3 Potential threatening processes**Nest predation**

There was no difference in predation rate of artificial nests between experiments (October and December) in Dryandra (chi-square, $\chi^2_2 = 0.20$, $P > 0.10$) or Yilliminning ($\chi^2_3 = 3.84$, $P > 0.10$), so data were combined to examine overall landscape differences. There was no difference in total nest predation rate between landscapes (Dryandra 36.9%, $n = 80$ vs Yilliminning 28.8%, $n = 80$, Fisher exact test, $P = 0.31$). Variation in predation rate was greatest in Yilliminning, being 40% for nests in the large grazed remnant and 20% for nests in the large ungrazed remnants (Figure 7.1), but there was no significant difference between the four habitat contexts ($\chi^2_3 = 1.52$, $P > 0.10$).

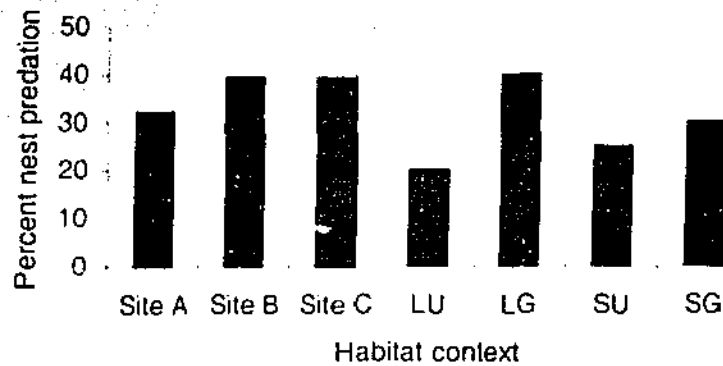


Figure 7.1 Differences in the level of nest predation between Sites A – C in Dryandra and the four habitat contexts in Yilliminning ($n = 160$).

For nests that were preyed upon ($n = 53$), nest predators were classified using the imprints left in plasticine eggs. The most common nest predators were small (47.8%) and large (34.8%) mammals; only 8.7% of nests were preyed upon by avian predators.

Nest-site selection

There was a significant difference in the structural characteristics of the nest sites used in Dryandra and Yilliminning (MANOVA, $F_{7,135} = 9.66$, $P < 0.001$). Post hoc comparisons showed smaller tree diameter at breast height (DBH), and tree and hollow height measures, and larger percent deadwood and hollow entrance size measures for nest sites in Yilliminning (Table 7.5).

The structural nest-site characteristics were included in a logistic regression model to assess relationships with nest success. This model identified hollow height as having a significant negative association with success. Average hollow height of successful nests was 4.8 m (± 0.49) and unsuccessful nests 7.1 m (± 0.52 , $n = 34$). Subsequent modelling that included hollow height with the measures detailed in Table 7.1 found that height was associated with the greatest change in model deviance, but grazing was still a significant predictor once hollow height had been considered (Table 7.6).

Table 7.5 Differences in the structural characteristics of nest trees and hollows in Dryandra and Yilliminning (mean \pm s.e.). Numbers in brackets are sample sizes. Characteristics marked with an asterisk are significantly different at $P < 0.02$ (Tukey's HSD). Table also shows a summary of transformations conducted prior to MANOVA.

Nest-site characteristic	Dryandra (90)	Yilliminning (43)	Transformation
Tree DBH (cm)*	46.8 \pm 1.89	38.5 \pm 2.26	
% deadwood*	37.2 \pm 2.99	60.5 \pm 5.10	Square root - arcsine
Tree height (m)*	16.3 \pm 0.48	11.2 \pm 0.59	
No. of hollows	6.6 \pm 0.58	6.5 \pm 0.80	Square root
Hollow height (m)*	8.5 \pm 0.37	6.4 \pm 0.40	
Spout angle ($^{\circ}$) ¹	67.9 \pm 2.53	68.7 \pm 2.76	
Hollow entrance size (cm)*	7.2 \pm 0.31	9.1 \pm 0.57	Log ₁₀
% canopy cover	37.6 \pm 3.39	36.1 \pm 4.81	Square root - arcsine

¹Spout angle was not included in parametric analyses as distribution could not be improved with data transformations.

Table 7.6 The final nest success model including hollow height and grazing as significant predictors of nest success ($n = 34$).

	df	Change in deviance	Residual df	Residual deviance	P
Null model			33	47.13	
+ Hollow height	1	10.54	32	36.59	< 0.005
+ Grazing	1	6.62	31	29.97	< 0.025
		Coefficients	s.e.		
Constant		7.474	2.647		
Hollow height		-0.641	0.292		
Grazing		2.307	0.973		

Food availability (provisioning rates)

There was a significant difference in provisioning rate between habitat contexts ($F_{3,46} = 7.01$, $P < 0.001$), but no difference between years ($F_{1,46} = 2.54$, $P > 0.10$). Provisioning rates in Dryandra were significantly higher than those in the large grazed and ungrazed remnants (Tukey's HSD, $P < 0.05$) and tended to be higher than those in small remnants ($P = 0.09$), but there was no difference in provisioning rates between the habitat contexts in Yilliminning (Figure 7.2).

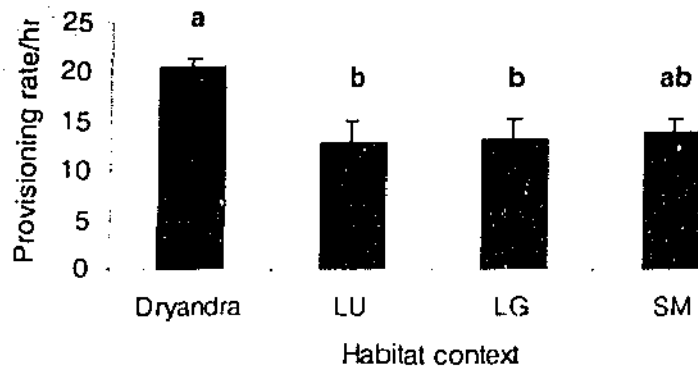


Figure 7.2 Provisioning rate/hr in each of the habitat contexts (mean \pm s.e.). Data from the three sites in Dryandra, and small grazed and ungrazed remnants (SM), were combined ($n = 54$ nests). Values with the same letter (above columns) are not significantly different (although there was a trend for provisioning rates in Dryandra to be higher than the small remnants – see text).

Total prey biomass delivered to nestlings was also significantly higher in Dryandra (190.1 ± 11.8) than Yilliminning (129.3 ± 9.11 ; $t_{18} = 4.08$, $P < 0.001$). The relative proportions of different sized prey items were similar between landscapes (Figure 7.3), so the difference in biomass was a result of the higher provisioning rates in Dryandra.

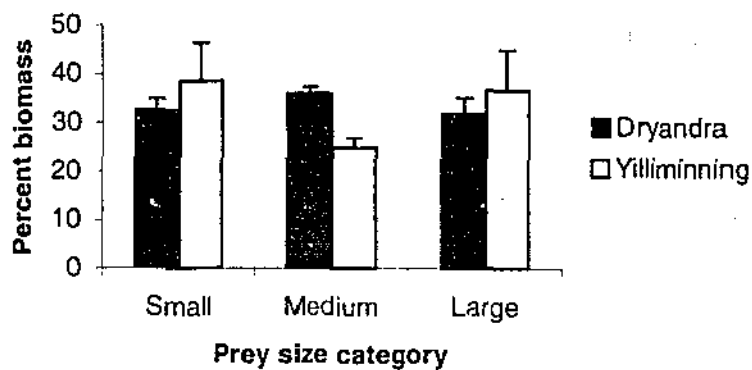


Figure 7.3 Percent biomass (mean \pm s.e.) of food delivered to nestlings in each prey size category in Dryandra and Yilliminning ($n = 20$ nests).

If food availability is lower in the agricultural landscape, nestling or fledgling weight may also be lower. I controlled for brood size (only using nests that produced two fledglings) and compared the weight of female fledglings between landscapes. There was no difference in the weight of fledglings between Dryandra

(27.3 grams \pm 0.34) and Yilliminning (28.6 grams \pm 0.51, *t*-test, $t_{45} = 1.47$, $P > 0.10$).

7.4 DISCUSSION

7.4.1 Patterns in reproductive success and survival

At the landscape level, the reproductive success of the Rufous Treecreeper in the fragmented agricultural district of Yilliminning was significantly lower than the continuously vegetated landscape of Dryandra. These results concur with the study of Saunders (1977) on White-tailed Black Cockatoos in the Western Australian wheatbelt, but are contrary to most other studies of hollow-nesting species (Matthysen and Adriaensen 1998; Nour et al. 1998). Interestingly, they also contradict the results of Walters et al. (1999), who studied the closely related Brown Treecreeper in the New England agricultural region of eastern Australia. Differences between the Brown and Rufous Treecreeper may be a result of variation in ecological characteristics or landscape type. Habitat disturbance in certain agricultural regions of New South Wales has resulted in a "variegated" landscape of variable native vegetation cover rather than one of discrete habitat fragments surrounded by an unusable matrix, as found in the Western Australian wheatbelt (McIntyre and Barrett 1992).

For Rufous Treecreepers, lower reproductive success in the agricultural landscape has significant implications for population persistence, particularly considering that the majority of reproductive output was confined to relatively few breeding groups. In Yilliminning, 64% of breeding groups ($n = 58$) produced \leq one fledgling per season. Consequently, only 36% of groups produced 77% of total fledglings ($n = 62$). These groups also tended to be spatially clumped in the same remnant or close group of remnants. If remnants containing clusters of productive groups are lost from the landscape, this may adversely affect population persistence (Chapter 8). In Dryandra, reproductive output was much more evenly spread. Only 30% of breeding groups ($n = 60$) produced \leq one fledgling and 70% of groups produced 88% of total fledglings ($n = 130$).

Landscape level patterns were consistent in both years of the study, but this masked the significant variability that occurred within landscapes. In Dryandra, Site

C produced more fledglings than the other sites owing primarily to Site C having larger group sizes and, on average, better quality territories (see Chapters 3 and 5). This demonstrates that variability between spatially discrete sites can occur in the same continuously vegetated landscape. In fragmented systems, researchers must be aware of other factors that may cause between remnant variability besides those specifically associated with fragmentation (e.g., remnant size or isolation).

In Yilliminning, nest success and group productivity differed between habitat contexts, but there was no consistent relationship between reproductive success and remnant size. Grazing appeared to be an important contributing factor to lower nest success (Table 7.3), but this relationship was strongly influenced by the results from the large grazed remnant. Although, most groups in the small grazed remnants also had low nest success.

Grazing may lead to soil compaction and reduce shrub and ground vegetation cover and complexity (Wilson 1990). In turn, this may alter invertebrate species assemblages (Abensperg-Traun et al. 1996; Bromham et al. 1999) possibly reducing food availability and subsequent reproductive success for ground-foraging insectivores like the Rufous Treecreeper. I have no evidence of lower food availability in grazed compared to ungrazed remnants. The use of foraging substrates in grazed remnants was similar to that recorded in Dryandra (Appendix 4.1), and provisioning rates to nestlings were similar to ungrazed remnants (Section 7.3.3). The relationship between grazing and food availability for ground-foragers needs to be assessed more directly by collecting data on invertebrate abundance and diversity.

Territory size was the only measure significantly correlated with group productivity in Yilliminning (Table 7.4); groups occupying smaller territories produced fewer fledglings. Territory size had no relationship with productivity in Dryandra where fledgling production was significantly related to territory quality (Chapter 5). In Yilliminning, territory size was negatively correlated with grazing and territory density. Territories were smaller and more densely packed in grazed remnants, but this appeared to put breeding groups at a reproductive disadvantage. This suggests that, in the agricultural landscape, reproductive success may be density dependent, mediated by habitat quality (see below).

A consequence of lower group productivity in Yilliminning was that fewer fledglings survived to independence compared to Dryandra. However, fledgling survival rate was similar between landscapes indicating no significant adverse relationship between habitat alteration and survival to independence. Survival rate was relatively low for fledglings in the large grazed remnant (Table 7.2), but sample size was very small. More importantly, there was a trend for juvenile survival rate to be lower in Yilliminning, particularly in the grazed remnants (once again sample sizes were small). This may have adverse consequences for population viability because it indicates a reduced number of potential future breeders.

7.4.2 Potential threatening processes

Nest predation

Nest predation appears to play a major role in the lower reproductive success of open-cup and ground-nesting species in fragmented landscapes (Robinson et al. 1995; Weinberg and Roth 1998). There is no evidence suggesting a similar relationship for hollow-nesters. In my study, relative predation rates on artificial nests did not differ significantly between landscapes or habitat contexts. Rates of predation were also relatively low compared to artificial open-cup or ground nests (Luck et al. 1999b; Zanette and Jenkins 2000), although this variation may be attributed to differences in methodology or predator assemblages.

There is some evidence to suggest that birds are common predators of open nests (Angelstam 1986; Andrén 1992; Zanette and Jenkins 2000) and may be more inclined to prey on artificial compared to natural nests (Willebrand and Marcstrom 1988; MacIvor et al. 1990). The abundance of generalist avian predators may also increase in fragmented landscapes or near habitat edges (Andrén 1992; Luck et al. 1999a). In my study, mammals appeared to be the main predators of artificial hollow nests based on imprints in the plasticine eggs. Habitat alteration of eucalypt woodlands may result in a reduced abundance of native mammal predators (e.g., Yellow-footed *Antechinus flavipes*) and a replacement of native predators by introduced species like the House Mouse *Mus musculus* and Black Rat *Rattus rattus*. Therefore, there may be no significant increase in the abundance of species likely to

prey on hollow nests. The lack of difference in predation rate between Dryandra and Yilliminning supports this possibility.

Importantly though, my study only measured predation rates on eggs. Nestling predation may be a significant cause of nest failure and may differ between landscapes. Predators of nestlings may also differ from predators of eggs and use different cues (e.g., nestling begging) to locate nests. For example, the Cat *Felis catus* may prey on nestlings, and the abundance of this species is likely to be greater in the agricultural landscape of Yilliminning owing to predator control measures in Dryandra.

Nest-site selection

A number of nest-site characteristics differed significantly between landscapes (Table 7.5) and these differences may have influenced variation in reproductive success. Nest hollows in Yilliminning had a larger mean entrance size, which may have exposed eggs and nestlings to a broader range of predators or greater microclimate variability. Hollow entrance size was one of only two characteristics identified by the regression model in Chapter 4 as being significantly associated with nest-site selection by the treecreeper in Dryandra. This indicates that restrictions to optimal entrance size selection may have adverse consequences. Restrictions to nest-site selection are likely to occur when hollows become limiting or competition for nest sites increases. Hollow density was significantly lower in Yilliminning (Chapter 6) and the abundance of some hollow nesters (e.g., Australian Ringneck *Barnardius zonarius* and Galah *Cacatua roseicapilla*) may increase in modified agricultural landscapes (Saunders and Ingram 1995). Current hollow density in Yilliminning does not suggest a critical shortage of this resource, but this situation may change in the future owing to relatively low seedling recruitment, especially in grazed remnants.

Hollow height, another potentially important nest-site characteristic, was significantly lower in Yilliminning (Table 7.5). Some studies have found a positive relationship between hollow height and nest success, as hollows lower to the ground may be more accessible to tree-climbing terrestrial predators (Hooge et al. 1999). Interestingly, I found a negative relationship between hollow height and nest success

in Yilliminning (Table 7.6). This non-intuitive result may reflect greater exposure of higher nests to climatic extremes in the agricultural landscape, particularly if coupled with large hollow entrance sizes. Also, nest-site characteristics not measured in my study (e.g., internal structure or microclimate variability) may have differed between landscapes, resulting in differences in nest success.

Food availability (provisioning rates)

Provisioning rates and total food biomass delivered to nestlings were significantly lower in Yilliminning providing inferential evidence for reduced food availability. Variation in provisioning rate and food biomass between landscapes corresponded with differences in reproductive success, but there was no consistent pattern between habitat contexts in Yilliminning. Lower food availability may result in lower fledging weights for nestlings (Saunders 1977), but I found no landscape differences in fledging weight for treecreepers. These data are limited because I was unable to control for differences in fledging date or time of measurement.

Recent studies have found that prey abundance for primarily ground-foraging insectivores may be reduced in small remnants (Burke and Nol 1998; Zanette et al. 2000). Zanette et al. (2000) established that lower invertebrate volume and dry mass in small remnants corresponded to fewer feeding visits by males to incubating females, and nestlings receiving fewer large prey items (although total provisioning rate to nestlings did not differ between large and small remnants). Therefore, estimates of the food biomass provided to incubating females and nestlings may serve as indicative measures of food availability if more direct measures are unavailable.

In fragmented landscapes, the influence of lower food availability on reproductive success may have been underestimated owing to the strong focus placed on nest predation and parasitism, and the difficulty of accounting for the extreme temporal and spatial variation that often characterises invertebrate distribution and abundance. Examining the importance of food availability for insectivores requires comprehensive studies of invertebrate assemblages, bird species diet and foraging behaviour (e.g., time budgets) and subsequent reproductive

success. In light of recent evidence, it appears that these studies are desperately needed.

7.4.3 Habitat quality and density dependence

There were significant differences in habitat structure and quality between landscapes (Chapter 6) and this may explain the differences in reproductive success. However, on the scale of individual territories, there were no correlative relationships between habitat quality and group productivity in Yilliminning. This is contrary to the results in Dryandra where there were strong correlations between territory quality and certain measures of reproductive success (Chapter 5). The mean quality index for each habitat context (see Figure 6.2 in Chapter 6) suggested a pattern of decreasing quality with increasing disturbance. Habitat contexts in Yilliminning were ranked, in order of decreasing quality; large ungrazed, small ungrazed, large grazed and small grazed. Interestingly, if all measures of reproductive success (i.e., nest success, group productivity and fledgling and juvenile survival rate) are used to rank habitat contexts from most to least successful (see Table 7.2), this ranking is similar to the one based on mean quality. The only difference is the transposition of large and small grazed remnants.

The average quality of a particular remnant or habitat context may be more closely associated with reproductive success than the quality of an individual territory. Processes that influence territory quality may operate at scales above that of individual territories. Food availability in one territory may influence availability in neighbouring territories despite differences in habitat structural characteristics. For insectivores, food distribution could be strongly influenced by the population dynamics of invertebrates, which are themselves responding to habitat changes associated with fragmentation. This type of situation may scale upwards, whereby processes operating in one remnant may influence neighbouring remnants regardless of habitat differences.

An important consequence of this scenario is that there may be a de-coupling of any relationship that exists between habitat structure and quality. In the relatively undisturbed landscape of Dryandra, structural habitat characteristics may indeed have some relationship with habitat quality (e.g., food availability) and provide cues

for potential breeders. The link between habitat structure and quality (if one exists) may be disrupted in Yilliminning owing to habitat disturbance and changes in ecosystem function. The important point is that if structural cues are used as indicators of habitat quality, but have no relationship with quality owing to other factors, then certain habitat patches may act as "ecological traps" (*sensu* Gates and Gysel 1978) whereby reproductive success in apparently suitable habitat is very low.

It is also possible that the measure of habitat quality derived in Dryandra, based on vegetation structure, has no relationship to the system in Yilliminning. This could occur if habitat structural characteristics are surrogate measures for other critical components of habitat quality (e.g., nutrient cycling) in Dryandra, but these components are missing or reduced in Yilliminning despite habitat structural characteristics still being present.

In the fragmented landscape, there were complex correlative relationships between reproductive success, grazing and territory size. Reproductive success was lower for treecreeper groups occupying grazed remnants or relatively small territories, but small territories occurred mostly in grazed remnants apparently as a result of territory packing. Consequently, population density was significantly higher in grazed than ungrazed remnants, but was similar to that recorded in Dryandra (Chapter 6). I propose that high population density in grazed remnants coupled with lower habitat quality led to lower reproductive success. That is, reproductive success in Yilliminning was density dependent. A similar relationship was not found in Dryandra because habitat quality was sufficient to support a relatively high population density with no adverse consequences for reproductive output.

Low reproductive success in habitats with high breeding densities has been noted in other studies (Vickery et al. 1992; Porneluzi et al. 1993; Purcell and Verner 1998) and illustrates the limitations of using density as an indicator of habitat quality (Van Horne 1983). Data must be collected on demographic parameters (e.g., fledging success) before any assessment of habitat quality can be made. Also, reproductive output per remnant (per unit area) should be determined because remnants with high breeding densities, but low per capita success, may produce a

similar number of offspring to remnants with low densities and higher success (this was not the case in Yilliminning – see Chapter 8).

There also appeared to be a level of spatial dependence in the reproductive success of treecreeper groups. All groups in the large grazed remnant had low success, whereas most of those in one of the large ungrazed remnants had relatively high success rather than there being a substantial degree of variability between territories in the same remnant. Therefore, any site-specific effects unique to a given remnant may be confounded with habitat context owing to the low replication of remnants in my study and the use of breeding groups as replicates. To address this problem, a large number of remnants (with different contexts) containing one or two randomly chosen territories would be required. However, this greatly increases the logistic demands of a project and does not address issues such as the influence of social organisation or territory density on reproductive success. From a conservation perspective, it is also extremely important to determine the overall productivity of remnants within a landscape to identify highly productive remnants that may warrant preferential protection.

**Appendix 7.1 STRUCTURAL CHARACTERISTICS OF TREES AND
HOLLOWS USED AS ARTIFICIAL NEST SITES
IN DRYANDRA AND YILLIMINNING**

Table 1 Nest-site characteristics of artificial nests (mean \pm s.e.). Numbers in brackets are sample sizes. Overall differences between nest sites are not significant (MANOVA, $F_{32,547} = 1.12$, $P = 0.30$).

Nest-site characteristics	Dryandra (80)	Yilliminning (80)
Tree DBH (cm)	29.3 \pm 1.85	29.6 \pm 1.61
% deadwood	71.0 \pm 5.59	66.7 \pm 5.70
Tree height (m)	12.4 \pm 0.69	10.2 \pm 0.84
No. of hollows	4.6 \pm 0.43	3.5 \pm 0.67
Hollow height (m)	2.3 \pm 0.34	2.2 \pm 0.14
Spout angle ($^{\circ}$)	77.8 \pm 2.62	73.5 \pm 3.17
Hollow entrance size (cm)	8.8 \pm 0.69	9.2 \pm 0.55
Hollow depth (cm)	24.3 \pm 2.87	29.4 \pm 2.99
% canopy cover	25.3 \pm 4.10	27.3 \pm 4.14

CHAPTER 8

SPATIAL STRUCTURE AND POPULATION DYNAMICS

SUMMARY

Documenting the spatial structure and demographic traits of subdivided populations living in fragmented landscapes is fundamental to assessing population viability. Metapopulation and source-sink theory have influenced ecologists' thinking on population dynamics in fragmented habitat. In this chapter, I assess the usefulness of these theories in interpreting the dynamics of the subdivided treecreeper population in Yilliminning.

I identified 12 local populations in Yilliminning based on the frequency of interaction between neighbouring breeding groups. For eight of these, I recorded the annual productivity of female fledglings, and primary female and juvenile survival rates to determine if each local population could replace itself without immigration. Only one local population was above replacement. Fledgling productivity and survival in the remainder were not sufficient to compensate for primary female mortality. Consequently, six of the eight local populations were predicted to decline to extinction within 20 years without immigration. A simulation model based on the average demographic rates for the entire Yilliminning population also predicted that it would decline to extinction within 20 years without new immigrants moving into the study area.

However, there appeared to be sufficient movement between local populations, and into the study area from nearby remnants, to slow or halt the decline of most local populations. Although population size declined slightly from 1998 to 1999, most local populations were close to equilibrium when levels of immigration and emigration were considered.

The temporal and spatial scale of my study precluded a comprehensive examination of metapopulation and source-sink theory, but within- and between-population dynamics appeared to be important to the persistence of treecreepers in the fragmented landscape. The level of movement between local populations suggested that the structure and dynamics of the subdivided population in Yilliminning fell somewhere along the continuum between a patchy population and a true metapopulation.

8.1 INTRODUCTION

8.1.1 Overview

In this chapter, I examine the spatial structure and dynamics of the subdivided treecreeper population in Yilliminning. This is fundamental to understanding population viability in the agricultural landscape. I also determine the level of movement between spatially discrete "local populations" and the importance of within- and between-population processes for the persistence of Rufous Treecreepers in Yilliminning. This is an empirical assessment of current spatial and demographic theory closely associated with habitat fragmentation. The aims of the chapter are to determine:

- a) how well spatially discrete groups of treecreepers fit the concept of local populations;
- b) the population dynamics (e.g., rates of replacement and population growth) of local populations without immigration or emigration;
- c) the level of movement occurring between local populations; and
- d) the spatial structure and dynamics of the local population network.

8.1.2 The dynamics of spatially structured populations

Metapopulation theory

Spatially structured populations may occur in heterogeneous environments where a species exhibits a preference for particular habitat types. A common approach to studying spatially structured populations is to view them as a metapopulation (Levins 1969; also see Chapter 1 p. 3 for definition). In the Levins (1969) metapopulation model, a balance between the extinction of local populations and re-colonisation of empty habitat via extant populations leads to the persistence of metapopulations through time. Metapopulation theory is frequently invoked by researchers studying the population dynamics of organisms living in anthropogenically fragmented landscapes (Opdam 1991; Verboom et al. 1991; Arnold et al. 1993). Fragmentation often creates spatially discrete habitat remnants with identifiable boundaries, which may contain, at least in a spatial sense, localised populations. Movement between these populations may be influenced by the location of habitat remnants.

Although the theory of metapopulation dynamics has become increasingly popular in recent times (see Figure 1 in Hanski and Simberloff 1997 p. 6), the approach still suffers from theoretical limitations and certain assumptions are difficult to test empirically. In a series of reviews on the empirical evidence for metapopulation dynamics, Harrison (1991, 1994) and Harrison and Taylor (1997) questioned any strict interpretation of the theory. They found that there is scant evidence in nature for the "classic" (i.e., Levins) metapopulation model where a collection of discrete, similar sized populations exist because of a balance between local extinction and colonisation. Harrison (1991) described a number of situations where populations are spatially structured yet differ from the Levins model in key aspects (Figure 8.1). These situations are referred to as:

- a) mainland-island (core-satellite) metapopulation consisting of a large, persistent population and a series of smaller, satellite populations prone to extinction;
- b) patchy population where movement between the local populations is so frequent that it functions as a single interacting population rather than a metapopulation;
- c) non-equilibrium metapopulation where local populations suffer extinction, but there is no re-colonisation; and
- d) an intermediate case that combines the features of the Levins metapopulation and the above three.

The observations of Harrison (1991) suggest that spatially structured populations lie along a continuum of varying population types. A spatially structured population may not fit into any of the above categories, but exhibit characteristics common to a number of categories. Given the variability of spatial structure and dynamics in real populations, broad application of metapopulation theory may not be appropriate (Harrison and Taylor 1997). However, various authors have suggested that the theory is useful in developing a mechanistic understanding of habitat fragmentation on the persistence of subdivided populations (Doak and Mills 1994; Harrison 1994; Hanski 1998; Holyoak and Ray 1999). It encourages researchers to collect data on movement and birth and death rates in different patch networks, which is vital in developing effective conservation strategies for

individual species. Empirical investigations of fragmented populations should consider all possible variations on the classic metapopulation structure and evaluate the relative importance of within- versus between-local-population dynamics on the persistence of a species.

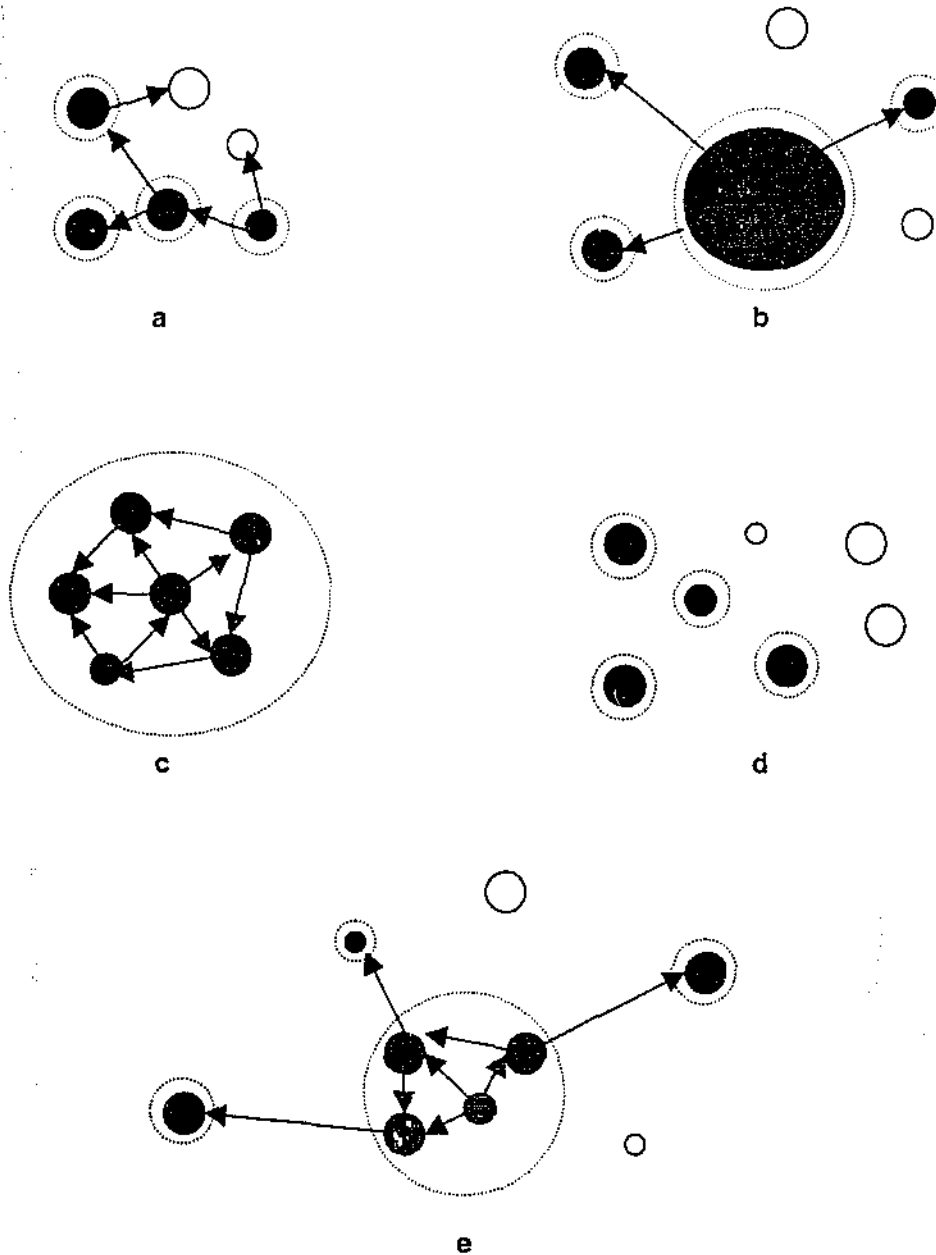


Figure 8.1 An example of five different metapopulations (modified from Harrison 1991). Circles represent habitat remnants; filled = currently occupied by the species of interest, unfilled = vacant. The size of circles is proportional to local population size and dotted lines represent local population boundaries. Arrows indicate movement between remnants. Metapopulation types are: a) Levins, b) mainland-island (core-satellite), c) patchy population, d) non-equilibrium, and e) an intermediate case.

Components of spatially structured population dynamics

In the study of subdivided populations, it is important to determine if spatially discrete local populations exist and the level of movement that occurs between them. Hanski and Simberloff (1997 p. 11) defined a local population as a "set of individuals that live in the same habitat patch and therefore interact with each other...populations living in such small patches that all individuals practically share a common environment." Based on this relatively broad definition, the presence of local populations is common to a number of studies of spatially structured populations (Harrison et al. 1988; Hanski and Thomas 1994; Driscoll 1998; Lindberg et al. 1998; Mousson et al. 1999), but the characteristics of these local populations may differ dramatically between studies. For example, Lankester et al. (1991) classified a small clan of badgers (up to seven individuals) occupying a single territory as a local population and interactions between clans as metapopulation dynamics. Spindelov et al. (1995) and Lindberg et al. (1998) considered large breeding colonies (in some cases > 1000 breeding pairs) of birds as local populations.

Although there is no numerical limitation in the definition offered by Hanski and Simberloff (1997), as local population size increases, demographic traits within populations (e.g., birth and death rates) may have more influence on population persistence than between population processes (e.g., migration). Before metapopulation theory is applied to spatially structured populations, researchers should carefully consider the relative importance of within- versus between-population dynamics (Harrison 1994).

Recording movement rates between local populations is extremely important in the study of spatially structured populations. Movement between local populations should have "...a significant impact on either the demography or genetic structure of each component population" (Stacey et al. 1997 p. 268). Empirical studies of spatially structured populations have documented movement rates varying from relatively low (Thomas and Jones 1993; Moilanen et al. 1998) to moderate or high (Verboom et al. 1991; Sæther et al. 1999). Frequent movement results in patchy population dynamics (Szacki 1999), whereas extremely low rates of movement may lead to non-equilibrium dynamics (Driscoll 1998). Movement rates may also differ

within species based on sex (Lindberg et al. 1998), age class (Sjögren-Gulve 1994) or the spatial characteristics of the habitat (Smith et al. 1996).

The consequences of variation in movement rates must be considered in relation to the ecological traits of the species being studied and the extinction probability of each local population. Infrequent movement is of relatively less concern if species are long-lived (which may increase population persistence time) or the extinction probability for local populations is low. Of greater concern are species with low movement rates, but short life spans and moderate to high extinction probabilities for local populations (e.g., the butterfly *Hesperia comma*, Thomas and Jones 1993).

Arguably the most important prediction from metapopulation theory is that the persistence of spatially structured populations results from a balance between the extinction and colonisation of local populations. Establishing the importance of extinction-colonisation dynamics for species living in fragmented habitat is critical to developing appropriate management strategies that ensure long-term persistence, but documenting extinction and colonisation events in nature can be extremely difficult.

One of the major problems that empirical investigations must confront is the temporal scale on which particular species operate. A number of species reported to exhibit Levins type (or similar) metapopulation dynamics are relatively short-lived making local extinctions easier to document (Hanski and Thomas 1994; Hanski et al. 1994; Moilanen et al. 1998). Spatial scale can also be a barrier to empirical investigations of extinction-colonisation dynamics. It is easier to track changes in local populations of invertebrates and small, dispersal-limited vertebrates, than larger, more mobile species. For long-lived species operating at large spatial scales, the importance of extinction-colonisation dynamics for population persistence may be difficult to determine.

8.1.3 Spatial variation in population viability

For species living in spatially structured populations, demographic rates (e.g., births and deaths) may vary between local populations. Spatial variability in demography can be modelled using the theoretical framework of source-sink

dynamics (Holt 1985; Pulliam 1988; Pulliam and Danielson 1991). In source-sink models, local populations occupy source habitat when reproduction exceeds mortality and a net surplus of individuals is produced, whereas when reproduction is less than mortality and there is a net deficit of individuals, populations occupy sink habitats (Pulliam 1988; Danielson 1992). Moreover, the stability of a network of local populations (e.g., a metapopulation) may rely on the dispersal of surplus individuals from source to sink habitat (Morris 1991; Dias 1996).

This net flow of individuals from sources to sinks is a key prediction of the source-sink model, which differentiates it from balanced dispersal models where equal movement occurs between all habitat patches (Doncaster et al. 1997; Diffendorfer 1998). Morris (1991) argued that dispersal to sink habitats is only an evolutionary stable strategy if some individuals return to sources. Therefore, sink habitats may play an important role in the persistence of subdivided populations by temporarily housing individuals that are able to return to fill vacancies in source habitats, and increasing total population size (Howe et al. 1991). The presence of highly productive source patches is critical to population persistence, but the potential contribution of sink habitats should not be underestimated. Also, habitat that is a sink to one species may be a source to others (McCoy et al. 1999).

A number of empirical studies have invoked the source-sink model when assessing differences in reproductive success between habitat remnants or landscapes that differ in the level of fragmentation (Donovan et al. 1995; Brawn and Robinson 1996; Hatchwell et al. 1996; Zquette 2000). However, recent reviews have highlighted the difficulty of identifying true source-sink dynamics (Watkinson and Sutherland 1995; Dias 1996; Diffendorfer 1998). Criticisms of empirical studies include a lack of detailed demographic data (including survival rates), little or no data on movement between habitats, and short temporal scales, which may not account for cyclic fluctuations in demographic traits. Density dependent effects may also complicate identification of true habitat sinks. "Pseudosinks" may exist where low reproductive success is a result of high population densities in poor quality habitat (Watkinson and Sutherland 1995; see Chapter 6 and 7). At lower densities, reproductive success may increase and the habitat may exhibit characteristics of a population source.

The importance of assessing source-sink dynamics in subdivided populations is well recognised (Dias 1996; Diffendorfer 1998). Although it may be difficult to identify true source and sink habitats, it is important to document differences in demographic traits and movements between local populations in a fragmented landscape. As with metapopulation theory, source-sink dynamics encourages a mechanistic understanding of the threats to population persistence. Empirical researchers should focus on the temporal and spatial differences occurring between local populations rather than attempting to apply inflexible classifications to particular systems (Thomas and Kunin 1999).

8.2 METHODS

8.2.1 Defining local populations

The first objective in examining the spatial structure of populations is to determine if local population boundaries can be identified. In Yilliminning, I delineated local population boundaries based on territory contiguity and level of interaction (actual or potential) between territory occupants (Figure 8.2). Interaction between territories could include territorial disputes or cross-territorial provisioning. A spatial cluster of territories was classified a local population if territories:

- a) were contiguous, confined to a spatially discrete habitat remnant and the likely or actual level of interaction between territory occupants was high (e.g., local population (LP) 1 – Figure 8.2);
- b) occurred in spatially discrete remnants, but the distance between remnants did not prevent regular interaction (e.g., LP 5); and
- c) occurred in the same remnant as other territories, but the distance between territories precluded regular interaction (e.g., LP 8).

Occasionally, single territories were considered local populations because they were spatially and demographically (based on the criteria above) discrete (e.g., LP 9 and 10 – Figure 8.2). Dispersal between territories was not used as a criterion to delineate local population boundaries because the number of recorded dispersals was relatively low (see Section 8.3.3). Local population boundaries could be modified with more extensive data on inter-territory movements. There was no numerical criterion for the delineation of local populations in Yilliminning, but all

populations were small enough to suggest that between population processes (e.g., dispersal) should have a significant influence on population persistence. My classification of local populations also fits the definition of Hanski and Simberloff (1997 – see Section 8.1.2) because all territory occupants shared a common environment. For comparative purposes, I also designated the three study sites in Dryandra as local populations (although they may be subsets of a continuous population). I did this to compare rates of increase and population projection models for the Dryandra sites with the local populations in Yilliminning.

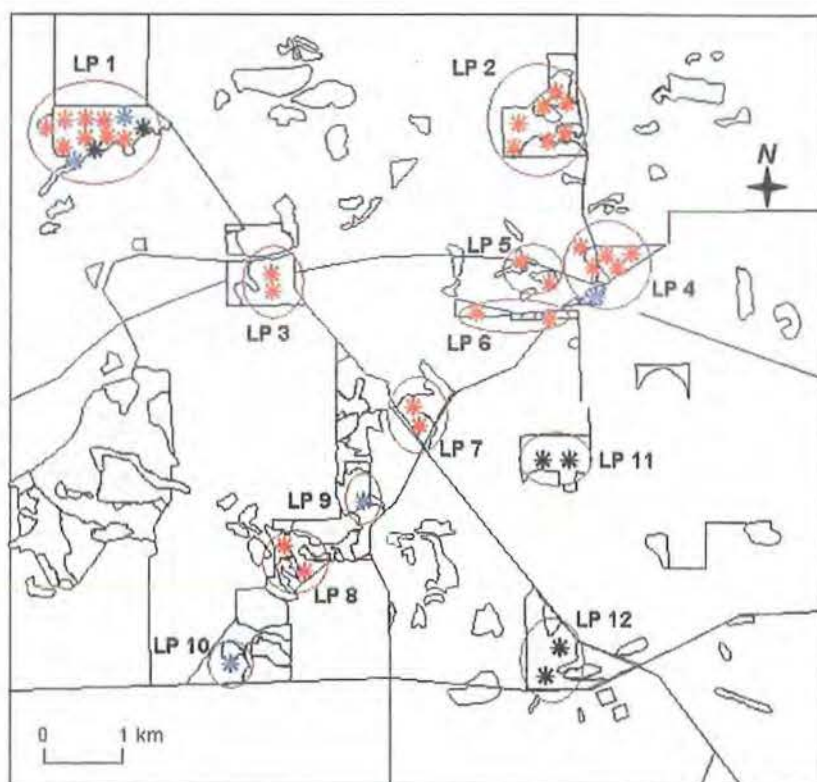


Figure 8.2 The location and boundaries (dark red ellipses) of local populations (LP) in Yilliminning. Red asterisks = the 30 closely monitored territories, blue asterisks = irregularly monitored territories with banded individuals, and black asterisks = irregularly monitored territories with unbanded individuals. Dark grey shading is remnant native vegetation or revegetation, and light grey shading is agricultural land. Solid lines between remnants are roads or other linear features associated with vegetation corridors.

8.2.2 The population dynamics of local populations

The survival rate of primary males and females in Yilliminning was determined using the methods described in Chapter 3 (Section 3.2.6). Survival rate for 1998 – 99 was calculated as the probability of a primary male or female surviving from the beginning of one breeding season to the next, and for 1999 – 00, the probability of surviving from the beginning of the 1999 breeding season to mid-July 2000 (the end of the study). Adult survival rate was compared between each habitat context in Yilliminning (i.e., large ungrazed, large grazed, small ungrazed and small grazed) and between Dryandra and Yilliminning using the computer program CONTRAST (Sauer and Williams 1989).

A complication in these calculations was the regular disappearance of entire groups from certain territories (see below). The fate of these groups was unknown because they were not re-located during the course of my study. It is possible that these disappearances represented group dispersals (to outside the study area) rather than mass mortality because new groups occasionally dispersed into vacated territories. They may also reflect a breaking up of groups and movement of individuals after the death of one of the primary birds (see Discussion). Irrespective of the reasons for group disappearances, primary individuals did not remain in the study area and did not contribute to the reproductive output of any local population. Therefore, I treated these disappearances as deaths in the calculations of survival rate.

I assessed local population dynamics in two ways to determine if a local population could persist without immigration or emigration. Firstly, I determined if recruitment within a local population was sufficient to compensate for adult mortality using three measures: a) the mean number of female offspring per primary female per year; b) juvenile survival rate (from fledging to the following breeding season); and c) primary female survival rate. The first two measures represent recruitment of female offspring into the breeding population. Juvenile survival rate was based on all juveniles rather than just females because the estimation of female only survival was complicated by high dispersal levels (see Chapter 3).

If a population is replacing itself then (following Pulliam 1988; Donovan et al. 1995)

$$(1 - \text{primary female survival rate}) = (\text{mean number of female offspring/primary female/year} \times \text{juvenile survival rate}).$$

If recruitment does not compensate for primary female mortality then the population is declining, or if it is greater than mortality the population is increasing. The calculation of each component of the equation was based on the methods described in Chapter 3 and the data collected from the local populations in Dryandra (the three study sites) and Yilliminning.

I also examined local population dynamics by constructing population projection models for each local population in the absence of immigration and emigration. These models predict population growth over time based on the survival and reproductive rates recorded during the study. Population growth was modelled following Donovan et al. (1995) as

$$N_{a(t+1)} = (N_{at} \times S_{at}) + (N_{at} \times F_t \times S_{jt}).$$

Here, t = year of simulation, N_a = number of primary females, N_{at} = the number of primary females in year t , S_{at} = the survival rate of primary females from one breeding season to the next, F_t = the mean number of female offspring per primary female in year t , and S_{jt} = the survival rate of juveniles in year t to the following breeding season ($t + 1$).

I used the number of all adult females (primary and helpers) in each local population at the beginning of the 1998 breeding season as the starting population for each model. If a local population contained irregularly monitored territories (e.g., LP 1 – see Figure 8.2), demographic rates (e.g., number of adult females and female offspring production) were assigned to these territories based on values averaged across all other territories in the same local population. I also constructed population projection models for the three sites in Dryandra to compare with Yilliminning. All rates used in the Dryandra and Yilliminning models were based on data averaged across the 1998 and 1999 breeding seasons, and population growth or decline was modelled over 20 years.

Population projection models were also constructed for the entire Yilliminning population based on all known territories. I averaged demographic

rates across all territories and modelled population growth or decline over 20 years. In these analyses, I examined the consequences of removal of certain local populations on overall population projection by re-calculating population growth or decline based on average values excluding the removed local population. This was a useful exercise because it simulated the consequences of the removal of habitat remnants from the landscape (e.g., through habitat clearance or fire) on the probability of persistence for the entire population.

8.2.3 Dispersal and group turnover

I recorded all inter-territory movement of banded birds in Yilliminning. This movement involved cross-territorial provisioning of nestlings (examined in Chapter 6), natal dispersal and other temporary movements. Dispersal by birds born prior to the commencement of the study (whose status as helper or primary individual was unknown) was considered to be natal rather than breeding dispersal (see Chapter 3 for definitions). These dispersers obtained a breeding position in their new territory while other individuals of the same sex remained in the originating territory. Therefore, the disperser was assumed to be a helper undertaking natal dispersal, and the individuals remaining in the originating territory were assumed to be the primary male or female.

Temporary movements involved the dispersal of an individual from its originating territory to another territory (or nearby area) in the study landscape where the individual remained in the area for a short period (1 – 2 months). The eventual fate of these dispersers was unknown. Group dispersals also appeared to occur because some vacated territories were occupied by adult birds with juveniles (assumed to be their offspring). The fate of groups that disappeared and the origin of new groups was unknown.

I calculated the distance of all natal dispersals and temporary movements by banded individuals. Dispersal distance was measured in a straight-line between the centre of the originating territory to the centre of the destination territory. Short dispersals (< 2 km) were measured directly in the field using a 100 m tape, pacing or an odometer. Dispersals > 2 km were measured from topographic maps.

I categorised dispersal distances into 1 km distance intervals (i.e., $0 < 1, \dots, 9 < 10$ km). The resulting distribution of distances was biased owing to a finite study area and uneven census effort in each territory. I adjusted the distribution using similar methods to Matthysen et al. (1995) and Calc (1999). For each territory containing banded individuals, I counted the number of territories in each distance interval (e.g., $1 < 2$ km) surrounding the territory, which were censused at least once during the study. These territories were weighted according to the number of census visits made during the study. This gave a weighted number of territories censused in each distance class surrounding every territory with banded individuals. These values were averaged across all territories to give a mean value per distance class. This value was used to weight the observed dispersals in each distance class to give an expected distribution of dispersals. I also examined the relationship between territory quality and natal dispersal using the quality index derived in Chapter 3 (Section 3.3.7).

Logistic regression was used to examine correlations between group disappearance and selected demographic and habitat variables (following the methods of Nicholls 1989). These variables were:

- a) territory quality – from the quality index derived in Chapter 6;
- b) group size – per Chapter 6;
- c) territory size – per Chapter 6;
- d) habitat context – large ungrazed, large grazed, small ungrazed and small grazed; and
- e) reproductive success – groups were considered successful if they produced at least one fledgling in a season.

8.2.4 Spatial structure and interactions between local populations

A comprehensive analysis of source-sink dynamics in a network of local populations requires knowledge of births (B), deaths (D), immigration (I) and emigration (E). Thomas and Kunin (1999) argued that rigid categorisation of local populations as sources or sinks may be inappropriate because elements of population dynamics may change over time reflecting characteristics of different categories.

The status of local populations defined by the four demographic parameters (B , D , I and E) may vary along a continuum reflecting changes in demographic traits.

The position of a local population can be plotted in “demographic space” at any given point in time (Thomas and Kunin 1999). This space is defined by the axes B minus D ($B - D$) and I minus E ($I - E$; Figure 8.3). For any given local population, the values of $B - D$ and $I - E$ can be used as coordinates to plot its location in demographic space. Populations with high positive values of $B - D$ and high negative values of $I - E$ could be considered population sources (Figure 8.3). These values can be expressed per capita by dividing them by local population size. This allows the comparison of the position of different sized local populations.

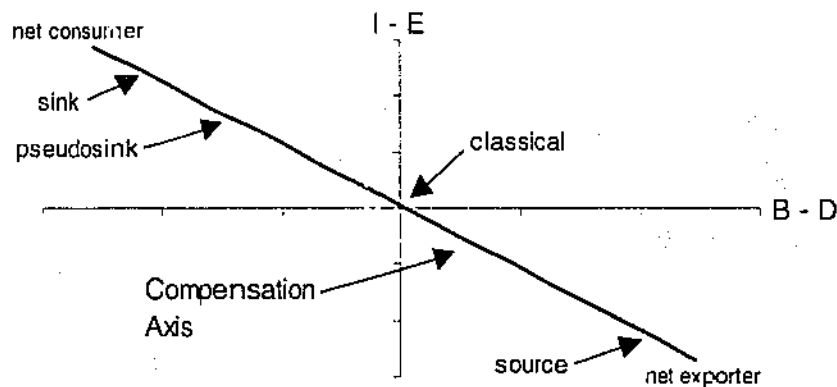


Figure 8.3 The demographic space defined by the axes births minus deaths ($B - D$) and immigration minus emigration ($I - E$; modified from Thomas and Kunin 1999). Local populations may be defined by their position along the compensation axis. This position may change over time reflecting variability in demographic rates.

The location of local populations in demographic space may fall along a line referred to by Thomas and Kunin (1999) as the “compensation axis” (Figure 8.3). This axis is defined by the equation $(B + I) - (D + E) = 0$. The compensation axis is a measure of population equilibrium and variability in the four demographic parameters. Local populations characterised by low demographic or environmental stochasticity and strong density dependence will be located close to the axis, whereas those with greater stochastic variation and weaker density dependence will be positioned further from the axis (Thomas and Kunin 1999). The important point

is that any given local population may change its position over time, fluctuating between source, sink and equilibrium status.

I used the methods of Thomas and Kunin (1999) to plot the location in demographic space of each local population in Yilliminning for the periods August 1998 – August 1999 (the beginning of the breeding season) and August 1999 – July 2000 (the end of the study). For comparative purposes, I also plotted the location of local populations (the three study sites) in Dryandra for 1997 – 1998 and 1998 – 1999. I calculated per capita measures of B, D, I and E for each local population as follows:

B = the number of female fledglings produced during each breeding season;

D = the number of primary females, and female fledglings failing to reach independence, disappearing from local populations during the defined periods;

I = the number of new females entering a local population and remaining for at least one breeding season (as breeder or helper); and

E = females born during the defined periods, reaching independence and subsequently disappearing.

Only considering the position of a local population along the compensation axis treats each population in isolation. If movement occurs between populations, the relative importance of interactions between populations in a network needs to be considered. To account for this, Thomas and Kunin (1999) proposed using a “mobility axis” defined as $(I + E) - (B + D)$. The position of a local population along the mobility axis gives some indication of the relative importance of movements in and out of the population on population dynamics (high positive values represent a high level of movement).

The mobility axis is orthogonal to the compensation axis and the location of a local population can be plotted in this new demographic space based on its value along each axis (Figure 8.4). The collective location of local populations in a network gives some indication of the nature of the subdivided population (e.g., a patchy population or source-sink). The position of a local population along the mobility axis also gives an indication of the relative importance of within- versus between-population processes. For example, the dynamics of local populations with

high positive values on the mobility axis would be strongly influenced by movement between populations (as in a patchy population). I plotted the location of each local population in Yilliminning and Dryandra in the demographic space defined by the compensation and mobility axes.

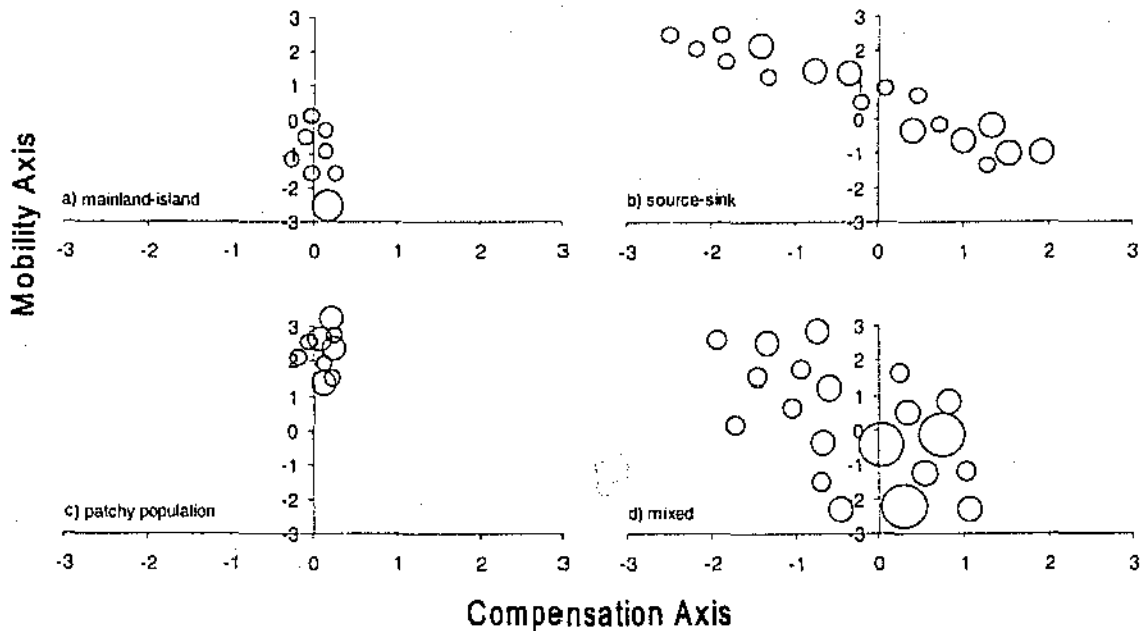


Figure 8.4 Examples of distributions of local populations (unfilled circles) on the compensation and mobility axes (from Thomas and Kunin 1999). The size of circles is proportional to local population size. The relative position of each local population in the network may be used to classify population structure: a) mainland-island (core-satellite), b) source-sink, c) patchy population, and d) mixed.

8.3 RESULTS

8.3.1 Local populations

I identified 12 local populations in Yilliminning based on inter-territory interaction between birds (see Figure 8.2). The number of territories in each local population ranged from one to 12 (3.3 ± 0.61) and local population size (for females only) ranged from one to 16 (3.9 ± 0.79 ; Table 8.1). The number of territories and local population size declined from 1998 to 1999, but no local population went “extinct” during this period.

Table 8.1 The number of territories and population size (females only) in 1998 and 1999 for each local population (LP) in Yilliminning.

Local population	No. of territories 1998	No. of territories 1999	Population size (♀) 1998	Population size (♀) 1999
LP 1	12	10	16	11
LP 2	7	6	9	8
LP 3	2	2	2	2
LP 4	6	6	9	6
LP 5	2	2	2	2
LP 6	2	1	2	1
LP 7	2	2	3	2
LP 8	2	2	2	2
LP 9	1	1	1	1
LP 10	1	1	1	1
LP 11	2	2	3	3
LP 12	2	2	3	3
Total	41	37	53	42

8.3.2 The population dynamics of local populations

Adult survival

On average, adult survival rate was lower in Yilliminning than Dryandra (Table 8.2), but there were no significant landscape differences between average primary male (Dryandra 0.77 ± 0.08 vs Yilliminning 0.63 ± 0.09 , CONTRAST, $\chi_1^2 = 1.35$, $P > 0.10$) or female survival rate (0.67 ± 0.09 vs 0.53 ± 0.09 , CONTRAST, $\chi_1^2 = 1.21$, $P > 0.10$) for the period 1998 – 99. Survival rate varied slightly between habitat contexts in Yilliminning (Table 8.2), but none of these differences were significant. The greatest variation was for males in 1998 – 99 (CONTRAST, $\chi_3^2 = 4.51$, $P = 0.20$).

Table 8.2 The survival rates of primary males and females in each habitat context in Yilliminning.

<i>Habitat context</i>	♂ survival		♀ survival	
	1998 - 99	1999 - 00	1998 - 99	1999 - 00
Large ungrazed	0.67 ± 0.17	0.78 ± 0.15	0.55 ± 0.18	0.89 ± 0.17
Large grazed	0.63 ± 0.18	0.63 ± 0.18	0.50 ± 0.19	0.63 ± 0.17
Small ungrazed	0.33 ± 0.21	0.50 ± 0.29	0.50 ± 0.22	0.80 ± 0.17
Small grazed	0.86 ± 0.14	0.71 ± 0.18	0.57 ± 0.20	0.67 ± 0.17
Overall	0.63 ± 0.09	0.73 ± 0.09	0.53 ± 0.09	0.78 ± 0.08

Rates of replacement

I modelled rates of replacement based on the actual mean number of female fledglings produced in each local population for 1998 and 1999 combined, and a range of primary female and juvenile survival rates. I used primary female survival rates ranging from 0.5 – 0.8 and juvenile survival rates from 0.1 – 0.4, close to the extremes recorded in my study. The results are presented in Table 8.3. In this table, actual productivity and survival rates for each local population (including Dryandra) are presented in bold text. Corresponding replacement levels (in red) indicate the number of female fledglings required for a local population to meet replacement at the observed survival rates. Non-bold text demonstrates how changes in the survival rates affect the number of fledglings required (in blue) for each local population to meet replacement (or as close as possible).

For example, in LP 1, actual primary female and juvenile survival rates were 0.6 and 0.1 respectively, and the mean number of female fledglings produced per territory was 0.19. At these survival rates, the local population would need to produce an annual average of four female fledglings per territory for the local population to replace itself without immigration (Table 8.3). If primary female and juvenile survival rates increased to the extreme values of 0.8 and 0.4 respectively, only 0.5 female fledglings per territory per year would need to be produced to meet replacement. This figure is still higher than the actual annual productivity recorded in LP 1, so improvements in primary female and/or juvenile survival rate and fledgling productivity are needed for the local population to meet replacement without immigration.

Table 8.3 The actual survival rates for primary females and juveniles (J), and fledglings produced (bold values), in each local population (LP) and the entire population at Yilliminning and Dryandra. Corresponding replacement values (in red) show the number of female fledglings required for each local population to meet replacement with the observed survival rates. Comparing values for mean fledglings and replacement provides an indication of how far behind or ahead of replacement local populations were. Population status indicates whether a local population was below replacement (-), meeting replacement (*) or above replacement (+). Non-bold values are the modelling results, which show how an increase or decrease in survival rates changes the level of replacement required (in blue).

Local population	Survival rate (♀)	Mean (♀) fledglings	Survival rate (J)	Replacement	Population status
LP 1	0.6	0.19	0.1	4.00	-
	0.8	0.19	0.4	0.50	
LP 2	0.8	0.47	0.4	0.50	*
	0.8	0.47	0.4	0.50	
LP 3	0.8	0.33	0.1	2.00	-
	0.8	0.33	0.4	0.50	
LP 4	0.6	1.20	0.2	2.00	-
	0.6	1.20	0.4	1.00	
LP 5	0.5	0.50	0.4	1.25	-
	0.8	0.50	0.4	0.50	
LP 6	0.7	1.33	0.3	1.00	+
	0.6	1.33	0.3	1.33	
LP 7	0.5	0.50	0.1	5.00	-
	0.8	0.50	0.4	0.50	
LP 8	0.5	0.50	0.4	1.25	-
	0.8	0.50	0.4	0.50	
Site A	0.7	0.80	0.4	0.75	*
	0.7	0.80	0.4	0.75	
Site B	0.8	0.90	0.4	0.50	+
	0.7	0.90	0.4	0.75	
Site C	0.8	1.30	0.4	0.50	+
	0.5	1.30	0.4	1.25	
Yilliminning	0.6	0.60	0.2	2.00	-
	0.8	0.60	0.4	0.50	
Dryandra	0.8	1.00	0.4	0.50	+
	0.6	1.00	0.4	1.00	

In contrast to LP 1, LP 2 was just meeting replacement at current productivity and survival rate levels. LP 6 was the only local population in Yilliminning that was ahead of replacement, producing 0.33 more female fledglings per territory per year than required (Table 8.3). Model results indicated that if female survival rate in LP 6 dropped to 0.6, the local population would just meet replacement all else being equal.

Out of the eight local populations studied in detail in Yilliminning, six (75%) did not meet replacement levels with the recorded survival and productivity rates. In contrast, all "local populations" in Dryandra either met or were ahead of replacement. Based on mean values across all local populations, the entire population in Yilliminning was well below replacement at recorded productivity rates and would only be slightly ahead of replacement if primary female and juveniles survival rates improved to the maximum recorded in my study (Table 8.3).

Population projection models

The trends identified in the analyses of replacement rates were mirrored in the population projection models for the local populations in Yilliminning and Dryandra. Without immigration, all local populations in Yilliminning, except LP 6, were predicted to decline over the next 20 years, most to extinction (Figure 8.5a). Local populations with small population sizes (two to three females) were particularly vulnerable, all declining to extinction within 10 years. The most dramatic decline was for LP 1, which went from a local population size of 16 females to extinction in approximately 11 years. This local population occupied the large grazed remnant, which had a high population density (Chapter 6), but very low levels of fledgling productivity (Table 8.3 and Chapter 7).

LP 6 was the only population where growth was predicted to occur (Figure 8.5a). This growth was the result of a single territory producing surplus female fledglings. LP 2 had a higher local population size (nine females) and although it declined over the 20-year period, it represented the most stable local population in the network. This population occupied the large ungrazed remnant, one of the most undisturbed remnants in the study area. In contrast to Yilliminning, all local populations in Dryandra were predicted to increase over the next 20 years. Sites B and C showed exponential growth, while growth in Site A was relatively marginal (Figure 8.5b).

Based on values averaged across all local populations (including unmonitored territories), the entire population in Yilliminning was predicted to decline to extinction within 20 years without immigration from outside the study area. With the selective removal of the more productive local populations, the time to extinction was shortened by approximately 5 – 6 years (Figure 8.5c).

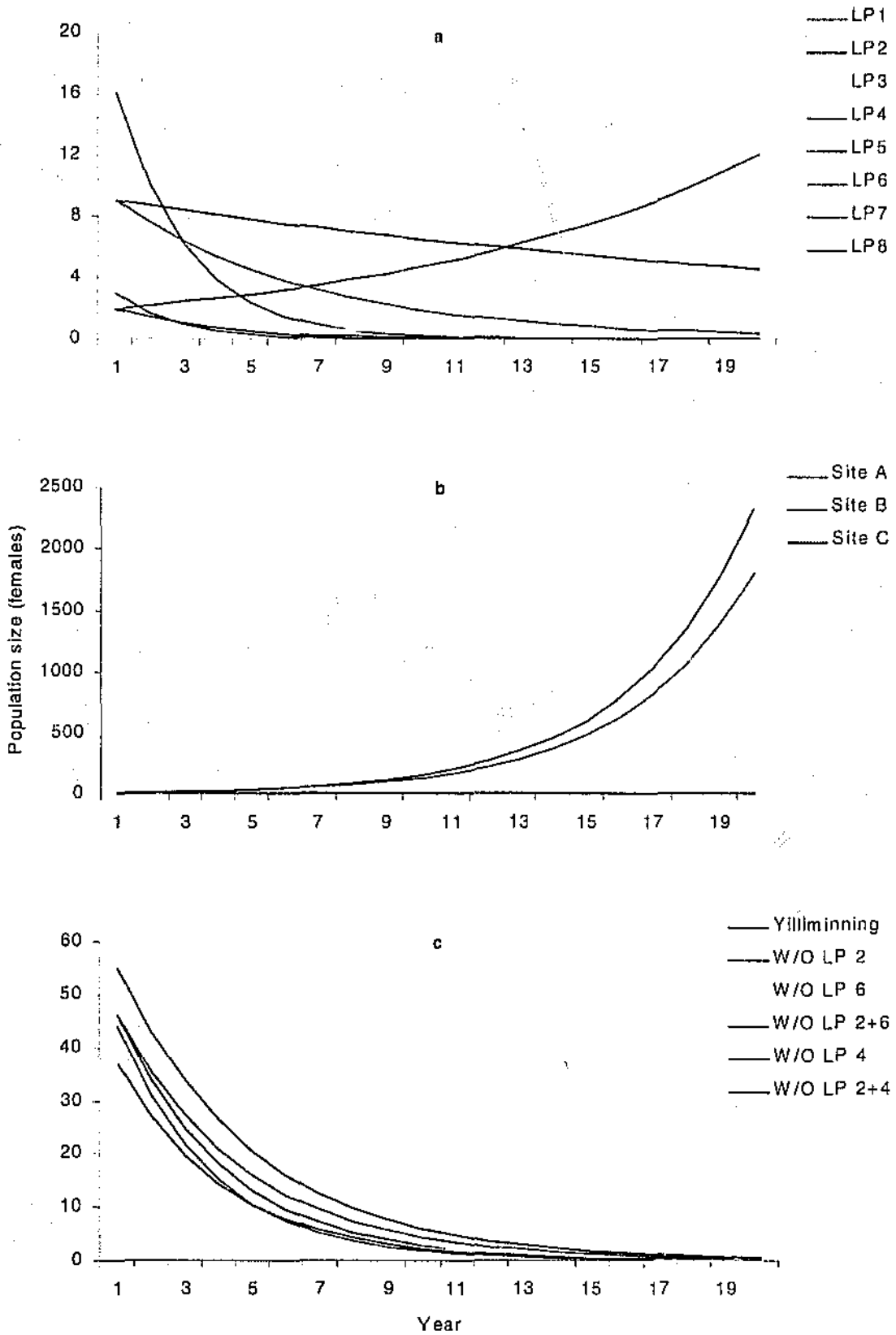


Figure 8.5 Population projection models for: a) each local population in Yilliminning, b) each study site (local population) in Dryandra, and c) the entire population in Yilliminning. The models predict population growth or decline over 20 years based on the demographic rates recorded during the study. Model (c) shows predicted population decline after the removal of certain local populations (w/o = without) from the landscape.

8.3.3 Dispersal and group turnover

Dispersal

I recorded nine natal dispersals and one temporary movement within the Yilliminning study area (Figure 8.6). A total of 50% of movements were to contiguous or nearby territories ($0 < 1$ km), but dispersals of up to 7 km were recorded (2.2 ± 0.8 km). Adjusting for census bias, short-distance dispersals tended to be overestimated and longer dispersals underestimated (Figure 8.7). Four dispersals were by males, three of these were to contiguous territories and one was 4 km (mean distance 1.2 km). In general, dispersals by females were longer than males; four out of six dispersals were ≥ 1 km (mean distance 2.5 km).

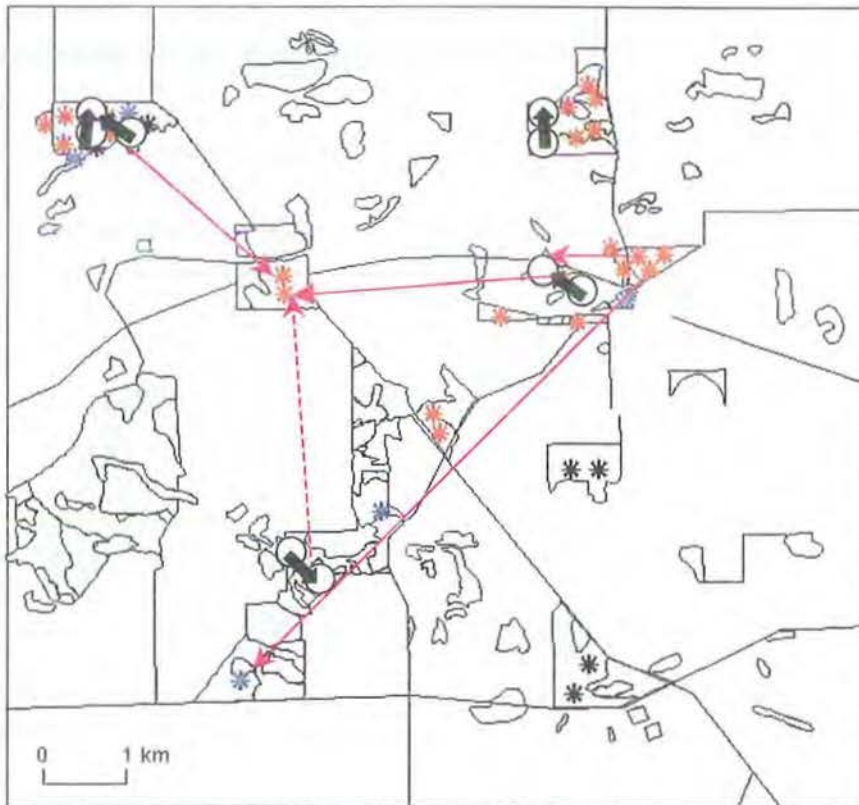


Figure 8.6 Natal dispersals and temporary movements of banded individuals in Yilliminning. Black arrows show natal dispersals to adjacent or nearby territories (indicated by white circles), pink arrows are long distance (> 1 km) natal dispersals (solid line) or temporary movements (dashed line).

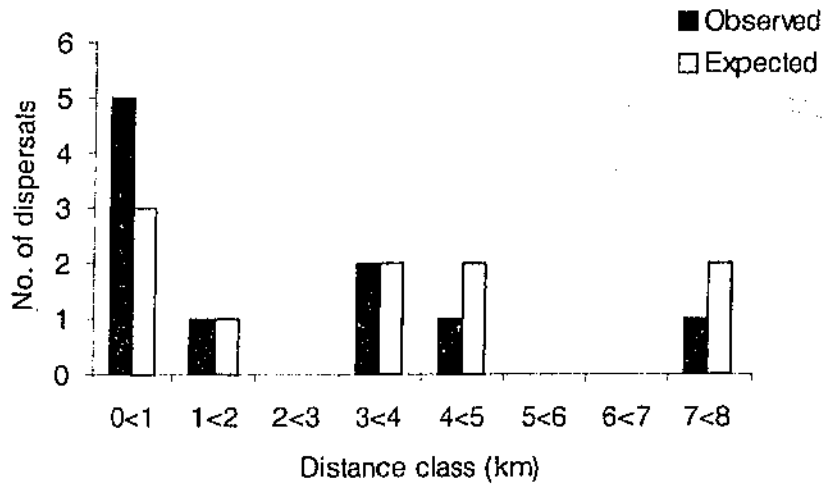


Figure 8.7 The number of dispersals recorded in each distance class during the study (observed) and the number expected after correcting for census bias.

In addition to the movement of banded birds, unbanded individuals were recorded dispersing into habitat remnants where all known residents were banded (i.e., there was a low probability of this being an intra-remnant movement). These dispersals were either temporary movements (six) or dispersals to a primary (breeding) position (eight). Most (71.4%) were by females, probably reflecting the female-biased dispersal recorded in Rufous Treecreepers (Chapter 3). The above evidence suggests that movements between habitat remnants in Yilliminning were not severely restricted.

Based on the territory quality index derived in Chapter 3, natal dispersal decisions did not appear to be influenced by territory quality. Out of the nine natal dispersals, just over half (55.6%) were to a higher quality territory.

Group turnover

During 1998 – 99, nine groups disappeared from territories in which they attempted to breed. Two territories were re-occupied by dispersers from adjacent or nearby territories, three territories were re-occupied by new groups (one pair and two groups of three) and four remained unoccupied to the end of the study. During 1999 – 00, seven groups disappeared, two were from the same territories that had been vacated by another group the previous year and only one territory had been re-colonised up to the end of the study.

In total, 16 groups disappeared from territories during the study. These disappearances almost always occurred post-breeding season during summer and autumn (January – May) and the fate of disappearing groups was unknown. I examined correlative relationships between group disappearance and the demographic and habitat (independent) variables described in Section 8.2.3 using logistic regression. None of the independent variables were highly correlated ($r \geq 0.7$). Only one variable was significantly related to the disappearance of treecreeper groups (Table 8.4). Groups were more likely to disappear if they failed to fledge a nestling during the breeding season. The timing of group disappearances and the fact that they occurred mostly after reproductive failure suggests that these disappearances may be movements rather than mass mortality.

Table 8.4 The final logistic regression model including reproductive failure as a significant predictor of group disappearance. Change in deviance is distributed as χ^2 .

	df	Change in deviance	Residual df	Residual deviance	P
Null model			31	43.86	
+Reproductive failure	1	10.62	30	33.24	< 0.005
		Coefficients	s.e.		
Constant		0.264	0.430		
Reproductive failure		1.276	0.430		

8.3.4 Modelling spatial structure

The local populations in Yilliminning were spread along the compensation axis defined by the values B – D and I – E (Figure 8.8). For the period 1998 – 99, LP 3, LP 7 and LP 8 showed characteristics of population sinks or pseudosinks, whereas LP 4 – 6 could be categorised as sources (Figure 8.8a). Interestingly, almost all local populations were positioned close to the compensation axis, characteristic of populations with a level of stability.

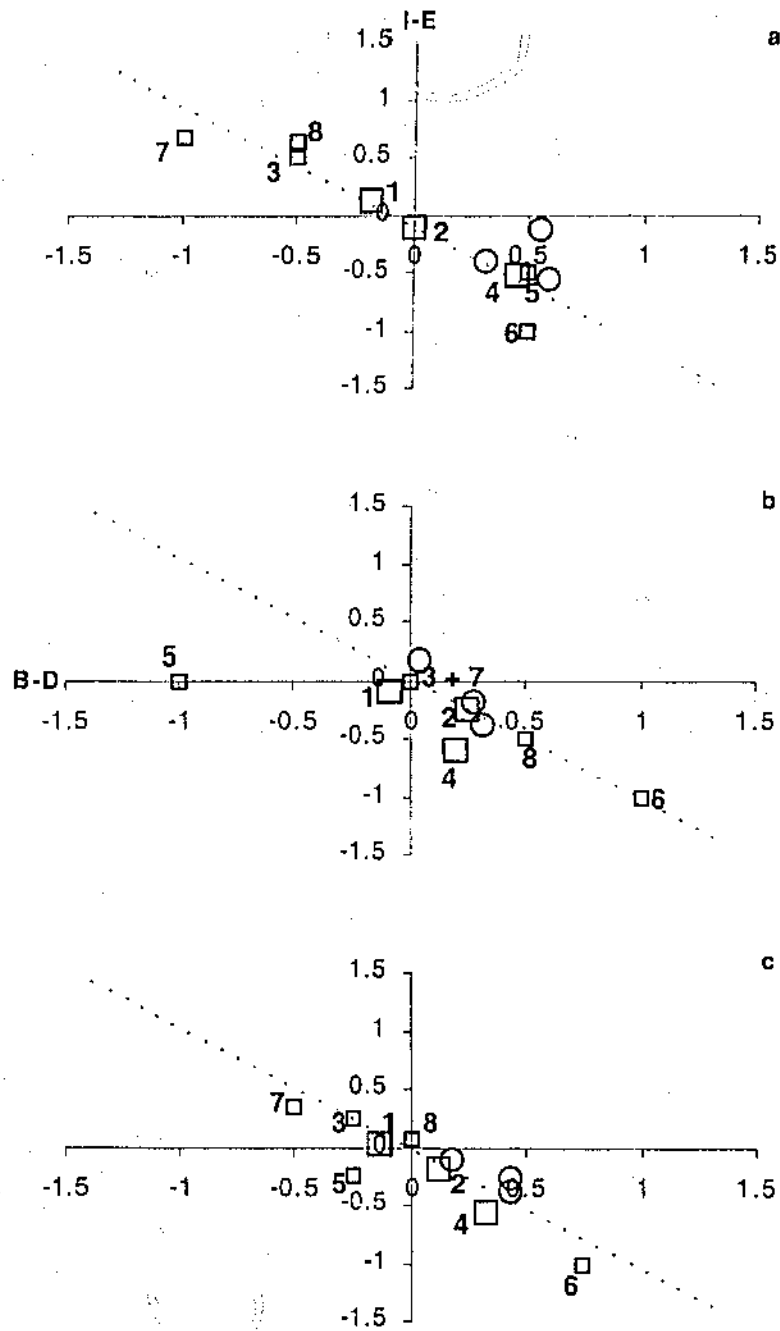


Figure 8.8 The position of each local population in Yilliminning (unfilled squares and bold numbers) and the three study sites in Dryandra (unfilled circles) in the demographic space defined by births minus deaths ($B - D$) and immigration minus emigration ($I - E$). The size of the squares is proportional to local population size and the dotted line is the compensation axis. The three figures show population status for: a) 1998 – 99 (1997 – 98 for the Dryandra sites), b) 1999 – 00 (1998 – 99 for Dryandra), and c) both periods combined.

The position of local populations for the period 1999 – 00 differed from the previous year (Figure 8.8b). No population showed clear sink characteristics except possibly LP 5, whereas LP 6 was the only population with clear source characteristics. Most local populations were positioned near the compensation axis and most exhibited the equilibrium dynamics of “classic” (balanced) populations. Importantly though, a number of populations were positioned differently in demographic space compared to the previous year. For example, LP 5 moved from a source towards being a sink, LP 2 moved from equilibrium towards being a source, LP 3 and LP 7 moved from sinks to equilibrium, and LP 8 swapped from sink to source (Figure 8.8b). The combined values for the two survey periods showed each local population (including the three sites in Dryandra) positioned on or close to the compensation axis with a distinct spread between population source and sink (Figure 8.8c).

The addition of a mobility axis yielded some interesting patterns in population structure (Figure 8.9). What is most striking about these patterns is that almost all local populations clustered near the centre of the demographic space, although there were movements from one year to the next (compare Figure 8.9a and b). Values along the mobility axis were mostly negative indicating that within-population processes (i.e., local births and deaths) had a stronger influence on population size than movements between populations. This would be expected from sedentary, resident species where dispersal into a local population generally only occurs when a breeding position becomes vacant.

The spatial structures illustrated in Figure 8.9 for the local populations in Yilliminning show a network at or near equilibrium, although the negative values along the compensation axis are indicative of a gradual decline in population numbers. Negative mobility values also suggest that any sudden decline in local population size is unlikely to be arrested by an influx of immigrants.

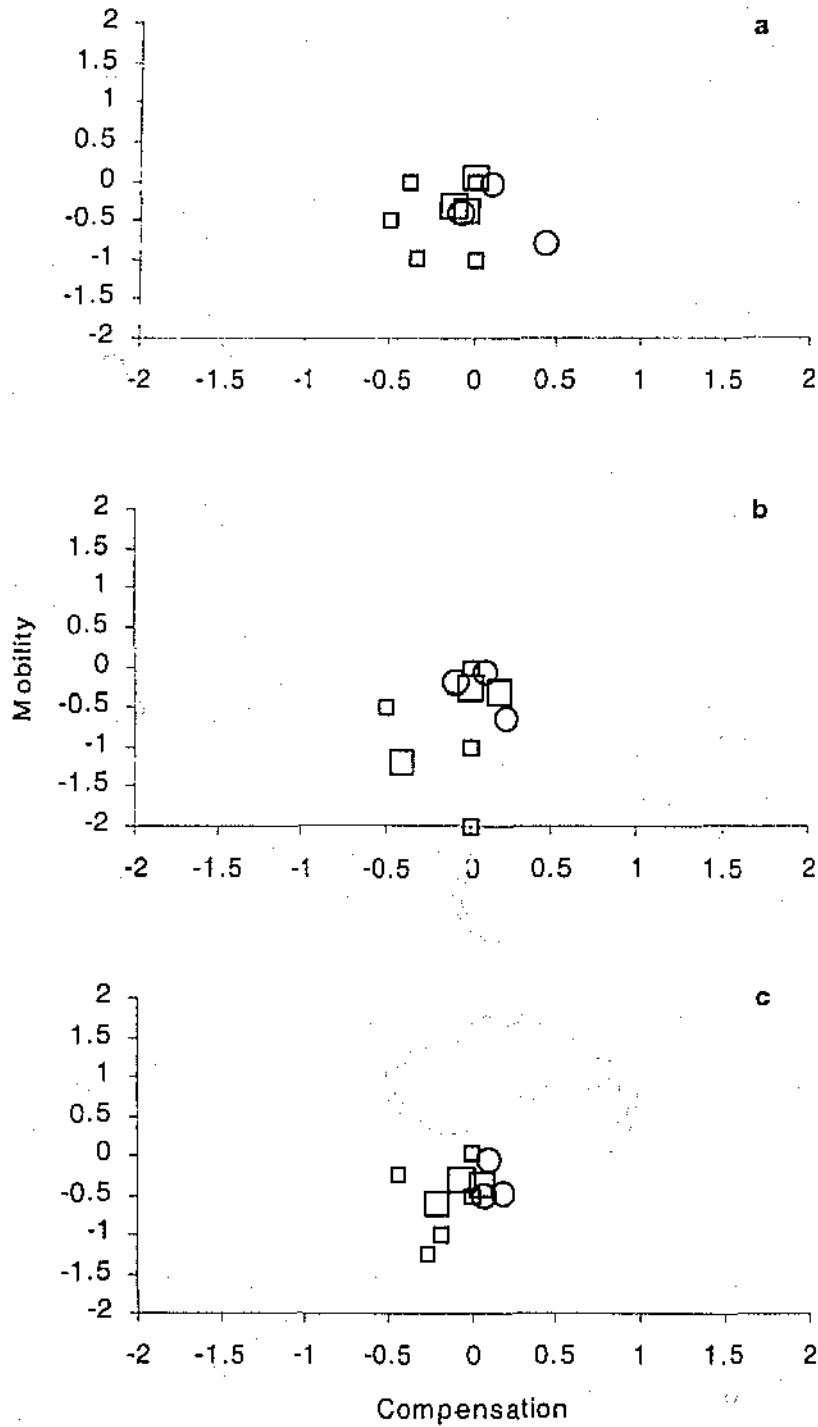


Figure 8.9 The position of each local population in Yilliminning (squares – size of square is proportional to local population size) and the three sites in Dryandra (circles) in the demographic space defined by the compensation and mobility axes. The three figures show population status for: a) 1998 – 99 (1997 – 98 for Dryandra), b) 1999 – 00 (1998 – 99 for Dryandra), and c) both periods combined.

8.4 DISCUSSION

8.4.1 The spatial structure of the subdivided population in Yilliminning

The treecreeper population in Yilliminning was divided into spatially discrete clusters of territorial groups occupying a single remnant or a close group of remnants. The level of interaction between territories within clusters was greater than between clusters. Movements between clusters generally involved natal dispersal to fill a breeding vacancy rather than frequent interaction between neighbouring groups. Although the temporal scale of my study precluded a detailed analysis of the level of interaction (e.g., dispersals) between clusters, current evidence suggests that this interaction was not sufficient to classify the collection of treecreeper territories as a single population with frequent mixing of individuals. The demographic discreteness occurring between the spatial clusters was probably adequate to categorise them as local populations, but the spatial and demographic structure of the population did not fit neatly into the classic (i.e., Levins) definition of a metapopulation. During my study, the subdivided population in Yilliminning fell somewhere along the continuum between a patchy population and a classic metapopulation.

No local population was large enough to be considered resistant to extinction. Analyses of replacement rates and population projection models indicated that all but one local population in Yilliminning would decline to extinction without immigration. The one local population that produced surplus individuals during the study period was comprised of two breeding groups in 1998 and one in 1999. Therefore, all local populations were projected to decline at observed demographic rates or were so small that they were at risk of extinction from demographic stochasticity (Shaffer 1981; Caughley 1994). Local population instability with all local populations at some risk of extinction is consistent with the Levins theory of metapopulation dynamics (Moilanen and Hanski 1998; Hanski 1998). This theory appears to be most appropriate when local population size is small (Moilanen et al. 1998) or stochastic and/or deterministic processes threaten the persistence of even relatively large local populations (Hanski and Thomas 1994; Hanski et al. 1994).

Population structure in Yilliminning was not characteristic of mainland-island (Harrison 1991) or core-satellite (Boorman and Levitt 1973) type metapopulations, but the spatial scale of my study and arbitrarily defined study area limit this interpretation. Some larger habitat remnants containing treecreepers occurred outside the study area. Although I am unaware of population size or demographic rates in these remnants, the area of suitable habitat was sufficient for them to act as possible mainlands to the "island" remnants in Yilliminning. Also, their distance from the study area (< 10 km) was within the dispersal range of the treecreeper (based on the longest dispersal recorded at Yilliminning), and it appeared that movements into and out of the study area were occurring. In retrospect, a much larger study area was required to adequately determine the population dynamics of the Rufous Treecreeper in the fragmented landscape. However, it was clear that the subdivided population at Yilliminning was unlikely to persist without immigration from surrounding remnants.

One of the key tenets of the Levins metapopulation model is that local populations persist in an equilibrium between local extinctions and colonisations (Harrison and Taylor 1997; Hanski 1998). During my study, no local population went extinct, but the limited temporal scale of my observations relative to the life span of the Rufous Treecreeper precluded a comprehensive analysis of this phenomenon. Breeding groups went "extinct" in that whole groups disappeared from territories, which were generally re-colonised by other groups or individual dispersers. Extinction-colonisation was observed at a level of organisation below that of local populations in what might be termed "metagroup" dynamics. This type of metagroup dynamics was rarely observed in the unfragmented landscape of Dryandra (Chapter 3).

Considering the small size of most of the local populations (nine out of 12 contained only one to two breeding groups), it is not difficult to "scale up" from metagroup dynamics to metapopulation dynamics characterised by local extinction and colonisation. Indeed, some local populations were close to extinction by the end of the study. For example, LP 3 contained only two single females in separate territories for the majority of 1999, and LP 6 comprised a single territory for most of

the study, as an adjacent, previously occupied territory remained unoccupied for 18 months.

The level of movement between local populations (and from outside the study area) appeared to be sufficient to rescue most from complete expiration (the "rescue effect"; Brown and Kodric-Brown 1977). This pushed the local population network along the structural continuum towards the patchy population dynamics described by Harrison (1991, 1994). One could argue that the subdivided population at Yilliminning consisted of a mixture of well defined local populations with infrequent dispersal between them (e.g., LP 1 and 2) and a patchy distribution of individual territories (e.g., LP 8 – 10).

The rescue effect is dependent on the number of potential dispersers, mortality rates during dispersal and the isolation of local populations. In years when there are few dispersers, small, isolated local populations may not be rescued from extinction. Dispersal decisions are also influenced by the ecology of the species in question. Being a cooperative breeder, the Rufous Treecreeper represents an interesting case because a certain proportion of young will remain philopatric. This reduces the number of dispersers that may rescue declining local populations from extinction. Conversely, it may help to maintain local population size over longer periods because all offspring do not automatically disperse from their natal territory.

Even infrequent dispersal may be sufficient to maintain metapopulation stability (Temple and Cary 1988; Simberloff et al. 1992), but the reproductive rate of breeding groups in Yilliminning was not sufficient to produce enough potential dispersers to fill vacancies caused by breeder mortality (disappearance). For example, in 1998, 18 female fledglings were produced. Using relatively high fledgling and juvenile survival rates (0.7 and 0.4 respectively), only five of these females would survive to the following breeding season. This calculation does not consider dispersal related mortality, but a recent study on two cooperatively breeding bird species found that dispersal mortality in another fragmented landscape in the wheatbelt was very low (i.e., 0.00072 and 0.00075; Brooker et al. 1999). With a relatively high primary female survival rate of 0.7, nine out of 30 females would die annually. Hence, the production of potential breeders in Yilliminning was about half that required to meet replacement.

The subdivided population at Yilliminning would not persist if the demographic rates observed during my study are consistent over the long-term. It appeared that dispersal from outside the study area assisted in maintaining population stability. Indeed, the location of the local population network in the demographic space defined by the mobility and compensation axes (Figure 8.9) suggested that the subdivided population was near equilibrium, although declining slightly (negative values on the compensation axis). Any observed short-term decline may also be a cyclic fluctuation in population dynamics and longer-term data are required for a comprehensive analysis of population stability.

Although current evidence suggests a population structure lying somewhere between classic metapopulation and patchy population dynamics, it is important to recognise the potential for change in dynamics over time. The network of local populations may move around in demographic space reflecting variability in B, D, I and E (Thomas and Kunin 1999). Changing the spatial scale of the investigation may also result in a re-classification of population structure (Thomas and Kunin 1999). Given these caveats, the persistence of the subdivided population at Yilliminning appeared to be dependent on both within-population dynamics of spatially discrete clusters of breeding groups and movement between clusters, and a metapopulation approach appears to be generally applicable.

8.4.2 Source-sinks and the demography of local populations

Significant differences in reproductive output between particular local populations in Yilliminning (e.g., LP 1 and 2; see Chapter 7) suggests that source-sink theory may be an appropriate framework for assessing population dynamics. However, the data on movement between local populations are insufficient to determine if the flow of movement is likely to be from local populations with relatively high productivity generating a surplus of potential dispersers (net exporter), to local populations with low productivity (net importer). This directional flow of movement is an important assumption of traditional source-sink models (Diffendorfer 1998). In species like the Rufous Treecreeper, directional flow cannot be inferred from differences in reproductive success because dispersal between local populations is a function of the mortality rate of breeders. A local population may

have relatively high reproductive output, but if breeder mortality is also high, it may not be a net exporter of individuals.

The position of each local population along the compensation axis defined by $B - D$ and $I - E$ (Figure 8.8) indicated that most fluctuated around population equilibrium. Some local populations exhibited traits of a source or sink in the first year of the study, but were positioned differently in demographic space in the second year. Local populations with demographic rates near replacement may fluctuate between being sources or sinks (Sæther et al. 1999). A fixed demographic categorisation of the subdivided population in Yilliminning is not appropriate because local populations may be spatially and temporally dynamic. Substantial changes in position in demographic space may be relatively more common among local populations with small population size, because minor changes in B , D , I and E could result in large differences in demographic characterisation from one year to the next. Only small changes in the position of larger populations should occur unless environmental stochasticity has a strong influence on population dynamics. This was the case for the local populations at Yilliminning (Figure 8.8) and would be expected from K -selected species living in a relatively stable environment.

Although there were no statistically significant differences between landscapes, adult survival rate in Yilliminning was slightly lower than Dryandra for both males and females. Variation in adult female survival rate may have a greater effect on population growth rates than changes in reproductive success (Lande 1988), particularly when reproductive output is less than replacement (Sæther et al. 1999). Improving survival rates may be extremely important for population viability. This may be achieved by improving habitat quality, although I found no relationship between quality and primary female survival in Dryandra (Chapter 5). It is also sobering to observe that six out of the eight local populations in Yilliminning were still below or just at replacement with a primary female survival rate of 0.8 (the maximum recorded in my study; Table 8.3). In some instances, an increase in reproductive output and/or juvenile survival rate would also be required for local populations to meet replacement.

The projected decline of all but one local population without immigration (Figure 8.5) suggests that the entire network of local populations in Yilliminning

may have been a population sink. For the population to persist, habitat remnants outside the study area would be required to act as sources. On an even larger scale, highly productive populations in the relatively undisturbed habitat of Dryandra may act as a source to areas like Yilliminning. This type of regional source-sink dynamics has been suggested in other studies (Brawn and Robinson 1996), but owing to the spatial scale involved it would be almost impossible to ascertain the influence of population dynamics in Dryandra on the subdivided population at Yilliminning with observational data only. Genetic data are required to provide an indication of the potential for mixing to occur between populations.

An important result from my study was that local population (and remnant) size was not related to source-sink status. LP 1 was the largest local population in Yilliminning, but had the lowest reproductive output and very low survival rates (Table 8.3). Interestingly, LP 1 could have been categorised as a pseudosink (Watkinson and Sutherland 1995) because low productivity appeared to be related to high population density (Chapters 6 and 7). At lower densities, LP 1 may exhibit the characteristics of a population source.

The temporal and spatial scales of my study were inadequate to make strong conclusions about source-sink dynamics, but there were demographic differences between local populations consistent with certain predictions from source-sink theory. Longer-term data on bird movements and possible manipulation of population density are required to contribute to our knowledge of source-sink dynamics in Yilliminning. The data on rates of increase and population projection models should also be interpreted with caution because they are based on observations from only two breeding seasons. The dynamics of the subdivided population in Yilliminning during 1998 – 2000 may have represented a temporary decline in a series of longer-term cyclic fluctuations. This is a consistent problem in short-term studies of long-lived species that operate over large spatial scales, but there is sufficient evidence to suggest that spatial variability in demographic rates and movement between local populations have an important influence on the persistence of the Rufous Treecreeper in the fragmented agricultural landscape.

8.4.3 Further differences between Dryandra and Yilliminning

With relatively few data on dispersal, it is difficult to determine if dispersal behaviour differed between landscapes. Increasing fragmentation may result in reduced dispersal (the *fusion* response) or an increase in dispersal distance and frequency (the *fission* response; Ims et al. 1993). A positive correlation between dispersal distance and level of fragmentation has been found for certain species (Diffendorfer et al. 1995; Matthysen et al. 1995) generally as a result of an increase in the distance between territories. Breininger (1999) found that Florida Scrub-jays *Aphelocoma coerulescens* living in an urban environment dispersed greater distances than those in a less modified environment containing groups of contiguous territories. I predict similar results for the treecreeper populations in Dryandra and Yilliminning. In Dryandra, any given territory was surrounded by many neighbouring territories within a relatively short distance, which represented potential destinations for a dispersing individual. The distance between territories was much greater in Yilliminning, particularly for individuals living in the small local populations. An increased distance between territories limits the opportunities for helpers to assess prospective territories for breeding positions (see Chapter 9).

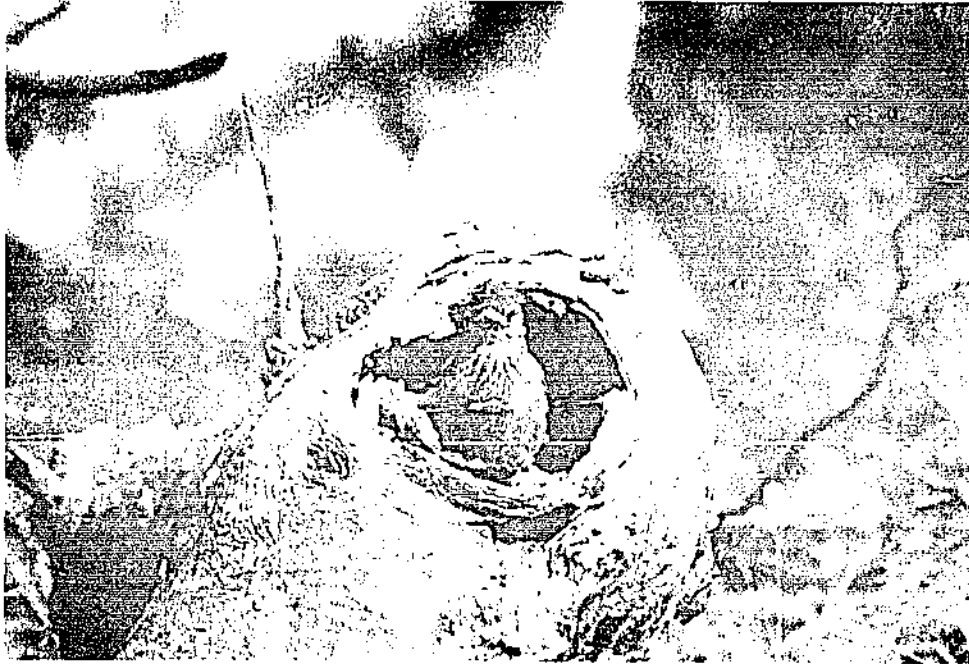
A striking difference between the treecreeper populations in Dryandra and Yilliminning was the rate of disappearance of entire breeding groups. In 90 group years in Dryandra, the loss of all territory residents within a short period of time (i.e., 1 month) occurred on only two occasions (2.2%). In Yilliminning, 16 groups disappeared in 59 group years (27.1%). The disappearances in Yilliminning were more likely to occur after reproductive failure.

Cale (1999) also recorded group disappearances in his study of the cooperatively breeding White-browed Babbler *Pomatostomus superciliosus* in the heavily fragmented Kellerberrin district of the Western Australian wheatbelt. Cale suggested that these disappearances represented group dispersals (where groups did not return to the study area) or visits (where groups eventually returned to the study area) rather than mass mortality or the breaking up of groups. Babbler groups were more likely to move in summer if their habitat supported a relatively low abundance of prey items (invertebrates) suggesting that habitat quality may have influenced this behaviour.

For Rufous Treecreepers, group disappearances may have been group dispersals to remnants outside the study area because new groups were occasionally recorded moving into vacated territories. It is possible that these disappearances were also a result of groups breaking up after the death (or disappearance) of one of the primary sexes. This is a possibility because many groups occurred in simple pairs and it may take a prolonged period for breeding vacancies to be filled. Therefore, some territories may be occupied by an individual bird for an extended period (this occurred in 1999, where four territories were occupied for at least 6 months by single birds). In these circumstances, an individual may decide to move rather than waiting for a disperser of the correct sex to locate their territory. This situation rarely occurred in Dryandra because most breeding vacancies were filled within a month (Chapter 3).

A greater probability of dispersal after reproductive failure has been recorded in other species (Doligez et al. 1999) and may reflect an adaptive response to sites yielding low success (Clark and Shutler 1999). This has significant implications for population dynamics in fragmented landscapes like Yilliminning where habitat quality and reproductive success were relatively low. It suggests a level of instability in territory occupancy, the possibility of small local populations going extinct, greater movement between remnants (and a possible increase in dispersal related mortality), and a reduction in the proportion of experienced breeders in the population. Experienced primary females had significantly higher reproductive success in Yilliminning (Chapter 6), but it is unclear if experienced females moving from one remnant to another between breeding seasons were at a reproductive disadvantage. The important point is that habitat familiarity is probably advantageous to breeding birds. This cannot occur with a frequent turnover of groups.

Part IV
CONCLUSION



"The future's uncertain, and the end is always near."
The Doors

CHAPTER 9 SYNTHESIS AND CONCLUSION

9.1 THE CONSEQUENCES OF HABITAT FRAGMENTATION FOR THE RUFIOUS TREECREEPER

9.1.1 Social and spatial organisation

This thesis attempted to determine the consequences of habitat fragmentation for the Rufous Treecreeper by comparing the ecological traits of the species in a relatively undisturbed landscape with those in a highly modified agricultural landscape. The “quasi-experimental” approach of comparing fragmented and unfragmented landscapes is a surrogate for more manipulative pre- and post-fragmentation comparisons, but for species that operate at relatively large spatial and temporal scales, it is one of the most viable options for assessing the threats to population persistence. I chose certain ecological traits for detailed comparison. Traits such as social organisation and cooperative breeding are more closely aligned with behavioural ecology than conservation biology, but some authors have recently highlighted the need to develop a stronger link between these disciplines (Lima and Zollner 1996; K. Martin 1998). A clear understanding of species behaviour can only strengthen conservation efforts, and a melding of behavioural ecology with other disciplines offers exciting prospects for future research (Lima and Zollner 1996; Sugg et al. 1996).

The social organisation of the Rufous Treecreeper appears to be hierarchically structured, influenced by habitat heterogeneity and the social dynamics of the species (Figure 9.1). Each level of the hierarchy can be identified by the frequency of interaction occurring between constituents. The basic unit at the lowest level is the breeding group where individuals interact on a daily basis. Breeding groups occupying contiguous or nearby territories may regularly interact under certain circumstances (e.g., the cross-territorial provisioning of nestlings during the breeding season) to form ecological or social neighbourhoods (*sensu* Cale 1999, but not used in the same context). Social neighbourhoods may be linked by frequent, short-distance dispersal to form dispersal neighbourhoods (Figure 9.1). Neighbourhood boundaries are likely to show temporal variability owing to changes

in the frequency of interaction among adjacent groups and variation in population dynamics.

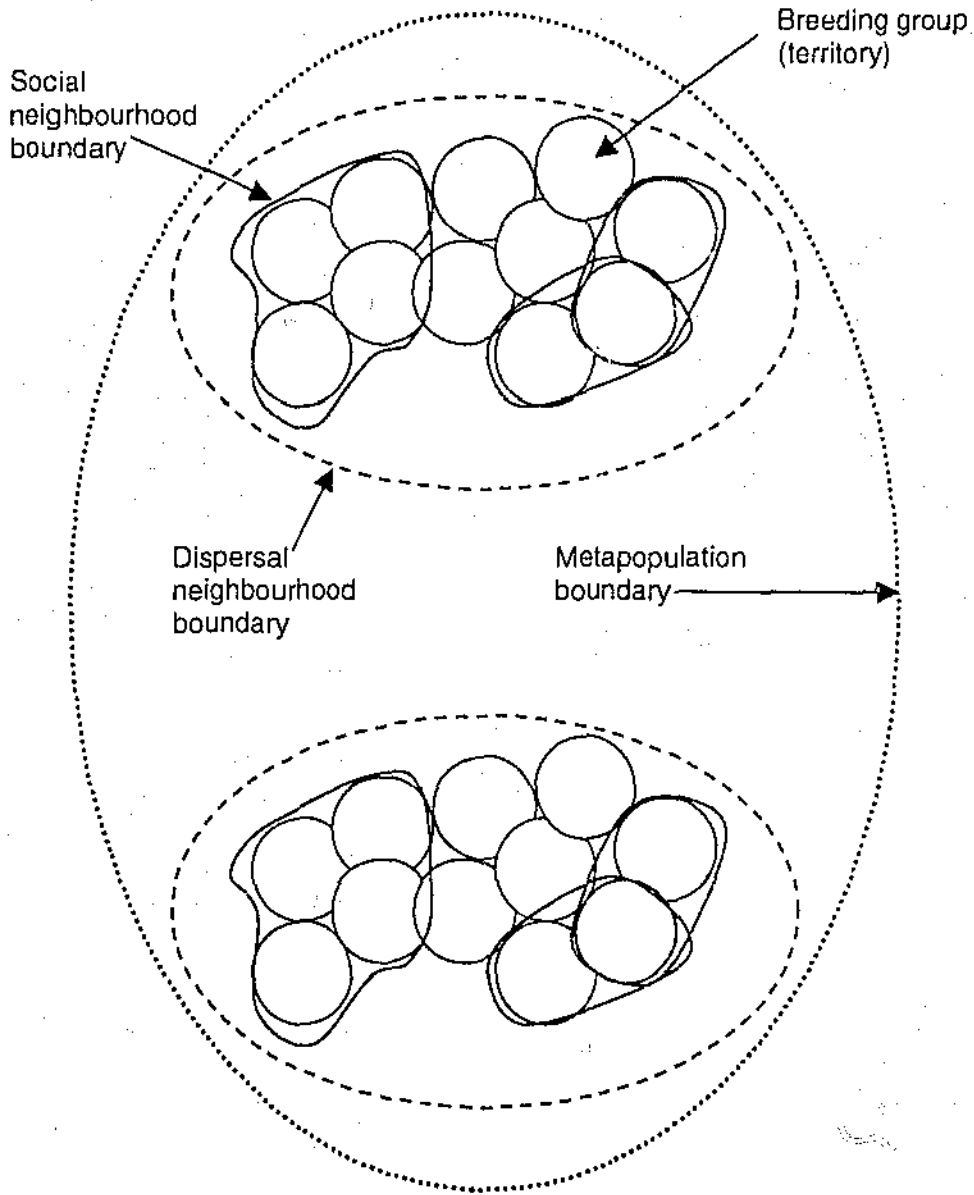


Figure 9.1 The hierarchical social organisation of the Rufous Treecreeper. Breeding group (territory) and social neighbourhood boundaries were identified during this study; dispersal neighbourhood (\approx local population) and metapopulation boundaries are hypothesised to exist based on evidence in the literature.

My data on treecreeper dispersal are not sufficient to determine if dispersal neighbourhoods exist for this species, but research on other cooperatively breeding birds suggests that dispersal frequency among nearby breeding groups is probably high (Zack 1990; Cale 1999; Daniels and Walters 2000). Dispersal neighbourhoods may be analogous to the local population concept from metapopulation dynamics (Hanski and Simberloff 1997). The level of interaction between dispersal neighbourhoods would then help to define the appropriateness of metapopulation theory to understanding the population dynamics of species with this type of demographic structure.

The demographic structure described above is similar to that proposed by Cale (1999) in his study of the White-browed Babbler *Pomatostomus superciliosus* in the highly fragmented central wheatbelt. This type of demographic structure may be imposed on a species by habitat fragmentation, but it appeared to be characteristic of the Rufous Treecreeper population living in the unfragmented landscape. Habitat heterogeneity coupled with the habitat selectivity of treecreepers (Chapter 4) would result in spatial subdivision in the distribution of the species even in continuously vegetated landscapes. Therefore, the Rufous Treecreeper has probably evolved to cope with a certain level of population discontinuity. The patchy distribution of populations characteristic of fragmented landscapes may not represent a significant disruption to the population dynamics of the species, especially if there are few restrictions to movement between spatially discrete groups. Indeed, spatial subdivision may reduce the threat of environmental stochasticity or catastrophes affecting all local populations simultaneously (Shaffer 1981; Goodman 1987; Letcher et al. 1998).

Too much subdivision is detrimental to population viability and a key area for future research is determining the level of habitat fragmentation particular species are able to cope with (Andr n 1994; With and Crist 1995; Fahrig 1998). If the maintenance of social and dispersal neighbourhoods is important for the persistence of the Rufous Treecreeper, then relatively fine-grained fragmentation that leads to neighbourhood subdivision is likely to have adverse consequences.

An important prediction from this assumption is that treecreeper populations in fragmented landscapes like the wheatbelt will be distributed in spatially clustered

groups more frequently than individual, isolated territories. The distribution of territories in Yilliminning provided equivocal evidence to support this hypothesis (see Figure 8.2), although the sample size was not sufficient for a robust assessment. Regional surveys of breeding group distribution are required. These surveys would contribute greatly to our understanding of the consequences of fragmentation for Rufous Treecreepers. Data on the incidence of a species in a wide range of remnants, particularly if collected over a time series, can also be input into "incidence function" models to assess metapopulation dynamics (Hanski 1994).

In addition to sociality, habitat suitability and quality influence the spatial aggregation of breeding groups and this must be considered when documenting the distribution of a species in fragmented landscapes. Although the absence of a species from a remnant may be the result of a myriad of factors, assessing the suitability of the habitat is fundamental to understanding this relationship. The habitat models developed in my study (Chapter 4) may assist others undertaking presence/absence surveys of Rufous Treecreepers to determine whether remnants are unoccupied simply because the habitat is unsuitable, or whether the habitat is suitable, but unoccupied owing to stochastic or deterministic processes affecting population dynamics.

Assessments of habitat selection in Rufous Treecreepers may be complicated by the apparent sociality of the species. If the maintenance of social neighbourhoods is important, non-preferred woodland types adjacent to Wandoo *Eucalyptus wandoo* may be used by some breeding groups so that neighbourhood interactions are maintained. This hypothesis predicts that non-preferred habitat will be used more frequently when it is close to preferred habitat that already contains treecreepers, and preferred habitat that is distant from other breeding groups (and may only support one or two territories) will remain unoccupied. This hypothesis is consistent with the theory of conspecific attraction (Smith and Peacock 1990; Muller et al. 1997) and could be tested by removing breeding groups from selected habitat patches and monitoring re-colonisation by new individuals.

The consequences of sociality are that individuals may repeatedly attempt to breed in poor quality habitat while more suitable habitat remains unoccupied. The viability of treecreeper populations in fragmented landscapes

would be enhanced by maintaining remnants of high quality habitat (old growth Wandoo) that are sufficiently large, or in close enough proximity, to support social and dispersal neighbourhoods.

9.1.2 Cooperative breeding and dispersal

Cockburn (1996) suggested that phylogenetic history might be an important determinant of cooperative breeding. This predicts that cooperative breeding will occur throughout a species' range. This is consistent with predictions from the life history hypothesis, which suggest that certain life history traits (e.g., low reproductive rates and high survival) predispose a species to breed cooperatively if environmental conditions (e.g., relatively stable climate) allow year-round territory occupation (Arnold and Owens 1998; Hatchwell and Komdeur 2000). The characteristic life history strategies of cooperative breeders are strongly *K*-selected, and are expected to occur in predictable environments supporting stable populations (MacArthur and Wilson 1967; Pianka 1970).

The phylogeny and ecological traits of the Rufous Treecreeper predispose the species to cooperative breeding (Chapter 3). Like many cooperatively breeding Australian passerines, its evolution is probably closely aligned with the aseasonality of the habitats it tends to occupy (Ford et al. 1988). Cooperation may be the best reproductive strategy for relatively stable populations living in aseasonal conditions. To assess the consequences of habitat fragmentation for the species, it is therefore important to determine if fragmentation and degradation disrupt ecological processes and population stability sufficiently to make cooperation a maladaptive trait in fragmented landscapes.

High annual survival is a primary factor believed to influence cooperative breeding in certain avian lineages (Arnold and Owens 1998). Habitat change leading to reduced survival rates may have adverse consequences for cooperative behaviour. In Yilliminning, the survival rate of primary males and females was lower than Dryandra (Chapter 8), although the difference was not statistically significant. There was also a weakly significant trend towards lower juvenile survival rates in the fragmented landscape (Chapter 7). The consequence of these trends is that breeding vacancies would occur more frequently in Yilliminning than Dryandra. This is

magnified by the fact that group disappearances were also much more common in Yilliminning. If we assume that restricted breeding opportunities is one factor leading to philopatric offspring, then philopatry may become a maladaptive trait under circumstances where breeding opportunities are much more common. In these situations, it may be more profitable for offspring to begin searching for a breeding position much sooner than would normally be the case.

The tendency for offspring to remain philopatric means that some breeding groups may be without a breeding male or female for extended periods. This could possibly lead to these groups breaking up and abandoning their territory. In Yilliminning, a number of territories remained unoccupied for > 12 months and some were occupied by single birds for periods of up to 6 months (see Chapter 8). This was not a result of there being insufficient potential breeders within the population, as a number of groups had additional males and females. I propose that this occurred because of the combined effects of the evolutionary trait of philopatry in offspring, and habitat fragmentation adversely affecting the ability of potential dispersers to locate breeding vacancies.

Many studies have examined the effects of habitat fragmentation on the movement of birds between relatively isolated habitat patches (Saunders and de Rebeira 1991; Haas 1995; Lynch et al. 1995; Sieving et al. 1996; Brooker et al. 1999), but few studies have determined the effects of fragmentation on dispersal behaviour (Martin et al. 2000). Movement is simply getting from point A to point B; dispersal is a process that involves decision making by individuals at a number of levels. For Rufous Treecreepers, the process may involve a complex cost-benefit trade-off between remaining philopatric, short-distance dispersal to familiar, adjacent territories, or long-distance dispersal to an unknown destination. The ability to move between habitat patches is only a component of the dispersal process.

In Yilliminning, sufficient movement occurred between remnants to suggest that the level of fragmentation in this landscape did not completely disrupt the ability of individuals to move between sites (Chapter 8). However, I contend that the fragmented landscape adversely affected the dispersal process for Rufous Treecreepers. Potential dispersers had limited opportunities to assess the quality or status of potential destination territories owing to fewer neighbours and an increase

in the distance between territories. In Chapter 3, I suggested that cross-territorial provisioning was an avenue for non-breeders to assess the quality and status of adjacent territories. This probably assists non-breeders to make informed decisions regarding dispersal, which has been suggested as an important component of the dispersal process (Zack 1990; Reed et al. 1999). Territory contiguity facilitates informed dispersal in treecreepers, but this is severely disrupted with increasing fragmentation.

Disrupting the dispersal process could result in high quality territories remaining unoccupied for extended periods or potential breeders remaining unpaired (Walters et al. 1999). The sparse distribution of territories in Yilliminning, which is likely to be characteristic of fragmented landscapes, means that dispersers must travel long distances before locating a breeding vacancy. Long-distance dispersal may be energetically costly and dangerous, particularly if vegetative cover providing protection from predators is sparse. Also, movement may only be possible in particular directions if birds use vegetation corridors as conduits and are reluctant to cross unvegetated gaps of a certain distance (Brooker et al. 1999). With little knowledge of the surrounding landscape and potential breeding vacancies, dispersers are likely to invest considerably more effort in their search for a breeding vacancy in fragmented compared to unfragmented landscapes.

Dispersal is a complex process that is poorly understood even for some of the most intensively studied species. Extremely long-term data sets are required to adequately assess dispersal behaviour in highly mobile and relatively long-lived organisms like birds (Daniels and Walters 2000; Koenig et al. 2000). Sex-biased dispersal and issues such as inbreeding avoidance (Pusey 1987; Pusey and Wolf 1996) also complicate interpretations of behaviour. There is a desperate need for comprehensive data on the consequences of habitat fragmentation for bird dispersal. The dispersal behaviour of individuals in fragmented landscapes is fundamental to assessing the validity of metapopulation theory, which is the current vogue in conservation biology.

9.1.3 Reproductive success and population dynamics

At the level of individual breeding groups, reproductive success in *Dryandra* appeared to be a factor of territory quality and possibly group size (Figure 9.2). It is difficult to determine the independent effects of either because better quality territories generally supported larger groups (Chapter 5). In Yilliminning, the factors correlated with reproductive success formed a much more complex model (Figure 9.3). Grazed remnants of low habitat quality supporting high population densities (and consequently, small territories) had very low success. Experimental manipulation of population density in grazed remnants would help to determine if reproductive success in Yilliminning is density dependent. If population density is a factor of sociality in treecreepers, as suggested above, this reinforces the need to improve the quality of the habitat occupied by the species.

Owing to low reproductive success and relatively low survival in Yilliminning, all but one local population was below replacement (Chapter 8). My definition of a local population was limited because of few data on dispersal frequency between clusters of territories. However, current evidence suggests that the entire population at Yilliminning is unlikely to persist without immigration into the study area. Within- and between-population dynamics appear to be important for the persistence of Rufous Treecreepers in this landscape.

The subdivided population at Yilliminning fulfilled reasonably well three of the four prerequisites required for regional persistence to be considered dependent on classic metapopulation dynamics (Hanski et al. 1995; Moilanen et al. 1998). Firstly, local populations occupied spatially distinct habitat patches owing to suitable habitat being patchily distributed among mostly unusable agricultural land or other native vegetation types (e.g., shrubland). Secondly, no local population was large enough to be considered resistant to extinction. Thirdly, local population dynamics were sufficiently asynchronous to suggest that simultaneous extinction of all local populations was unlikely. Independent fluctuations in demographic rates may reflect localised differences in habitat quality. I have limited data to assess the fourth condition, which predicts that migration (dispersal) is distance dependent and population dynamics are strongly influenced by the spatial configuration of the habitat.

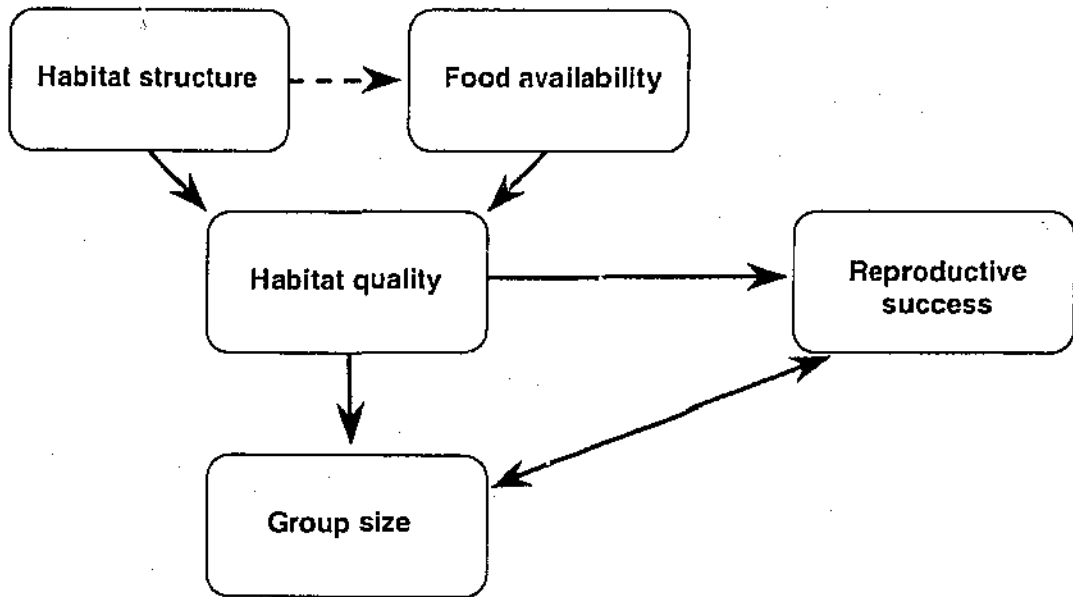


Figure 9.2 The interactions between factors that are likely to influence reproductive success in the unfragmented landscape of Dryandra. Solid arrows are probable relationships, dashed arrows are possible relationships. Habitat structure and food availability defines habitat quality, which in turn is correlated with reproductive success. Higher quality territories support larger groups, and group size is also correlated with reproductive success. A feedback loop occurs between group size and success because the size of a breeding group is generally defined by prior reproductive output.

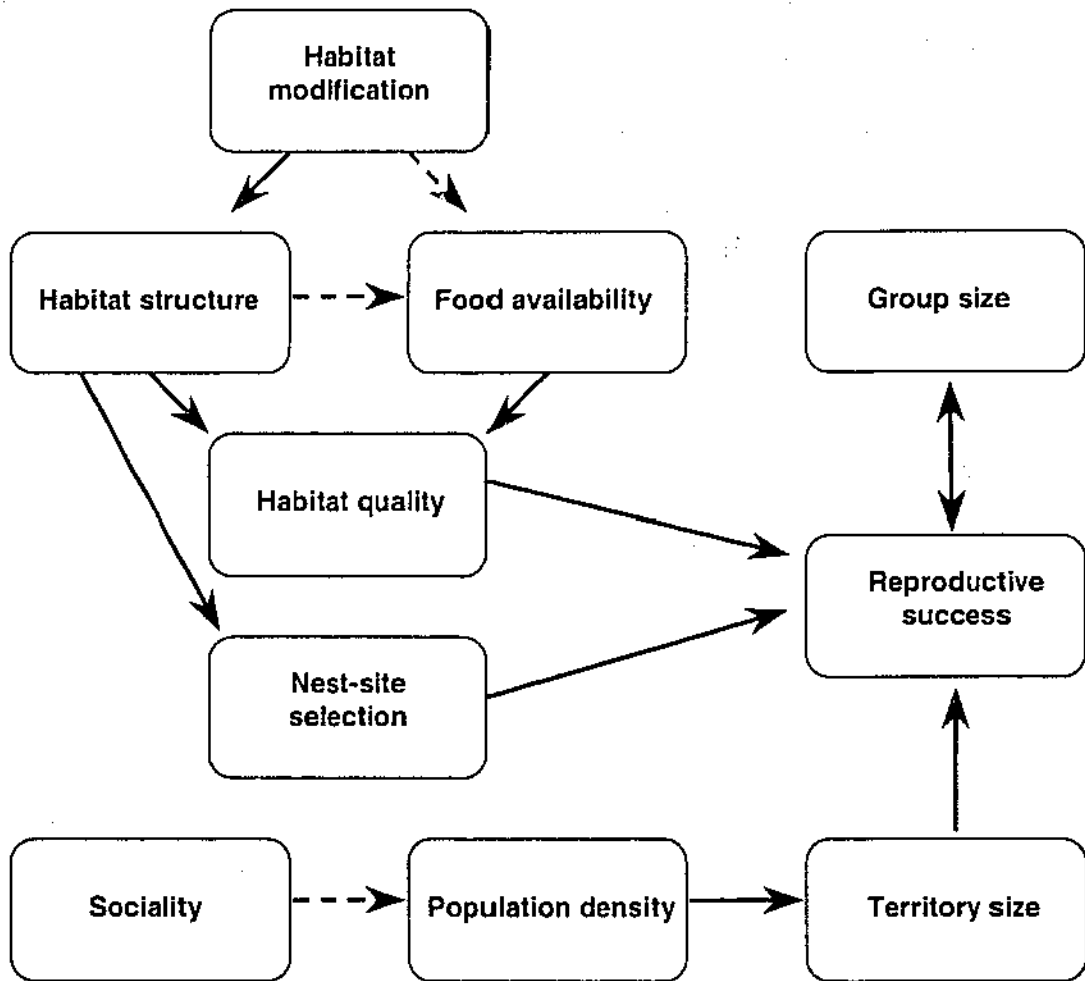


Figure 9.3 The interactions between factors that are likely to influence reproductive success in the fragmented landscape of Yilliminning. Solid arrows are probable relationships, dashed arrows are possible relationships. Habitat modification affects habitat structure and probably food availability, which is detrimental to habitat quality and subsequently reproductive success. Changes in habitat structure may also limit nest-site selection affecting nest success. Sociality may lead to high population densities and small territories, which appears to have adverse consequences for reproductive success if the underlying habitat quality is low.

9.2 RESEARCH LIMITATIONS AND FUTURE DIRECTIONS

My study was limited in a number of ways. Replication of territories or sites within remnants or landscapes is, in essence, pseudoreplication (Hurlbert 1984). At least one more unfragmented and fragmented landscape would have strengthened my conclusions, but replication at large scales is extremely difficult (Hargrove and Pickering 1992). Even if suitable replicates can be located, there are logistic constraints to monitoring large areas. In this instance, it is best to treat research such as mine as a case study of a particular region(s), and to use the results to generate hypotheses that can be tested in similar landscapes. It would be wrong to extrapolate my results to all fragmented landscapes in the wheatbelt.

It was apparent in Yilliminning that the 10,000 ha study area was not large enough to comprehensively document the population dynamics of treecreepers (Chapter 8). This is a constant problem when studying highly mobile species like birds. Populations bounded by natural or anthropogenic barriers (e.g., confined to oceanic islands) may be sufficiently "closed" that most influences on dynamics occur within a clearly defined area. However, the distribution of the Rufous Treecreeper spans thousands of square kilometres and any arbitrarily defined population may be open to influences from adjacent populations such that its dynamics are difficult to understand in isolation. It is yet to be determined if the level of fragmentation in the wheatbelt is sufficient to create disjunct populations that are effectively closed to external influences. It would be extremely valuable to identify and study such populations.

Conclusions from short-term studies of relatively long-lived species also need to be cautious. Cyclic fluctuations in dynamics may be misinterpreted as longer-term trends, or non-linear responses may provide misleading results (Wiens 1994). There is an urgent need in ecology for detailed, long-term case studies on selected species or systems (Brussard 1991; Golley 1998). This is beyond the scope of a single PhD study, but the opportunity exists for future research to build on the work presented here with the aim of generating long-term (e.g., 20+ year) data sets on the consequences of habitat fragmentation for the Rufous Treecreeper and other woodland birds.

Single-species studies have been criticised because of limited generality to conservation planning and the fact that we do not have the time or resources to study the dynamics of every organism (Franklin 1993; Wiens 1994; Lambeck 1997; Simberloff 1998; Mönkkönen and Reunanen 1999). To address the issue of generality of single-species research, approaches that use certain species as surrogates for others in the community have been proposed. These include the indicator (Landres et al. 1988), umbrella (Launer and Murphy 1994; Williams and Gaston 1994), keystone (Paine 1995) and focal (Lambeck 1997) species approaches. Each differs in emphasis and methodology, but a general premise in all approaches is that by managing for the requirements of a single or selected suite of species, other species in the same community will also be preserved. The attractiveness of this approach is that we would only need to know a few species well to effectively manage entire ecosystems. Although these concepts have theoretical appeal, unequivocal empirical evidence of their validity is lacking (Simberloff 1998; Lindenmayer 1999).

The use of surrogates attempts to meld single-species research with the pursuit of general ecological principles. One of the most important questions in ecology is whether general principles exist, or if every species needs to be treated as a special case (Lawton 1999). The search for generality must continue, but not at the expense of detailed empirical investigations of selected species. Single-species studies have contributed substantially to the development and testing of ecological theory (e.g., metapopulation dynamics). General theories may be severely limited without a detailed understanding of a species' biology (Simberloff 1994). Conversely, single-species research should be conducted and interpreted within the appropriate theoretical frameworks. It is the combination of natural history and underlying theory that drives ecology forward.

9.3 THE CONSERVATION OF WOODLAND BIRDS IN AGRICULTURAL LANDSCAPES

The future of woodland birds in the agricultural regions of Australia is in the balance (Recher 1999; Ford et al. 2001). Studies of the mechanisms of decline and the ecological traits of species that make them susceptible to the adverse consequences of habitat fragmentation are desperately needed (Mac Nally et al.

2000; Ford et al. 2001). These studies are best focussed on declining species that were once common in the agricultural region of interest rather than historically rare species or those near the limits of their distribution (Barrett et al. 1994; Reid 1999).

The once common Rufous Treecreeper is a declining species and the wheatbelt of Western Australia is arguably the centre of its distribution (Ford 1971). My study provides an insight into the complexity of processes that threaten the persistence of this species in agricultural landscapes. It is this complexity that undermines approaches to predict species-specific responses to fragmentation based on a few key ecological traits (Mac Nally and Bennett 1997; Mac Nally et al. 2000). However, generating and testing predictions is a valuable approach to understanding the consequences of habitat fragmentation. My study generates a number of predictions about the effects of fragmentation on the Rufous Treecreeper and future research should be designed to assess these predictions.

Conserving woodland birds in agricultural landscapes requires the active management and restoration of remnant native vegetation. Future directions for landscape restoration have been outlined in detail by other researchers (Recher 1993; Barrett et al. 1994) and the results of my study support these conclusions. In summary, management actions must involve removing disturbance (e.g., grazing) from remnant vegetation, ensuring regeneration of endemic species and maintaining important habitat characteristics (e.g., large trees). A key result from my study was the strong correlation between habitat quality (at the territory scale) and fitness in the Rufous Treecreeper population in Dryandra (Chapter 5). The consequence of this is that habitat modification is likely to result in reduced fitness.

I contend that increasing remnant size and improving landscape connectivity will not be sufficient to conserve many woodland birds in agricultural landscapes unless subsequent improvements are made to habitat quality. Good quality habitat for the Rufous Treecreeper appears to be Wandoo woodland (or similar, e.g., Salmon Gum *E. salmonophloia*) characterised by a high density of large trees, hollows and hollow logs. The challenge for future studies is determining what constitutes good quality habitat for the many other woodland birds that are declining in the agricultural regions of southern Australia.

A narrow management focus on just remnant native vegetation is unlikely to ensure the persistence of all species. Sympathetic management of the entire landscape is required that addresses the effects of current land-use practice on native species. An important area for future research is the consequences of changing the predominant land use (e.g., from cropping to agroforestry) on the processes occurring in remnant vegetation.

The conservation of woodland birds, and all other species, will not be achieved by managing ecological processes and threats in isolation. The underlying causes of the conservation crisis are social, political and economic (Brussard 1991; Daily 1997; Czech 2000; Naveh 2000; Prugh et al. 2000). Substantial changes to the current socio-economic and political environment are required to ensure the preservation of our biological diversity. This is a major challenge for society, but it is a challenge we all must face as we search for the road to sustainability.

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