Mallee Emu-wren (*Stipiturus mallee*): multi-scale habitat requirements and population structure

by

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Submitted in fulfilment of the requirements for the degree of

Doctor of Philosophy

Deakin University

June, 2011
I am the author of the thesis entitled:

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A naturalist's life would be a happy one if he had only to observe
and never to write

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Preface

This thesis has been written with a view to publishing all data chapters (2-5) as stand-alone bodies of work. This approach has lead to repetition in the Introduction and Methods sections. I am the principal contributor to all chapters in this thesis, and the primary author on all publications arising from this thesis.

All work was conducted under Deakin University Animal Ethics Committee approval (A35/2005) and research permits issued by the Department of Sustainability and Environment Victoria (10003389) and the Department of Environment and Heritage South Australia (G24995, 29/2005-M1).

Chapter 2 was published in Biological Conservation. Rohan Clarke and Michael Clarke carried out the initial work on ecological niche factor analysis of the Mallee Emu-wren, whilst I was the principal author of the distance analysis and interpretation of the entire chapter. I designed the approach to collection of genetic material and conducted the majority of the laboratory work and analyses. Additional marker loci and analyses were conducted by Katherine Harrisson under my direction. Co-contribution on the interpretation of analyses was provided by Paul Sunnucks and Katherine Harrisson (Chapter 5).

All field assistants collected data under my supervision. These volunteers contributed labour in the field and played no part in the analysis or interpretation of results. Volunteers generally assisted in the capture of birds. Some individuals assisted in the collection of data for habitat use (Chapter 3) and vegetation data (Chapters 2 & 3), acting as a scribe. Sally Cowan identified all insect material (Chapter 3). All field assistants are mentioned in the acknowledgements section.
Acknowledgements

I thank my supervisors, Prof. Andrew Bennett and Dr. Rohan Clarke, for their valuable advice, support and enthusiasm provided throughout this study. Their input significantly contributed to the quality of this research and thesis. In particular I thank Andrew for his mentorship, overall guidance, constructive crit of drafts, and patiently assisting me with statistical analyses. I have learned much. I thank Rohan for joining this project and sharing his knowledge on the ecology of mallee birds (or any bird!!) with unbounded enthusiasm - the research output is much the richer.

My office companions and friends have been a great support and encouragement to me. I wish to thank Tanya Pyk, Mike Sale and Meagan Underwood for assistance in the field, and their companionship when we all felt a little forgotten in the various office moves. Also thank-you to Dr. Janet Gwyther, for ensuring that we were not left without resources and assistance during these moves. I thank Natasha Schedvin for drawing on her recent Ph.D. experience on how to keeping my data files in a sensible order and for help with the use of ArcView. Thanks also to Martin Schulz for advice and lend of filament mist nets. Thank-you to my sister Rachael for assistance with figures.

I thank staff within the School of Life and Environmental Sciences for providing support with ethics, permits, accounts and grant applications. My particular thanks to the Landscape Ecology Group: Angie Haslem, Greg Holland, Jim Radford and Alistair Stewart. I especially thank members of the Mallee Fire and Biodiversity Team from Deakin and La Trobe Universities for their help and providing a stimulating research environment; Luke Kelly, Dale Nimmo, Simon Watson, Rick Taylor and Kate Callister. Simon, Rick and Alistair provided valuable assistance in bird surveys for Chapter 2. I am humbly thankful to Alistair for his patient assistance with GIS and to Simon and Dale for assistance with modelling and the use of the R package. I thank Assoc. Prof. Mike Clarke for his initial encouragement and ongoing advice on mallee birds. Thank-you to Prof. Bill Buttemer for his guidance and discussion on micro-habitat selection.

Colleagues in South Australia kindly assisted in organising permits and the collection of genetic material from Ngarkat Conservation Park. They include Peter Cale, Jody Gates, Leanne Mladovan, and Claire Treilibs.
I thank the Deakin University CCMB laboratory for the generous use of their facilities for the molecular work. Thanks to David Freestone for pointing me in the correct direction for laboratory equipment. Thank-you to Assoc. Prof. Paul Sunnucks, Dr. Sasha Pavlova and Dr. Birgita Hansen from Monash University for assistance and advice on population genetic analyses and for bringing me up-to-date on the finer points of this fast-paced area. I thank Katherine Harrisson for efficiently providing additional hypervariable nuclear loci, re-analysing the larger data-set and her contribution to the genetics chapter.

Thank-you to the staff at Hattah Kulkyn, the Murray Sunset and Wyperfeld National Parks assisted in logistic support and ensuring that I was safely at camp each night – particularly Phil Murdoch. Thank-you to Robert McNamara for introducing me to the Mallee Emu-wrens at Pink Lakes National Park.

The following volunteers, colleagues and friends assisted in various ways in the field or provided advice: Malcolm Brown (patiently taught and assisted me with obtaining my mist netting licence), Rebecca Boulton, Phil Cassey, Peter Colins, Sally Cowan, Leonnie Daws, Shirley Diez, Birgita Hansen, Alex Hawtine, Ash Herrod, Kim Kitchen, Richard Loyn, Ken Mableson, Mark MacKinnon, Mel Mitchell, Hilary Thompson, Michael Wood, Chris Sanderson, Rosalind and Steve Sheers and Eleanor Russell.

This work would not have been possible without funding. I wish to thank several organisations and benefactors for their generous financial and logistic support of the research including; the Holsworth Wildlife Research Endowment, Winifred Violet Scott Foundation, Birds Australia – Victoria Group, Parks Victoria, Mallee Catchment Management Authority and the Department of Sustainability and Environment. This scope of this project would not have been achieved without the generous support from Winifred Violet Scott Foundation and Holsworth Wildlife Research Endowment. Financial support was also provided by Deakin University.

Last, my loving and extra-special thanks to my four-legged furry companion Sabre, who always missed me on my absences, and made the long stints at the computer tolerable with his regular taps on my shoulder for a scratch, snuggle or feed. You were sorely missed during the final write-up.
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Abstract

This study is a multi-disciplinary investigation of the conservation ecology of the Mallee Emu-wren *Stipiturus mallee*, a species of global conservation concern. The Mallee Emu-wren is one of the smallest members of a distinctive element of the Australasian bird fauna, the family Maluridae. The Mallee Emu-wren is a restricted-range endemic that occurs in semi-arid mallee vegetation in south-eastern Australia. Little is known of the distribution, life-history or ecology of this tiny inconspicuous species.

The Mallee Emu-wren has declined precipitously in recent decades, attributed to widespread wildfires combined with drought and habitat fragmentation. The remaining populations are relatively secure from clearing of habitat for agricultural purposes, as they occur within large conservation reserve systems of north-western Victoria and adjacent reserves in South Australia. However, wildfire and altered fire regimes are identified as the major threat to the species. A series of landscape-scale wildfires in 1998, 2003 and 2005, compounded by prolonged drought, have extirpated most of the western and south-western populations in Billiatt, Ngarkat and Big Desert conservation reserves, leaving the Murray-Sunset reserve system in north-western Victoria as possibly the remaining stronghold of the species.

The precipitous decline of the Mallee Emu-wren and its limited (global) geographic distribution mean that there is an urgent priority for study into aspects of the species' distribution, habitat requirements and population structure. These data are fundamental to effective conservation management.

In this study, I investigated the global population size and distribution of the Mallee Emu-wren using field surveys and habitat modelling techniques. Organisms respond to different environmental variables at different scales, and therefore a multi-scale investigation of the species' habitat requirements was undertaken. In north-west Victoria, habitat use and selection by the Mallee Emu-wren were measured at the landscape-scale, local scale and at the scale of resource selection by individual birds. Because Mallee Emu-wrens occur in a fire-prone dynamic ecosystem, temporal scales were implicitly included.
Genetic analysis enables the elucidation of micro-evolutionary processes that mould the contemporary population structure of species. Fire is a major cause of disturbance that results in spatially and temporally dynamic landscapes and may have genetic consequences. Thus, the second disciplinary approach undertaken in this study was to investigate the population genetic diversity and structure of the Mallee Emu-wren across its global range.

At the landscape scale, I used ecological niche factor analysis, habitat suitability modelling and distance sampling to determine the habitat requirements and the population distribution and density across vegetation types and fire-age classes. Extrapolation of these data was used to estimate the global population size. Populations were detected in only five of seven reserves which they had occupied in 2000. The global population size was estimated to be about 17,000 individuals (range 8,607 to 39,280), with the Murray-Sunset and Hattah-Kulkyne reserve complex containing the majority (~92%) of the global population. The Mallee Emu-wren is a habitat specialist, primarily occurring in vegetation that has not been burnt for at least 15 years. The highest densities were in vegetation associations containing at least 15% cover of the hummock grass Triodia scariosa; however, time since the habitat was last burnt was the overriding factor in determining density. Specifically, Woorinen Sands Mallee and Loamy Sands Mallee were found to be key Ecological Vegetation Classes for the Mallee Emu-wren, and the 16-29 year fire age-class contained the greatest density.

Modelling of environmental variables that influence the local distribution of the Mallee Emu-wren and the closely allied Striated Grasswren Amytornis striatus found that both species were strongly associated with T. scariosa, although different aspects of T. scariosa structure explained the presence of each species. The growth-phase and total volume of T. scariosa best explained habitat use by the Mallee Emu-wren, whilst the percent cover of T. scariosa best explained the presence of the Striated Grasswren. The differences in model responses may reflect subtle niche differences between the species. The structural attributes of T. scariosa that the Mallee Emu-wren prefers are strongly dependent on time-since-fire, directly linking this key resource requirement of the Mallee Emu-wren to the temporal element of scale – the fire regime of mallee ecosystems.
Examination of the biophysical variables and behavioural decisions that explain micro-habitat selection by the Mallee Emu-wren found that individuals select mature growth-phase hummocks of *T. scariosa* that have relatively high volume as a favoured site for a range of behavioural activities. Specifically, they select healthy mature growth-phases.

Genetic analyses of partial sequences from the ND2 gene of mitochondrial DNA and of twelve hypervariable nuclear loci were used to examine the population structure and processes within this species. Populations of the Mallee Emu-wren exhibited a low to moderate level of genetic diversity, and evidence of genetic drift and bottlenecks. Fine-scale autocorrelation analyses found non-random genetic structure at less than 2 km, most likely reflecting local kin associations. Bayesian clustering methods revealed weak genetic population structure across the species’ global range. These findings are inferred to be a consequence of both low to moderate genetic variability inherited from an evolutionary ancestor and contemporary population processes. Spatial and temporal patterns of fire in mallee ecosystems result in population bottlenecks, serial local extinctions and subsequent recolonisation, all of which interact to erode genetic diversity in this species. Movement among temporally and spatially shifting habitat, mediated by fire, appears to maintain long-term genetic connectivity. A plausible explanation for the observed genetic patterns is that recolonisation by founders, not *in-situ* survival, is the prominent driver of population recovery and metapopulation processes for this species. These findings suggest that for species that occupy highly dynamic landscapes, the spatial characteristics of refugia and habitat mosaic may have profound demographic and genetic consequences for species.

This study has made a significant contribution to understanding the distribution, habitat requirements, and population size structure of the Mallee Emu-wren. I have identified two pervasive processes that threaten this species; i) population and habitat loss due to landscape-scale fires and inappropriate fire regimes, and ii) adverse genetic and demographic consequences within small and isolated populations or groups. These two threats are likely to be directly or indirectly exacerbated by global warming.
Evaluation of the global population status, and the risk to remaining populations from wildfire, warranted recent reclassification of the Mallee Emu-wren from Vulnerable to Endangered according to IUCN Red List categories and criteria.

The work presented in this thesis provides a basis to inform conservation actions specific to the Mallee Emu-wren: components of which are relevant to other sedentary and specialist bird species of the semi-arid mallee ecosystem and also to species occupying similar dynamic ecosystems.
CHAPTER 1

Introduction: towards an understanding of the ecology of the
Mallee Emu-wren

Figure 1.1 Mallee shrublands, Hattah-Kulkyne and Murray-Sunset National Parks,
Victoria.
1.1 Avian conservation

1.1.1 Avian declines

A conservation issue of global concern is the declining status of many bird species caused by habitat loss and modification from land-use practices and climate change (Andrén 1994, Wormworth and Mallon 2006, BirdLife International 2008). A synthesis in 2008 of the global status of bird species listed 1,226 species (one in eight) of the world’s avifauna as facing global extinction. Of these, 190 species are listed as Critically Endangered, 363 as Endangered, and 669 as Vulnerable (BirdLife International 2008). Characteristically, those listed tend to have a limited distribution, small population size, or occur in low density. More disconcerting, is that many formerly abundant and widespread species may be also rapidly declining (Ford et al. 2001, BirdLife International 2008).

In Australia, avian taxa qualifying as Threatened or Near Threatened, have increased from about 7% of the avifauna during early-post-European settlement, to 17.3% in 2000 (Garnett and Cowley 2000, BirdLife International 2008) and the rate of taxa qualifying to higher categories of threat status continues to increase (Brooke et al. 2008). More than 80% of Threatened bird species in Australia are identified as being affected by a combination of habitat loss, fragmentation and degradation (Garnett and Cowley 2000), with nearly half also affected by altered fire regimes (Woinarski and Recher 1997, Garnett and Cowley 2000).

Mallee vegetation of semi-arid southern Australia supports a high proportion of species of conservation concern (Garnett and Crowley 2000, Baker-Gabb 2004, Clarke 2005). This fire-prone ecosystem is characterised by eucalypt shrublands, 3-10 m tall, in which individual trees are multi-stemmed (i.e. the 'mallee' growth form) (Fig. 1.1). The most threatened bird species in the ecosystem are mallee endemics, or near endemics, that characteristically are highly site tenacious, have low fecundity and specialist habitat requirements (Garnett and Crowley 2000, Baker-Gabb 2004, Clarke 2005ab)(Box 1.1). Despite the high level of conservation concern for many of these species, relatively little is known of their spatial distribution, habitat preference, breeding biology and dispersal ability. One species of conservation concern is the Mallee Emu-wren (*Stipiturus mallee*), a species endemic to south-eastern Australia.
The ecology and conservation biology of the Mallee Emu-wren is the focus of this thesis.

### Box 1.1 Bird species of conservation concern in mallee ecosystems

Mallee ecosystems of southern Australia contain a disproportionate number of threatened avian taxa (Woinarski and Recher 1997, Garnett and Cowley 2000). Several endemic or near-endemic species have declining populations caused by the loss, degradation and fragmentation of habitat and by inappropriate fire regimes (LCC 1987, Benshemesh 1992, 2000, Clarke et al. 2005). Since 1998, a series of landscape-scale wildfires (>100 000 ha) in the Murray Mallee of south-eastern Australia has burnt significant portions of habitat, and has been directly associated with population losses of the Mallee Emu-wren, the Black-eared Miner (*Manorina melanotis*) and the likely local extinction of the eastern form of the Western Whipbird (*Psophodes nigrogularis leucogaster*). Studies on the Black-eared Miner and Mallee Fowl (*Leipoa ocellata*) have provided insights into aspects of their breeding ecology, habitat requirements, fire age-class preference and resource availability (Benshemesh 1992, 2000, Clarke et al. 2005). Nevertheless, although facing similar ecological threats, there is a paucity of data on other species of conservation concern.

<table>
<thead>
<tr>
<th>Avian species of conservation concern in the Murray Mallee region</th>
<th>State †</th>
<th>EPBC Act 1999#</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Endangered</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black-eared Miner <em>Manorina melanotis</em></td>
<td>E (SA Vic NSW)</td>
<td>E</td>
</tr>
<tr>
<td>Mallee Emu-wren <em>Stipiturus mallee</em></td>
<td>E (SA V(Vic))</td>
<td>V*</td>
</tr>
<tr>
<td><strong>Vulnerable</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mallee Fowl <em>Leipoa ocellata</em></td>
<td>E (NSW Vic V(SA))</td>
<td>V</td>
</tr>
<tr>
<td>Western Whipbird <em>Psophodes nigrogularis leucogaster</em></td>
<td>CE(Vic) E(SA) $</td>
<td>V</td>
</tr>
<tr>
<td>Red-lored Whistler <em>Pachycephala rufogularis</em></td>
<td>E(Vic NSW V(SA))</td>
<td>V</td>
</tr>
<tr>
<td><strong>Least Concern</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chestnut Quail-thrush <em>Cinclonoma castanotus castanotus</em></td>
<td>NT(Vic V(NSW) R(SA))</td>
<td>NT</td>
</tr>
<tr>
<td>Gilbert’s Whistler <em>Pachycephala inornata</em></td>
<td>V(NSW)</td>
<td>LC</td>
</tr>
<tr>
<td>Shy Heathwren <em>Hylocola cauta</em></td>
<td>V(NSW)</td>
<td>LC</td>
</tr>
<tr>
<td>Striated Grasswren <em>Amytornis striatus striatus</em></td>
<td>V(NSW) R(SA)</td>
<td>NT</td>
</tr>
<tr>
<td>Southern Scrub-robin <em>Drymodes brunneopygia</em></td>
<td>V(NSW)</td>
<td>LC</td>
</tr>
</tbody>
</table>

† State level: Vic = Victoria, SA = South Australia, NSW = New South Wales
# Federal level: *Environment Protection and Biodiversity Conservation Act 1999*
CE = critically endangered, E = endangered, R = rare, V = vulnerable, NT = near threatened, LC = least concern
$ Possibly extinct in eastern Australia
* Re-classified from Vulnerable to Endangered, IUCN Red List May 2008
1.1.2 Threatening processes and their ecological implications

Habitat loss, fragmentation and degradation

Changes in the abundance and distribution of species and local extinction of birds and other fauna in the Murray Mallee region, have been attributed to land degradation caused by the introduction of grazing stock and feral animals, exacerbated by the plague invasion in 1880 of the European rabbit (*Oryctolagus cuniculus*) (LCC 1987, Harris 1990, Menkhorst and Bennett 1990, Schodde 1990). Further compounding the detrimental effects of vegetation degradation on species' distribution in the Murray Mallee, is the extensive loss and fragmentation of habitat caused by the clearing of millions of hectares for agricultural settlement in the early 20th century (LCC 1987, Harris 1990).


Habitat loss and fragmentation are processes that result in the remaining patches of habitat becoming smaller in area, and increasingly isolated as the level of vegetation clearance increases (McIntyre and Hobbs 1999). Resources such as food, shelter and nesting sites are less abundant in smaller patches and therefore they support smaller populations (Berger 1990, Gardner 1998). Populations inhabiting small patches typically are susceptible to detrimental processes associated with 'edge effects' (Luck et al. 1999, Lindenmayer and Fischer 2006) and are more prone to extinction from demographic stochastic processes (Pimm et al. 1988, McCarthy et al. 1994), Allee effects (Stephens et al. 1999, Stephens and Sutherland 1999, Berec et al. 2007), environmental events (Fahrig and Merriam 1994, Harrison and Taylor 1997, Weins 1997, With and King 2001) and genetic stochasticity (Lacy 1987, 1993, Young and Clarke 2000). Habitat specialists, which are less able to adapt to or occupy other habitat types, are particularly vulnerable (Simberloff 1995, Wiens 1995, Clarke et al. 2005).
Climate change and fire regimes

Where ecosystems are already stressed from habitat degradation and modification and the effects of introduced species, climate change adds a further degree of complexity which is likely to exacerbate those stresses (Mac Nally et al. 2009, Steffen et al. 2009). Biodiversity has been identified as the global sector most vulnerable to the effects of climate change reflecting the very low adaptive capacity of ecosystems to respond rapidly to environmental change (IPCC 2007). The threats to biodiversity from climate change arise because of changes in the physical and chemical environment (e.g. water flux and pH) which underpin all ecosystem processes. Individual species will be affected by these changes in different ways, potentially leading to trophic cascades and potentially altered ecosystem processes (Steffen et al. 2009).

Since 1960 the mean temperature in Australia has increased by about 0.7°C. The year 2007 was the warmest on record in Victoria with a mean annual temperature 1.2°C above the long-term average (Australian Bureau of Meteorology 2010). It has been predicted that Victoria will warm at a slightly faster rate than the global average, especially in the north and east of the state (Department of Sustainability and Environment 2008). Annual rainfall totals are expected to decrease and evaporation to increase, exacerbating the overall drying trend (Department of Sustainability and Environment 2008, Steffen et al. 2009).

Climate warming is expected to alter the distribution of species in mallee ecosystems (Chambers et al. 2005, Crick 2006, Wormworth and Mallon 2006). Relatively minor temperature changes, coupled with reduced rainfall, are predicted to lead to severe contraction in the geographical ranges and the possible extinction of habitat specialists such as the Malleefowl and the Mallee Emu-wren (Brereton et al. 1995). Periods of reduced rainfall are linked to reduced bird numbers because dry spells reduce food resources such as insects and nectar (White 2008, Williams et al. 2008, Mac Nally et al. 2009). Furthermore, climate change is predicted to increase the intensity and frequency of fires (Hennessy et al. 2005, Department of Sustainability and Environment 2008).

Fire is an integral component of mallee ecosystems (Heisler et al. 1981, Bradstock 1990, Bradstock and Cohn 2002, Haslem et al. 2011) and is a major driver of plant structure and function (Bradstock 1989, Turner et al. 2008, Haslem et al. 2011) which
in turn influences the fauna of these ecosystems (Friend 1993, Kelly et al. 2010). Many published studies describe avian responses to fire in Australian ecosystems (reviewed by Woinarski and Recher 1997) and yet, among these few describe the underlying processes of species’ responses to fire (Whelan et al. 2002, but see Brooker 1998 for an example). The complexity of environmental variables (e.g. the nature of a given fire event, fire history, seed bank, post-fire rainfall, grazing pressure) make understanding the causes and effects of species responses to fire – particularly long-term responses – difficult to interpret and predict (Whelan et al. 2002).

The practice of prescribed burning is an issue of concern, with regard to species’ decline (Clarke 2008, Driscoll et al. 2010). Prescribed burning is a common feature of Australian landscape management (Burrows and Wardell-Johnson 2004, Bradstock et al. 2005) and is a tool currently used in mallee ecosystems to reduce the risk of wildfire burning extensive areas and homogenising the landscape (Sandell et al. 2006). The use of prescribed burning adds to the challenge faced by conservation managers to conserve species already threatened by multiple processes. Prescribed burning can be used for ecological management, by manipulating the age-structure of vegetation to provide for species that require a particular seral stage after fire. However, there is the potential for prescribed burning to affect biodiversity adversely because of an inadequate understanding of species’ responses to fire (Whelan 1975, Russell and Rowley 1998, Whelan 2002, Clarke 2008, Driscoll et al. 2010). There is a risk that inadvertent and irreversible changes may lead to the loss of local populations or even to species’ extinctions (Russell and Rowley 1998, Baker 2000).

It is important, therefore, that managers improve our understanding of the patterns and processes of how species respond to fire including the scale, frequency and the landscape context of fire (Gill and McCarthy 1998, Bradstock et al. 2005), and interactions between fire and other environmental factors and with species’ life history traits. This requires improved knowledge of the ecology and habitat requirements of organisms that inhabit fire-prone environments and of how they respond to the spatial and temporal dynamics of their environment.
1.2 Species-environment models

1.2.1 Habitat use and selection

The species-environment relationship is a central issue in ecology and is important in describing and explaining species’ distributions. Advances in geographic information systems (GIS) and remote sensing, coupled with a wide variety of statistical methods, have enabled researchers to develop predictive models of species’ distributions based on environmental variables, for a wide variety of species (Guisan and Zimmermann 2000, Rodríguez et al. 2007). The underlying premise of species-environment models is that predictable relationships exist between the occurrence of species and specific environmental elements (niche)(Heglund 2002), and that the distribution of a species has an adaptive significance (Rozenweig 1981, 1991). Studies of habitat use and habitat selection (see Box 1.2 for terminology) enable managers to identify what constitutes important habitat for a given species and to develop predictive models for species occurrence, ultimately aiding conservation planning.

Habitat selection is viewed as an hierarchical process with multiple processes operating at different spatial and temporal scales (Wiens 1989a, Orians and Wittenberger 1991, Luck 2002b, Suorsa et al. 2005). Habitat selection refers to a hierarchical process of behavioural responses that result in a disproportionate use of a particular component of the environment (Hutto 1985, Johnson 1980, Jones 2001). At one end of the hierarchical spectrum, organisms select habitat at the geographical regional scale (Suorsa et al. 2005) and are restricted by aspects of their physiology, ecology, morphology, behaviour and evolutionary origins (Wiens 1989b). At an intermediate landscape-scale, more proximal factors are at work and individuals select suitable patches of habitat within the landscape (Luck 2002b, Suorsa et al. 2005). At an even finer scale, specific resources, such as territories, and nesting and foraging sites, are selected by individuals (Luck 2002a and b, Rowley and Russell 2002).

1.2.1 Patterns, processes and scale

Given the hierarchical nature of habitat selection, patterns of use observed in habitat selection studies not only vary depending on the spatial scale at which they are viewed (Wiens 1989a), but different variables may emerge as determinants of local abundance and distribution, depending on the scale at which the study is undertaken (Levins 1969, Wiens 1989a, Finlayson et al. 2008). The use of broad environmental variables
from digital layers in a GIS may be suitable for identifying landscape-scale processes in habitat selection (Van Horne 2002), but this approach is more limiting for identifying process-orientated influences on habitat selection at the patch scale. Studies in habitat use and selection at fine-scales may enable the identification of more causal predictors or mechanisms for a given species’ distribution (Huston 2002).

**Box 1.2 Terminology and definitions in habitat studies**

Species-environment studies have a key role in conservation planning and management. It is important for researchers to be consistent in their use of terminology so as to eliminate ambiguities and inaccuracies in the interpretation of studies (Hall 1997).

**Habitat**: The physical space within which the animal lives and the abiotic and biotic entities in that space. Habitat is not synonymous with vegetation.

**Habitat use**: the way in which an individual or species uses a collection of physical or biological components to meet its life history needs. The pattern observed will depend on the scale at which data are recorded.

**Habitat selection**: is an hierarchical process involving a series of innate and learned behavioural decisions made by an animal about what habitat it will use at different scales in the environment (i.e. decision-making process). Habitat selection carries the connotation of understanding complex behavioural and environmental processes, that habitat use does not; habitat use patterns are a result of habitat selection processes.

**Habitat preference**: is the consequence of the habitat selection process, resulting in the disproportional (or relative) use of some locations over others.

**Habitat availability**: refers to the accessibility and procurability of physical and biological components of a habitat by animals (in contrast to abundance).

**Habitat quality**: relative ability of an area to provide conditions appropriate for individual and population persistence.

(Adapted from Hall et al. 1997, Jones 2001, Morrison and Hall 2002)
Frequently, as in the case of inconspicuous or rare species, little knowledge of habitat use or habitat selection exists for a species of interest and researchers often lack guidance as to the appropriate scale at which to undertake such studies. Undertaking studies at multiple-scales may overcome the possible shortcomings of a single-scale study. In this way researchers may not only describe broad patterns influencing a species’ distribution, but also identify elements that are biologically meaningful in the processes that determine those patterns observed (Orians and Wittenberger 1991, Brambilla et al. 2009).

1.3 Population and landscape genetics

Genetic patterns can also elucidate the underlying processes of how species respond to variation in the environment in space and time. Genetic patterns among individuals and populations and among related taxa, can provide insights into some fundamental processes including metapopulation dynamics, species’ population structure, and speciation (Storfer et al. 2007); and at fine-scales, movements of individuals, dispersal, gene flow and natural selection (Manel et al. 2003, 2007) (Box 1.3).

In traditional studies of population genetics, the study of genetic variation has largely focused on genetic structure relative to the actual distance between populations, major geographical features or historical factors (Britten et al. 1995, Paetkau et al. 1998, Taberlet et al. 1998). However environmental variables such as climate, vegetation types or riparian systems may in fact explain the variation in genetic patterns (Kozak et al. 2008). Landscape genetics (Manel et al. 2007, Kozak et al. 2008, Storfer et al. 2007) now makes it feasible to investigate environmental correlations with evolutionary processes by coupling innovations in GIS with the availability of hypervariable genetic markers (Manel et al. 2003, Holderegger and Wagner 2006, Storfer et al. 2007, Kozack et al. 2008) and multivariate statistical analysis, model comparison and validation (Storfer et al. 2007). Because landscape genetics has the scope to integrate environmental variables in both space and time with population genetics, it more closely resembles natural population dynamics (Holderegger and Wagner 2006).
Box 1.3 Levels of genetic analysis in time and space

All individuals, except identical twins and clones, differ in the DNA sequence of their genomes. Embedded in the DNA sequence of a genotype are signals to the natural events that have moulded its evolutionary history. The genetic patterns reflected in individuals and populations are a consequence of evolutionary processes at multiple scales influenced by the interaction of environmental variation over space and time, together with the intrinsic characteristics of the individual or species (Kozak et al. 2008).

Three levels of analysis provide information at different levels in time and space;

Genotypic analysis: provides information at the finest spatial and shortest temporal scale (contemporary; several to many generations) and is based on the DNA genotypes of individual organisms. This type of analysis is used for elucidating relationships among individuals and close neighbours (kinship), dispersal over small landscape distances, estimation of Ne for populations. Genotypic analysis uses highly variable loci such as microsatellites, Amplified Fragment Length Polymorphisms (AFLPs), Single Nuclear Polymorphisms (SNPs) and highly variable mitochondrial DNA (mtDNA) genes.

Genic analysis: provides information at medium spatial scales, and recent past temporal scale (e.g. several to many generations). The same data sets described above can be analysed for allele or genic frequencies. Gene frequencies in populations change more slowly than individual genotypes and record biological events over many generations. Genic frequency-based analysis is often used to investigate medium-term population structuring and gene flow.

Genealogical analysis: provides information at large spatial scales and distant past temporal scales. Slowly evolving genes are analysed for changes in their DNA sequence as a result of spontaneous mutations. New variants arise at a relatively slow pace, and usually reflect patterns and processes at large spatial scales and deep back in time. Genealogical analysis is used for studying biodiversity, systematics and evolutionary relationships among biota. DNA sequences of slowly evolving genes, usually single locus co-dominant genes (e.g. Cytochrome Oxidase), are typically used.

(Adapted from Sunnucks 2000, Garrick and Sunnucks 2006)
1.4 Thesis overview and aims

This study is a multi-disciplinary investigation of the conservation ecology of the Mallee Emu-wren; an avian species of conservation concern. In this study I investigate the global population size and distribution of the Mallee Emu-wren, the global population diversity and structure by using genetic analysis, and multi-scale habitat requirements and habitat selection by the species in north-west Victoria, Australia.

1.4.1 Family Maluridae

The Mallee Emu-wren is one of the smallest members of a distinctive element of the Australasian bird fauna, the family Maluridae. Five genera currently are recognised within the family, with members occurring in Australia and New Guinea. The enigmatic Emu-wrens (Stipiturus) and Grasswrens (Amytornis) are endemic to Australia, Tree-wrens (Sipodotus) and Russet-wrens (Clytomyias) to New Guinea, whilst the Fairy-wrens (Malurus) occur across both regions. All members of the family are small (about 5 – 40 g), feed and breed in the lower strata of vegetation, are poor fliers, and are easily recognised by their characteristic cocked tail (Schodde 1982b, Rowley and Russell 1997, Higgins et al. 2001).

Emu-wrens and Fairy-wrens are closely allied groups within the family Maluridae (Christidis and Boles 1994, Rowley and Russell 1997) and share many life history and behavioural traits (Rowley and Russell 1997, Maguire and Mulder 2004, Maguire 2006a and b, Maguire and Mulder 2008). There have been exemplary long-term studies on several species of Fairy-wren (Russell and Rowley 1993a and b, Brooker and Brooker 1994, 2001) and the ecology, social systems, demography and dispersal patterns of these taxa are well understood (Rowley and Russell 1997, Double et al. 2005). Notably, Fairy-wrens exhibit two distinctive behavioural traits; cooperative breeding (Russell and Rowley 1993a and b, Mulder 1995, Dunn et al. 1995, Webster et al. 2004) and extraordinarily high rates of extra-pair fertilisation (Mulder et al. 1994, Rowley and Russell 1997).

The genus Stipiturus comprises three members; the Southern Emu-wren (Stipiturus malachurus), the Rufous-crowned Emu-wren (Stipiturus ruficeps) and the Mallee Emu-wren. Several sub-species of the Southern Emu-wren are distributed across the south and south-east of mainland Australia and Tasmania. The Rufous-crowned Emu-wren
occurs in the semi-arid zone of north-central Australia (Rowley and Russell 1997, Higgins et al. 2001). Only the Southern Emu-wren has been studied in detail and it has also been subject of major conservation efforts (Wilson and Paton 2004). The ecological and life-history traits of the Southern Emu-wren are in many respects similar to those of the Fairy-wrens although, in contrast to Fairy-wrens, cooperative breeding is uncommon and facultative and extra-pair paternity are comparatively low (Maguire and Mulder 2004, Maguire 2006a and b, 2008).

1.4.2 Mallee Emu-wren (Stipiturus mallee) Campbell 1908

The Mallee Emu-wren is one of the smallest (about 4-6 g body weight) members of the Maluridae. Little is known of the life history or ecology of this inconspicuous species. Anecdotal observations indicate it probably has similar breeding and life cycle characteristics to the Southern Emu-wren (Schodde 1982b, Rowley and Russell 1997). The occurrence of breeding pairs in September indicate the Mallee Emu-wren is likely to be monogamous (McGilp and Parsons 1937), and they are known to produce a clutch size of three (rarely two) (Schodde 1982b). There are suggestions that territories may break down after the breeding season and that groups congregate and forage together through autumn and winter (Higgins et al. 2001). There have been no studies of marked birds, although researchers consider them to be resident (Rowley and Russell 1997) or probably sedentary (Schodde 1982b). They are a habitat specialist, living in dense understorey containing the hummock grass Triodia scariosa (hereafter refered to as Triodia) (Schodde 1982b, Rowley and Russell 1997, Higgins et al. 2001).

Early 20th Century records show that the Mallee Emu-wren once occupied a region extending from the Annuello Fauna and Flora Reserve in the north-west of Victoria to eastern South Australia where its distribution was bounded by Billiatt Conservation Park, Nadda, Peebinga and Pinnaroo and Comet Bore (Ngarkat Conservation Park) (Howe and Burgess 1942, McGilp 1943, Eckert 1977, Hatch 1977, Carpenter and Mathews 1986, Garnett 1992). Its northern range limit was the northern Sunset Country (Murray-Sunset National Park) and in the south it extended to the south of the Big Desert at Yanac (Howe 1933, Howe and Burgess 1942, Chisholm 1946) (Fig. 1.2).
Populations of the Mallee Emu-wren have perished from those areas under agricultural cultivation and the status of the species in the smaller conservation reserves is unclear. The remaining populations are relatively secure from clearing for agricultural purposes, inhabiting the large reserve systems of north-western Victoria and South Australia (Fig. 1.2). However, wildfire and altered fire regimes are identified as the major threat to the species (Garnett and Crowley 2000, Baker-Gabb 2004). A series of landscape-scale wildfires in 1998, 2003 and 2005, compounded by prolonged drought, have extirpated the west and most of the south-western populations in the large reserves (i.e. Billiatt, Ngarkat and Big Desert conservation areas), leaving the Murray-Sunset reserve system in north-west Victoria as possibly the remaining stronghold of the species.

Figure 1.2 The global distribution of the Mallee Emu-wren. The approximate historic distribution is represented by light grey stippling. Solid grey represents the reserve system in Victoria and South Australia. Vic = Victoria, S.A. = South Australia, N.S.W. = New South Wales, FFR = Fauna and Flora Reserve.
1.4.3 Study site and vegetation

This study was undertaken in the reserve system of north-west Victoria, with samples also collected for genetic analysis from Ngarkat Conservation Park, South Australia (Fig. 1.2). The region is semi-arid, with hot dry summers and mild winters, and most precipitation occurring during the months of April-October (Bureau of Meteorology, 2010). The distribution of the Mallee Emu-wren traverses two major landforms comprised of sandy dunefields; the Woorinen Formation in the northern range of distribution and the Lowan Sands in the south (Wasson 1989). Each landform contains floristically and structurally variable vegetation communities, reflecting the complex origins of the soils and overlaying sands, the topology of the dunefield systems, and the disturbance history - notably fire regimes (Cheal and Parkes 1989, Hill 1989, Wasson 1989, Menkhorst and Bennett 1990).

Within the Woorinen Formation the vegetation community pertinent to the Mallee Emu-wren is open *Eucalyptus* mallee (3-10m tall, multi-stemmed *Eucalyptus* spp.) with an understorey comprised of a mix of sclerophyllous shrubs and *Triodia* (Fig. 1.3a). *Triodia* is an important habitat component for fauna in mallee ecosystems (Bennett et al. 1989) and in some locations continuous swathes of *Triodia* dominate the understorey (Fig. 1.3b). *Triodia* is a sclerophyllous grass which forms large hummocks up to several metres in diameter. These hummocks grow outward as they mature, leaving dead or dying material in the centre, creating a characteristic concentric ring (Specht 1981b) (Fig. 1.4a).

Lewan Sands is the dominant landform in the southern part of the species' range. The vegetation communities in the Lowan Sands are mallee-heath and heath-like communities. They have a structurally dense, sclerophyllous shrub-layer with or without scattered *Triodia* and typically lack a mallee eucalypt overstorey (Cheal and Parks 1989, Menkhorst and Bennett 1990, Ross 1993, Mercer 1998) (Fig. 1.4b).
Figure 1.3 a & b  Vegetation of the Woorinen Formation, Mallee-\textit{Triodia} vegetation type; a) showing a mix of sclerophyllous understorey and \textit{Triodia}, and b) continuous swathes of \textit{Triodia}.

Figure 1.4 a & b  a) Concentric ring form of a mature \textit{Triodia} plant, and b) Mallee-heath, Ngarkat Conservation Park, South Australia. Note the absence of mallee eucalypt overstorey.

1.4.4 Study objectives

The precipitous decline of the Mallee Emu-wren and its limited (global) geographic distribution mean that there is an urgent priority for study into aspects of the species' distribution, habitat requirements and population structure. These data are fundamental to effective conservation management. This study focuses on the multi-
scale habitat requirements of the Mallee Emu-wren in north-west Victoria. I also investigate the genetic diversity and population structure of the Mallee Emu-wren using genetic analysis.

The specific objectives of my research are to:

- determine the global abundance and distribution of the Mallee Emu-wren and assess the global conservation status based on IUCN Red Book criteria;
- identify fine-scale habitat elements at the patch level that are important to the distribution and ecology of this species;
- investigate habitat selection by the Mallee Emu-wren in relation to the biotic and abiotic attributes of Triodia scariosa;
- examine the genetic diversity and population structure of the Mallee Emu-wren across its global range; and
- evaluate and synthesise key elements of the ecology and habitat requirements of the Mallee Emu-wren to enhance its conservation management.

1.4.5 Chapter outlines

These objectives are addressed in four data chapters that present the results of detailed field investigations and analyses of genetic markers from samples across the species’ range. Additional material is presented in the Appendixes. The first data chapter (Chapter 2) determines the global distribution and population status of the Mallee Emu-wren and assesses its conservation status based on IUCN Red List criteria (IUCN 2001). In this chapter, broad-scale habitat requirements are examined based on ecological niche factor analysis and distance-sampling techniques. GIS, distance-sampling and habitat modelling were integrated to determine the population size of the Mallee Emu-wren in the Victorian reserve system and to determine its habitat requirements at the landscape-scale. In May 2008, in part resulting from this work, the global conservation status of the Mallee Emu-wren was re-assessed to a higher category of threat, from Vulnerable to Endangered, in accordance with IUCN Red List criteria (Birdlife International 2008, Chapter 2 this thesis). A follow-up survey of the species to determine population trends was carried out in 2009, the results of which are presented in Appendix II.
The following two chapters (Chapters 3 & 4) investigate habitat use and habitat selection by the Mallee Emu-wren in Hattah-Kulkyne National Park, north-west Victoria. These chapters complement the broad-scale modelling described in Chapter 2 by elucidating the underlying processes that influence the distribution of the Mallee Emu-wren at fine-scales.

Chapter 5 relates to the second disciplinary approach undertaken in this thesis - to investigate the genetic diversity and global population structure of the Mallee Emu-wren. Samples were selected with the intention of undertaking a multi-scale analysis of genetic structure, including meta-population structure and fine-scale micro-evolutionary patterns and processes. In addition, samples were selected from two fire-age classes to investigate environmental influences on genetic diversity. The results provide insights into the role of fire as a process in influencing population structure of this presumably sedentary species.

All data chapters were written with a view to publishing as stand-alone bodies of work. This approach has lead to repetition in the Introduction and Methods sections. Chapter 2 has been published in Biological Conservation. The remaining chapters will be prepared for papers in the future.

The final chapter presents a synthesis of the results and discusses the implications for management of the Mallee Emu-wren. I conclude this synthesis with suggested approaches for fire management, for reintroductions and translocation programs and for further research.

Appendix III presents morphological measurements collected for each individual caught throughout the project. Appendix IV briefly discusses the phylogenetic relationship of Emu-wrens.

1.5 Limitations of the research

It is relevant to note several limitations experienced in researching the Mallee Emu-wren which resulted in major changes to the objectives of an initial project design. First, conventional mist netting techniques proved to be ineffective in trapping Mallee Emu-wrens. I spent many hours and several trials developing a net that would enable me to capture them by hand (see Appendix I).
Second, the colour bands available proved to be inappropriate for such a small bird. A colour marking study to investigate breeding chronology and population demography was abandoned after the first field season. Some data on territory size were obtained from a few individuals and are referred to throughout the thesis.

Third, field work on the Mallee Emu-wren was labour intensive due to their patchy distribution, their inconspicuous nature and low density. Many hours were taken to find groups of Mallee Emu-wrens (especially as a prolonged drought continued to affect numbers adversely) and then set-up nets or capture individuals by hand nets. It was estimated that an average of 12 person hours was taken to collect each genetic sample during this study.

All work was conducted under Deakin University Animal Ethics Committee approval (A35/2005), the Australian Bird and Bat Banding Scheme (authority number 2714), and research permits issued by the Department of Sustainability and Environment (10003389) and the Department of Environment and Heritage, South Australia (G24995, 29/2005-M1).
CHAPTER 2

Global population distribution, size and status of the Mallee Emu-wren


*The content of this chapter is identical to the published version and has been presented to be consistent in style with the remaining thesis.

Figure 2.1 Woorinen Sands Mallee, Murray-Sunset National Park, Victoria.
2.1 Abstract

The Mallee Emu-wren (*Stipiturus mallee*) is a Threatened, narrow-range passerine endemic to south-eastern Australia. To inform future conservation measures for this poorly known species, we used ecological niche factor analysis, habitat suitability modelling and distance sampling to determine landscape-scale habitat requirements and estimate the population size. Using GIS software, we integrated digital layers of ecogeographic variables with; 1) presence-only observations to derive and validate a habitat suitability model using ecological niche factor analysis, and 2) distance sampling to determine population distribution and densities across vegetation types. We detected populations in only five of seven reserves which they had occupied in 2000. We estimate the global population size to be about 17 000 individuals (range 8 607 to 39 280), 70% greater than the previously estimated 10 000 individuals, with a single large reserve containing the majority (~92%) of the global population. The Mallee Emu-wren is a habitat specialist, primarily occurring in mallee-*Triodia* vegetation that has not been burnt for at least 15 years. The highest densities were in vegetation associations containing at least a 15% cover of *Triodia*, however, time since the habitat was last burnt was the overriding factor in determining densities. Large-scale wildfires are a pervasive threat to the global status of the Mallee Emu-wren, and the risk to remaining populations is exacerbated by the adverse impact of prolonged drought and the potential for altered fire-regimes caused by global warming. Evaluation of the global population status, and the continued wildfire threat warranted recent reclassification of the Mallee Emu-wren from Vulnerable to Endangered according to IUCN Red List categories and criteria.
2.2 Introduction

An issue of global concern is declining bird species caused by landscape-scale habitat changes from human land-use practices (BirdLife International 2004). Land-use practices such as vegetation clearance result in habitat loss, fragmentation and degradation, altering species' population dynamics and distribution (Pulliam and Danielson 1991, Fahrig and Merriam 1994). Fragmented and isolated populations are more prone to extinction from intrinsic stochastic processes (e.g. demographic variability) and environmental events (e.g. wildfire, vegetation succession and climate change) (Harrison and Taylor 1997, With and King 2001). Habitat specialists, unable to adapt or occupy other habitat types, are particularly vulnerable (Simberloff 1995, Clarke et al. 2005).

In Australia, more than 80% threatened birds are affected by a combination of habitat loss, fragmentation and/or degradation, with nearly half affected by altered fire regimes (Woinarski and Recher 1997, Garnett and Crowley 2000). In particular, fire-prone mallee habitats (semi-arid eucalypt shrublands <10m tall, in which individual trees are multi-stemmed) support a suite of threatened or near-threatened bird species; many of which are habitat specialists (Schodde 1990, Garnett and Crowley 2000).

One species of particular conservation concern is the Mallee Emu-wren (*Stipiturus mallee*). The Mallee Emu-wren is a tiny (4-6 g) passerine that is endemic to the semi-arid mallee vegetation in the southern Murray Mallee region of south-eastern Australia (Fig. 2.2) (Schodde 1982b, Menkhorst and Bennett 1990, Higgins et al. 2001). They inhabit mallee vegetation typically dominated by an understorey of dense, prickly spinifex grass (*Triodia scariosa*, hereafter referred to as *Triodia*) or medium-sized, dense heaths and shrubs with scattered *Triodia* (Cheal and Parkes 1989, Menkhorst and Bennett 1990, Mercer 1998). Little is known of the life history or ecology of this inconspicuous species. It is thought to be sedentary, with low fecundity, although there has been no detailed study of individually marked birds. The Mallee Emu-wren has short rounded wings, and a long filamentous tail that make them poor flyers and they are adapted to scurrying through dense undergrowth (Schodde 1982b, Rowley and Russell 1997). It is suspected to have a high degree of habitat specialisation, and a locally patchy distribution (Schodde 1982b, Rowley and Russell
1997, Higgins et al. 2001). These attributes are likely to limit the ability of the species to disperse and re-colonise, making them particularly vulnerable to environmental change.

Historical records indicate that the Mallee Emu-wren once occurred across much of north-western Victoria and neighbouring areas in eastern South Australia, south of the Murray River (Fig. 2.2, for review see Higgins et al. 2001). Wide-scale vegetation clearance in the 1920s-60s (Harris 1990) has resulted in the extinction of Mallee Emu-wrens from agricultural areas and confined extant populations to two large regions and several isolated reserves (Silveira 1999). In 2000, in the absence of any substantive data, the global population was estimated to be no more than 10 000 individuals within seven reserves (Garnett and Crowley 2000).

In recent decades large wildfires (>10 000 ha), compounded by prolonged drought, have led to precipitous population declines. In 1989 a reserve-scale fire (60 000 ha) is thought to have brought about the extinction of Mallee Emu-wrens from Billiatt Conservation Park (CP) in South Australia (Gates 2003). A further series of fires in 1998, 2003 and 2005, razed 287 400 ha of vegetation in the contiguous Ngarkat, Big Desert and Wyperfeld reserves in the southern half of the species’ range (Fig. 2.2). A small population covering 20-60 territories persists in Ngarkat CP in South Australia (P Cale pers. comm.). However, the impact of these fires on Mallee Emu-wrens within the Victorian reserves (i.e. Big Desert and Wyperfeld) is unknown. Given the large-scale fires within the southern reserves and the apparent extinction of Mallee Emu-wrens in Billiatt CP, the Murray-Sunset and Hattah-Kulkyne reserves within Victoria are the only areas remaining likely to contain significant numbers (Fig. 2.2).

The global decline of the Mallee Emu-wren in recent decades and the paucity of data on the distribution and population size highlighted the need for an examination of the species’ distribution and population size within the Victorian reserve system. In this paper we present recent (1999-2006) records of Mallee Emu-wrens and quantitative data from the Victorian reserve system. We apply ecological niche factor analysis (ENFA) and habitat suitability modelling (Hirzel et al. 2002) to identify landscape-scale attributes influencing the distribution. Distance sampling data from the Murray-Sunset and Hattah-Kulkyne National Parks (NPs) are combined with digital data and satellite imaging to determine the densities of Mallee Emu-wrens in different
vegetation types and fire age-classes and arrive at total population estimates in the Victorian reserves. From these findings we evaluate the risk of threat from fire and the role of drought and climate change as threatening processes to the persistence of the Mallee Emu-wren. We review the threats to the Mallee Emu-wren and the current global conservation status in accordance with IUCN Red List Criteria (IUCN 2001).

![Map of the reserve system within the southern portion of the Murray Mallee region, south-east Australia. The Murray Mallee region encompasses the border area of New South Wales (N.S.W.), South Australia (S.A.) and Victoria (Vic.). Grey hatching shows the approximate historical occurrence of Mallee Emu-wrens, Solid Grey shows the major reserves, FFR = Fauna and Flora Reserve.](image)

**Figure 2.2** The reserve system within the southern portion of the Murray Mallee region, south-east Australia. The Murray Mallee region encompasses the border area of New South Wales (N.S.W.), South Australia (S.A.) and Victoria (Vic.). Grey hatching shows the approximate historical occurrence of Mallee Emu-wrens, Solid Grey shows the major reserves, FFR = Fauna and Flora Reserve.

### 2.3 Methods

#### 2.3.1 Study Site

Surveys were conducted within the Murray-Sunset and Hattah-Kulkyne National Parks, the northern portions of the Big Desert Wilderness Park that adjoins a known Mallee Emu-wren population in Ngarkat Conservation Park, Wyperfeld NP and two
smaller reserves: Bronzewing (12 415 ha) and Wathe (5 600 ha) Flora and Fauna Reserves (FFR) (Total area; 34°30'S–35°15'S; 141°00'N– 143°00'N)(Fig. 2.2). Annuello FFR was also considered for carrying capacity because reliable sightings were reported in 1998 (P Murdoch, pers. comm.), though an on-ground assessment in this reserve was not conducted. The region comprises of narrow, linear east-west dunefields with discrete vegetation communities within the dunes, slacks and swales. Vegetation is both structurally and floristically variable, reflecting the complex origins of soils and overlaying sands of the dunefields (Cheal and Parkes 1989, Hill 1989).

2.3.2 Digital data layers

Digital maps for the Murray Mallee reserves in Victoria were prepared using ArcView 8.1 or ArcMap 9.0 (ESRI). Digital data for vegetation types (Ecological Vegetation Classes (EVCs), see Table 2.1 for descriptions) and fire footprints (Department of Sustainability and Environment 2004) were layered and delineated. For Ecological Niche Factor Analysis (ENFA) and habitat suitability modelling (see below), EVCs and fire footprints were respectively derived from the EVC_BSC100 and LASTBURNT100 data layers (Department of Sustainability and Environment 2004). The LASTBURNT layer contains details of the last time an area was burnt by either a wildfire or prescription burn. Precision for the LASTBURNT layer was considered to be 10-100 m (Department of Sustainability and Environment 2004). For population estimates using distance analysis (Buckland et al. 1993) (see below), we used more refined fire footprints that became available partway through the project, prepared from satellite images available from 1972 onwards (Mallee Fire and Biodiversity Project, La Trobe and Deakin Universities).

2.3.3 Mallee Emu-wren records and transect survey

Records of Mallee Emu-wrens were obtained from the following sources; 1) standardised transect surveys for threatened mallee birds, 2) records collated from the Birds Australia Atlas Scheme (Barrett et al. 2003), 3) the Victorian Wildlife Atlas (Department of Sustainability and Environment, Victoria), 4) records provided by an environmental consulting company (BIOSIS Research Pty. Ltd., (Smales et al. 2005)), 5) the Mallee Fire and Biodiversity Project (Deakin and La Trobe Universities), and 6) incidental encounters during work in the region (see Table 2.2 for source of data and analysis treatment).
Table 2.1 Composition and benchmarks (%) for key Ecological Vegetation Classes (EVCs) of the Murray Mallee region included in this study.

<table>
<thead>
<tr>
<th>EVC</th>
<th>Broad Description</th>
<th>Key Understorey Composition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Woorinen Mallee</td>
<td>Mallee woodland to 12m tall</td>
<td>Sub-shrubs</td>
</tr>
<tr>
<td></td>
<td>Open chenopod understorey</td>
<td>Herbs</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Grasses</td>
</tr>
<tr>
<td>Woorinen Sands Mallee</td>
<td>Mallee shrubland to 7m tall</td>
<td>Hummock grass (Triodia spp.) 15%</td>
</tr>
<tr>
<td></td>
<td>Hummock dominated understorey</td>
<td>cover</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Medium shrub</td>
</tr>
<tr>
<td>Lowan Sands Mallee</td>
<td>Low woodland mallee to 7m tall</td>
<td>Healthy understorey</td>
</tr>
<tr>
<td>Loamy Sands Mallee</td>
<td>Low mallee shrubland to 5m tall</td>
<td>Hummock grass (Triodia spp.) 5%</td>
</tr>
<tr>
<td></td>
<td>Scattered shrubs above a hummock grass layer</td>
<td>cover</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Medium shrub</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Small shrub</td>
</tr>
<tr>
<td>Red Swale Mallee</td>
<td>Dense to whipstick mallee to 6m tall</td>
<td>Medium shrub</td>
</tr>
<tr>
<td></td>
<td>Sparse understorey</td>
<td>Small shrub</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Soil crust</td>
</tr>
<tr>
<td>Chenopod Mallee</td>
<td>Open to very open mallee woodland to 12m tall</td>
<td>Saltbush</td>
</tr>
<tr>
<td>Parilla Mallee</td>
<td>Open mallee to 10m</td>
<td>Semi-succulent understorey</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Highly variable floristic understorey</td>
</tr>
<tr>
<td></td>
<td></td>
<td>and/or well-developed woody shrub</td>
</tr>
<tr>
<td>Sandstone Ridge Mallee</td>
<td>Low open mallee (3m) with tall shrubby understorey or</td>
<td>Medium shrub 40% cover</td>
</tr>
<tr>
<td></td>
<td>shrubland with emergent mallee</td>
<td></td>
</tr>
</tbody>
</table>

Table 2.2 Data sources employed for analysis of; a) global distribution, b) ecological niche factor analysis (ENFA), habitat suitability modelling (HS) and validation, and c) population density using distance sampling. n = number of Mallee Emu-wren records.

<table>
<thead>
<tr>
<th>Source</th>
<th>Season(s) and year</th>
<th>Global distribution</th>
<th>ENFA and HS</th>
<th>ENFA and HS validation</th>
<th>Population density</th>
</tr>
</thead>
<tbody>
<tr>
<td>Transect (Clarke et al. 2005)</td>
<td>Spring and Autumn 2001-2003</td>
<td>√</td>
<td>n=41</td>
<td>n=28</td>
<td></td>
</tr>
<tr>
<td>Transect (This study)</td>
<td>Spring 2006</td>
<td>√</td>
<td></td>
<td>n=15</td>
<td></td>
</tr>
<tr>
<td>BA Atlas (Barrett et al. 2003)</td>
<td>1999-2003</td>
<td>√</td>
<td>n=16</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Victorian Wildlife Atlas (Department of Sustainability, Victoria)</td>
<td>1999-2003</td>
<td>√</td>
<td>n=15</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BIOSIS (Ian Smale, 2005)</td>
<td>2005</td>
<td>√</td>
<td></td>
<td>n=26</td>
<td></td>
</tr>
<tr>
<td>Unpublished PhD. study (S Brown)</td>
<td>2005-2006</td>
<td>√</td>
<td>n=34</td>
<td>n=5</td>
<td></td>
</tr>
<tr>
<td>Mallee Fire and Biodiversity Group</td>
<td>Spring 2006</td>
<td>√</td>
<td></td>
<td>n=12</td>
<td></td>
</tr>
<tr>
<td>S.A. Data (Peter Cale, pers. comm.)</td>
<td>2006</td>
<td>√</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
During Autumn and Spring in 2001-03, Mallee Emu-wren records were collected during transect surveys for the Black-eared Miner (*Manorina melanotis*) (Clarke et al. 2005). In September 2006, a portion of these transects was repeated and additional transects were conducted in previously unsurveyed areas. Areas targeted were those supporting *Triodia* vegetation associations (i.e. Woorinen Sands Mallee and Loamy Sands Mallee). However, given the nature of the mallee topography and vegetation, other vegetation types were also traversed (Table 2.1). Systematic transects of 500 m length were traversed on foot by experienced observers. Transects were continuous with the end of each transect equating to the start of the next. A total of 1105 km of transects was covered. As the landscape was dominated by east-west dune-swale systems, a representative sample of vegetation communities was obtained within each transect by aligning transects perpendicular (i.e. north-south) to the dune-swale systems where possible. Searches commenced at dawn and continued until about 1530 hrs unless conditions were deemed unsuitable (windy, wet or hot weather). At the start of each 500 m transect, a single 60 second sound recording of Mallee Emu-wren contact and alarm calls (©David Stewart/Nature Sound) was played through an MP3 player (iRiver T30MX) and amplified speaker system (Sony SRS A27 or JBL OnTour). Call playback was followed by either a 30 or 60 second listening period.

Detailed information was gathered for each group of Mallee Emu-wrens encountered. This included the number of individuals present, their sex, the vegetation type they occupied and notes on breeding activity. When birds were located whilst traversing transects, both the bird and observer’s co-ordinates were recorded on a Garmin GPS. The perpendicular distance from the fixed transect line was calculated (m) and used for subsequent distance analysis.

2.3.4  Ecological niche factor analysis, habitat suitability modelling and model validation

ENFA overcomes potential survey bias associated with a failure to detect rare or inconspicuous species by requiring presence-only data for modelling. As such, Mallee Emu-wren records are particularly suited to this multivariate statistical treatment. The principles and procedure of ENFA, based on the niche concept by Hutchinson (1957), have been described in detail elsewhere (Hirzel et al. 2002). Briefly, ENFA computes suitability functions by comparing the species’ distribution in the ecogeographical variable space with that of all grid squares in the study area. The expectation is that a species is non-randomly distributed with regard to ecogeographical variables and
should occur preferentially in grid squares lying within the species' optimum range on that variable. ENFA summarizes the overall information under the form of two types of factor. The first factor is 'marginality'; a measure of how the species mean differs from the global mean. It maximizes the multivariate distance of the ecogeographical variable between the cells occupied by the species and the cells within the whole reference area. A high marginality value indicates that the species' niche deviates from the average habitat condition in the study area. The second and subsequent factors, 'specialization(s)', account for the decreasing residual variance after removal of upper-ranked explanatory factors, and denote to what extent the species' ecogeographical variables distribution is narrow, with respect to the overall distribution of the ecogeographical variables in the whole reference area. A high specialisation value indicates that a species does not tolerate large variation in the habitat features compared with the overall range of conditions in the study area. Marginality and specialization are uncorrelated factors, with the major information contained within the first factors (Hirzel et al. 2002).

For ENFA and habitat suitability modelling, the software BioMapper 3.0 (Hirzel et al. 2004) was used. All key ecogeographical variables included in the analysis model are GIS layers depicting mallee vegetation types and fire footprints of known or estimated age. Five vegetation types and 11 grouped fire age-classes were employed for ENFA (16 input layers; Table 2.3). Unique GIS layers displaying the presence and absence of each variable were produced for each ecogeographical variable. In all instances, raster resolution was 141x141 m (2 ha). This was considered a suitable compromise between available resolution and accuracy of input data (including point data for Mallee Emu-wren presence), and areas over which Mallee Emu-wrens are likely to be sensitive to variation in vegetation community and time since last fire. Vegetation types were converted to frequency of occurrence maps with the calculation for each 2 ha grid cell based on the percentage frequency of occurrence of that ecogeographic variable within a radius of 35 grid cells (~5 km). Fire footprints displayed discrete distributions within the study area. Given this, and the fact that fire represents a disturbance in the landscape, distance maps were computed for these ecogeographic variables.
Table 2.3 Summary statistics for ecogeographical variables employed in Ecological Niche Factor Analysis for the Mallee Emu-wren in the Murray-Sunset reserve complex, Victoria. Values presented are mean ± SD.

<table>
<thead>
<tr>
<th>Ecogeographical variable</th>
<th>Study area</th>
<th>Mallee Emu-wren</th>
</tr>
</thead>
<tbody>
<tr>
<td>Last burnt 63-70 years ago¹</td>
<td>215.2 ± 148.4</td>
<td>147.7 ± 70.3</td>
</tr>
<tr>
<td>Last burnt 48-50 years ago¹</td>
<td>455.0 ± 215.1</td>
<td>305.0 ± 177.8</td>
</tr>
<tr>
<td>Last burnt 44 years ago²</td>
<td>218.9 ± 156.3</td>
<td>175.1 ± 158.2</td>
</tr>
<tr>
<td>Last burnt 37-41 years ago¹</td>
<td>153.2 ± 95.9</td>
<td>105.9 ± 61.2</td>
</tr>
<tr>
<td>Last burnt 32-36 years ago¹</td>
<td>193.7 ± 113.0</td>
<td>185.0 ± 86.3</td>
</tr>
<tr>
<td>Last burnt 27-31 years ago¹</td>
<td>73.4 ± 70.0</td>
<td>35.5 ± 26.2</td>
</tr>
<tr>
<td>Last burnt 24-26 years ago¹</td>
<td>79.7 ± 80.9</td>
<td>18.7 ± 26.2</td>
</tr>
<tr>
<td>Last burnt 21 years ago²</td>
<td>104.5 ± 127.0</td>
<td>127.6 ± 109.0</td>
</tr>
<tr>
<td>Last burnt 12-15 years ago¹</td>
<td>148.5 ± 85.9</td>
<td>171.3 ± 76.9</td>
</tr>
<tr>
<td>Last burnt 7-11 years ago¹</td>
<td>110.0 ± 73.4</td>
<td>78.6 ± 45.3</td>
</tr>
<tr>
<td>Last burnt 3-6 years ago¹</td>
<td>85.7 ± 89.6</td>
<td>29.2 ± 33.9</td>
</tr>
<tr>
<td>Sandstone Ridge Mallee²</td>
<td>1.9 ± 6.0</td>
<td>2.5 ± 4.2</td>
</tr>
<tr>
<td>Chenopod Mallee²</td>
<td>24.9 ± 21.3</td>
<td>17.0 ± 9.3</td>
</tr>
<tr>
<td>Lowan Sands Mallee²</td>
<td>28.6 ± 29.1</td>
<td>12.4 ± 18.6</td>
</tr>
<tr>
<td>Red Swale Mallee²</td>
<td>1.1 ± 4.2</td>
<td>2.8 ± 7.1</td>
</tr>
<tr>
<td>Woorinen Sands Mallee²</td>
<td>42.9 ± 21.9</td>
<td>65.0 ± 16.6</td>
</tr>
</tbody>
</table>

¹ Fire footprint variables show the mean number of 2 ha cells that separate and fire footprint of interest and a) every cell in the study area or b) cells containing Mallee Emu-wren records.

²Vegetation class variables show the mean number of 2 ha cells containing the vegetation class of interest within a 35 cell radius of a) every cell within the study area and b) cells containing Mallee Emu-wren records.

Based on the ENFA model, a habitat suitability map was generated by means of a median algorithm. Habitat suitability varies from 0 (least suitable habitat) to 100 (best habitat) and indicates how the environmental combination of a single cell suits the requirements of the focal species. Many studies that generate habitat suitability maps designate an arbitrary threshold above which habitat is considered suitable and below which all habitats are unsuitable (e.g. 70%) (e.g. Hirzel et al. 2004). Such an approach has little biological justification and here all habitat suitability classes are displayed. Given that the Mallee Emu-wren is thought to have a relatively small home range and
are unlikely to disperse widely given their poor flying ability, narrow classes of habitat suitability within each habitat suitability map were chosen for display; 10 classes whose boundaries were defined by quartiles show all areas of suitable habitat in habitat suitability maps.

The predictive power of habitat suitability models and map was assessed using a cross-validation process that computed a confidence interval about the predictive accuracy of the habitat suitability model. BioMapper 3.0 does this following the method described by Boyce et al. (2002). Each map is reclassified into $b$ bins. Each bin $i$ covers some proportion of the map’s total area ($A_i$) and contains some proportion of the validation points ($N_i$) (validation points are those observations left out during the cross-validation process). The area-adjusted frequency is computed for each bin as $F_i = A_i / N_i$. A completely random habitat suitability will have $F_i = 1$ for all bins, and high habitat suitability will be $>1$ with a monotonic increase in between. A Spearman-rank correlation between area-adjusted frequency of cross-validation points within individual bins and the bin rank was calculated for each cross-validation model. A Spearman-rank correlation $>0.65$ indicates the model displays a good predictive power, while values below are indicative of a weak model. Initially, all variables within a study area were included. However, in some instances where correlations existed between GIS variables, some variables were found to bias the results. This included Loamy Sands Mallee EVC and was excluded from the analysis. To test the validity of the conclusions of the habitat suitability modelling based on 1999-2003 data, we use additional samples collected between 2005 and 2006 (Table 2.2).

Mallee Emu-wren records provided by the Mallee Fire and Biodiversity Project were collected as part of three-State study targeting a range of mallee species in diverse vegetation and fire age-classes. Records obtained from a current study of the Mallee Emu-wren (S Brown), were unpublished results from a presence/absence design survey at the landscape-scale at Hattah-Kulkyne NP. Records from a consulting company (BIOSIS Pty. Ltd., Smales et al. 2005) were from a survey of threatened vertebrate species in Crown land adjacent to Hattah-Kulkyne NP. As the habitat suitability map generated using 1999-2003 data was not referred to during more recent surveys the validation data set was considered independent of the previously obtained presence records.
2.3.5 Estimate of densities using distance analysis

The program DISTANCE (Thomas et al. 2002) was used to estimate the group densities of Mallee Emu-wrens across the landscape. Mallee Emu-wrens forage in breeding pairs or family groups during the breeding season and individuals within a group generally forage in close proximity (<15 m) to one another (S Brown, pers. obs.), therefore no attempt was made to ascertain the centre of the group. The first sighted bird was used to determine the perpendicular distance for that group. Data points were assigned to one of eight 6.25 m intervals after manually creating several histograms from the raw data and, following Buckland et al. (1993), truncating outliers to exclude points beyond 50 m. Visual inspection of the histograms of sighting distances excluded uniform or negative exponential as suitable detection curve models. Four models (half-normal with cosine expansion, half-normal with simple polynomial expansion, half-hazard with cosine expansion, half-hazard with simple polynomial expansion) were considered for analysis. The model with the lowest Akaike’s Information Criterion (AIC) was automatically selected. Group densities of Mallee Emu-wrens (groups ha⁻¹) were determined by EVC and/or fire age-class stratum.

2.3.6 Estimation of population size within the Murray-Sunset, Hattah-Kulkyne and Annuello Reserves

The total number of groups of Mallee Emu-wrens for each reserve was determined by multiplying the average densities for each EVC and fire age-class by the corresponding area (km²) within each reserve. As the number of individuals within each group was not consistently collected during the surveys, population size was extrapolated from the average size of breeding groups (2.1 birds/group) obtained from surveys at the same time of year from an intensively studied population at Hattah-Kulkyne NP (S Brown, unpublished data). Emu-wrens are thought to reach sexual maturity before the breeding season (Maguire and Mulder 2004), and fledglings rarely occur in breeding groups this early in the breeding season (S Brown, pers. obs.). Therefore the breeding groups encountered during the census were likely to be exclusively adults.
2.3.7 Estimation of effective population size

The effective population size ($N_e$) is defined as the number of breeding individuals of a census population ($N$) in an ideal randomly breeding population of equal adult sex ratios, with equal chance of breeding, and offspring frequencies in a Poisson distribution. $N_e$ is an important parameter in influencing the genetic structure of small populations and is regarded as a measure of population viability (Frankel and Soulé 1981). For this reason it is used to specify risk categories in IUCN Red List Criteria (IUCN 2001). In a theoretically ideal population $N$ (the total number of sexually mature individuals) approximates $N_e$; however, natural populations typically deviate from the ideal population commonly causing $N_e < N$ (Crow and Kimura 1970, Nunney 1993). In evaluating the conservation status of threatened taxa such as the Mallee Emu-wren, it is important to estimate the relationship between the total number of adults in the population ($N$) and $N_e$. Unpublished data and anecdotal observations obtained from a colour-marked population at Hattah-Kulkyne NP show the adult population deviates from the ideal, with a slight bias towards males. When the adult sex ratio deviates from parity, $N_e$ can be estimated by the formulae $4 (1-p)N$ where $p$ is the proportion of males in a population of size $N$ (Crow and Kimura 1970). We use the adult sex ratio of survey data from the Hattah-Kulkyne NP population to estimate $N_e$ (1.3M:1F, n=15; S Brown, unpublished data).

2.4 Results

2.4.1 Regional distribution and declines

A total of 192 recent records (48 transect records and 144 incidental records; post 1999) delimit the current distribution of the Mallee Emu-wren within the reserve system in Victoria. Mallee Emu-wrens are locally patchy, but widely distributed across much of the Murray-Sunset reserve complex within an estimated area of occupancy of 989 km² (Fig. 2.3a, Table 2.4). Records for Hattah-Kulkyne NP found that Mallee Emu-wrens have a wider distribution within this reserve than previously known, with individuals recorded in both the northern and southern extremities of the reserve (Fig. 2.3a).
**Figures 2.3 a & b**  a) Mallee Emu-wren records for 1999-2006 in the Murray-Sunset reserve complex, Hattah-Kulkyne NP and Annuello FFR. The map shows the extent of the current fire age-classes for key EVCs (Woorinen Sands Mallee, Loamy Sands Mallee and Woorinen Mallee). b) Habitat suitability map based on 1999-2003 Mallee Emu-wren records. White dots represent recent records obtained in the period 2004-2006 and used in model validation. Here, the darkest-shaded (black) areas represent the inner core habitat that contains the top 10% of records with the smallest median value, while the white-shaded areas represent the outermost envelope containing the most distant 10% of records. This outermost quantile was treated as unsuitable habitat and discarded. The eight intervening classes each represent 10% of all records (palest grey for outer 80-90%, darkest grey for inner 10-20% of records).
Table 2.4 Total number of Mallee Emu-wren groups, number of individuals (N) and effective population size (Ne), for each EVC and fire age-class variable in each reserve. Included is the projected carrying capacity of Annuello FFR. N was determined from an average group size of 2.1 birds/group, and Ne from 4 (1- p)N where p is the proportion of males in the population.

<table>
<thead>
<tr>
<th>Data Type</th>
<th>Reserve</th>
<th>EVC</th>
<th>Area (km²)</th>
<th>Total No. of Mallee Emu-wrens Groups</th>
<th>Total No. of Individuals N</th>
<th>Effective Population Size Ne</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Total (16+)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>&gt;29</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>16-29</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Sub-Total</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Quantitative</td>
<td>Murray-Sunset</td>
<td>LSM</td>
<td>212</td>
<td>246 (64 - 933)</td>
<td>3303 (1948 - 5014)</td>
<td>3549 (2012 - 6548)</td>
</tr>
<tr>
<td></td>
<td>reserve complex(1)</td>
<td>WM</td>
<td>92</td>
<td>209 (24 - 1754)</td>
<td>807 (88 - 1078)</td>
<td>516 (112 - 2828)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>WSM</td>
<td>156</td>
<td>815 (240 - 2790)</td>
<td>2485 (1358 - 4573)</td>
<td>3300 (1598 - 7363)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sub-Total</td>
<td>460</td>
<td>1270 (328 - 5477)</td>
<td>6995 (3394 - 11260)</td>
<td>7365 (3722 - 16738)</td>
</tr>
<tr>
<td></td>
<td>Hattah - Kylkynie NP(1)</td>
<td>LSM</td>
<td>119</td>
<td>26 (6 - 98)</td>
<td>83 (49 - 142)</td>
<td>109 (55 - 240)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>WM</td>
<td>48</td>
<td>19 (2 - 164)</td>
<td>3 (0 - 11)</td>
<td>22 (2 - 175)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>WSM</td>
<td>107</td>
<td>95 (28 - 327)</td>
<td>21 (27 - 91)</td>
<td>116 (55 - 418)</td>
</tr>
<tr>
<td></td>
<td>Sub-Total</td>
<td>275</td>
<td></td>
<td>146 (36 - 589)</td>
<td>107 (76 - 244)</td>
<td>247 (112 - 833)</td>
</tr>
<tr>
<td></td>
<td>Annuello FFR (1,2)</td>
<td>LSM</td>
<td>121</td>
<td>26 (7 - 100)</td>
<td>82 (48 - 140)</td>
<td>108 (55 - 240)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>WM</td>
<td>33</td>
<td>12 (1 - 100)</td>
<td>4 (1 - 14)</td>
<td>16 (2 - 114)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>WSM</td>
<td>160</td>
<td>81 (24 - 279)</td>
<td>70 (38 - 129)</td>
<td>151 (62 - 408)</td>
</tr>
<tr>
<td></td>
<td>Sub-Total</td>
<td>254</td>
<td></td>
<td>119 (32 - 479)</td>
<td>156 (87 - 283)</td>
<td>275 (119 - 729)</td>
</tr>
<tr>
<td></td>
<td>TOTAL</td>
<td>989</td>
<td></td>
<td>1529 (391 - 6545)</td>
<td>6358 (3557 - 11787)</td>
<td>7887 (3953 - 18333)</td>
</tr>
<tr>
<td></td>
<td>Wyperfield/Big Desert</td>
<td></td>
<td></td>
<td>~1</td>
<td>~50</td>
<td>~45</td>
</tr>
<tr>
<td>Complex (1)</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Watie FFR (1)</td>
<td>N/A</td>
<td></td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Bronzewing FFR (1)</td>
<td>N/A</td>
<td></td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Ngarkat CP (3)</td>
<td>N/A</td>
<td></td>
<td>42-126 (4)</td>
<td>39-115</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Billab CP (5)</td>
<td></td>
<td></td>
<td>Extinct (5)</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>

(1) this study
(2) carrying capacity
(3) Peter Cole, pers. comm.
(4) based on 20-60 territories comprising 2.13 birds/territory
(5) the last confirmed sighting was of a single individual at the boundary of the park in 2003 (pers. ob. R Clarke)
(6) estimated area of occupancy

N/A = data not available
LSM = Loamy Sands Mallee
WM = Wooreen Sands Mallee
WSM = Woorinen Sands Mallee
PAC = fire age-class
EVC = Ecological Vegetation Class
Despite a large survey effort in Wyperfeld NP (210 km of transects), only one group of Mallee Emu-wrens was found within the species’ southern range - in Loamy Sands Mallee in the south-east section (Table 2.4). Given that only two additional records have been obtained for this region since 1999 (Barrett et al. 2003), it seems likely that the Mallee Emu-wren is now extremely rare within the southern complex. An extensive survey of nearby Wathe FFR (38.6 km of transects) failed to detect Mallee Emu-wrens. Likewise, no Mallee Emu-wrens have been observed in Bronzewing FFR despite frequent surveys by experienced ornithologists since 1997. Although the Mallee Emu-wren was purported to occur in these latter two reserves prior to the 1970s (Silveira 1999), we conclude from these systematic surveys that the Mallee Emu-wren is now extinct within these reserves.

2.4.2 ENFA regional-scale habitat requirements and preferred age since fire

Ecological niche factor analysis was based on 72 records obtained within the Murray-Sunset reserve complex for the period 1999 to 2003 (Table 2.2). This represented 64 grid cells in which Mallee Emu-wrens had been recorded in the region from a total of 328 258 available two-hectare grid cells. A habitat suitability map (Fig. 2.3b) was generated using ENFA based on 16 input layers (Table 2.3). The four factors that were retained in the model explained 87.9 % of the total variation observed in the model (Table 2.5). Model quality was good with a mean Spearman correlation coefficient of 0.70 after area-adjusted-frequency cross validation. Model results demonstrate that the Mallee Emu-wren selects specific habitats from those available within the Murray Sunset reserve complex. The species is positively correlated with Woorinen Sands, Mallee and Red Swale Mallee and negatively correlated with Lowan Sands Mallee and Chenopod Mallee on the marginality factor (Table 2.5).

Mallee Emu-wrens displayed a mixed response to fire age-classes, although three of the four highest ranked fire age-classes on the marginality factor were last burnt 24 or more years ago (Table 2.5). Whilst there are particularly close associations with habitats last burnt 24 to 26 and 27 to 31 years ago (Table 2.5), a conservative interpretation is that the species displays a mixed response to fire age-classes with preference for older unburnt habitats.
Table 2.5 Score values for the four retained factors (out of 16 generated) modelling the habitat preferences of Mallee Emu-wren in the Murray-Sunset, Hattah-Kulkyne and Annello reserves using Ecological Niche Factor Analysis. Marginality of the focal species is expressed in units of standard deviations of global distribution; i.e. 0 = species distribution approaches the global mean. The higher the absolute value for specialisation values (in brackets), the more restricted is the range of the focal species for that variable. Grid cells n=64, for the study period 1999-2003, r-values ≥0.25 are significant at p=0.05 (significant EVCs and fire age-classes are highlighted in bold text).

<table>
<thead>
<tr>
<th>Marginality factor</th>
<th>Specialisation factors</th>
<th>Factor 3 (15%)</th>
<th>Factor 4 (11%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Factor 1 (26%)</strong></td>
<td><strong>Factor 2 (35%)</strong></td>
<td>Lowan Sands Mallee (-0.66)</td>
<td>Lowan Sands Mallee (-0.61)</td>
</tr>
<tr>
<td>Woorinen Sands Mallee (0.49)</td>
<td>Last burnt 21 years ago (0.63)</td>
<td>Woorinen Sands Mallee (-0.51)</td>
<td>Woorinen Sands Mallee (-0.46)</td>
</tr>
<tr>
<td>Last burnt 24-26 years ago (0.37)</td>
<td>Last burnt 48-50 years ago (0.61)</td>
<td>Chenopod Mallee (-0.51)</td>
<td>Last burnt 44 years ago (0.37)</td>
</tr>
<tr>
<td>Last burnt 48-50 years ago (0.34)</td>
<td>Last burnt 63-70 years ago (-0.29)</td>
<td>Sandstone Ridge Mallee (-0.14)</td>
<td>Chenopod Mallee (-0.35)</td>
</tr>
<tr>
<td>Last burnt 3-6 years ago (0.31)</td>
<td>Last burnt 44 years ago (-0.27)</td>
<td>Red Swale Mallee (-0.10)</td>
<td>Last burnt 21 years ago (-0.21)</td>
</tr>
<tr>
<td>Lowan Sands Mallee (-0.27)</td>
<td>Last burnt 32-36 years ago (-0.15)</td>
<td>Last burnt 48-50 years ago (-0.08)</td>
<td>Last burnt 48-50 years ago (0.19)</td>
</tr>
<tr>
<td><strong>Last burnt 27-31 years ago (0.26)</strong></td>
<td>Chenopod Mallee (0.12)</td>
<td>Last burnt 44 years ago (-0.07)</td>
<td>Last burnt 12-15 years ago (0.18)</td>
</tr>
<tr>
<td>Last burnt 37-41 years ago (0.24)</td>
<td>Last burnt 3-6 years ago (-0.12)</td>
<td>Last burnt 63-70 years ago (0.06)</td>
<td>Last burnt 27-31 years ago (-0.13)</td>
</tr>
<tr>
<td>Last burnt 63-70 years ago (0.22)</td>
<td>Last burnt 27-31 years ago (0.07)</td>
<td>Last burnt 24-26 years ago (0.06)</td>
<td>Last burnt 24-26 years ago (-0.13)</td>
</tr>
<tr>
<td>Last burnt 7-11 years ago (0.21)</td>
<td>Lowan sands mallee (0.06)</td>
<td>Last burnt 12-15 years ago (-0.04)</td>
<td>Sandstone Ridge Mallee (-0.11)</td>
</tr>
<tr>
<td>Red Swale Mallee (0.20)</td>
<td>Last burnt 24-26 years ago (-0.05)</td>
<td>Last burnt 27-31 years ago (0.03)</td>
<td>Red Swale Mallee (-0.06)</td>
</tr>
<tr>
<td>Chenopod Mallee (-0.18)</td>
<td>Woorinen Sands Mallee (0.05)</td>
<td>Last burnt 3-6 years ago (-0.02)</td>
<td>Last burnt 7-11 years ago (-0.04)</td>
</tr>
<tr>
<td>Last burnt 44 years ago (0.14)</td>
<td>Last burnt 32-36 years ago (-0.04)</td>
<td>Last burnt 32-36 years ago (-0.01)</td>
<td>Last burnt 32-36 years ago (-0.04)</td>
</tr>
<tr>
<td>Last burnt 12-15 years ago (-0.13)</td>
<td>Sandstone Ridge Mallee (0.03)</td>
<td>Last burnt 7-11 years ago (0.01)</td>
<td>Last burnt 63-70 years ago (-0.03)</td>
</tr>
<tr>
<td>Last burnt 21 years ago (-0.09)</td>
<td>Last burnt 12-15 years ago (-0.03)</td>
<td>Last burnt 21 years ago (0.01)</td>
<td>Last burnt 37-41 years ago (0.02)</td>
</tr>
<tr>
<td>Sandstone Ridge Mallee (0.05)</td>
<td>Red Swale Mallee (0.01)</td>
<td>Last burnt 21 years ago (0.01)</td>
<td>Last burnt 3-6 years ago (-0.01)</td>
</tr>
<tr>
<td>Last burnt 32-36 years ago (0.04)</td>
<td>Last burnt 37-41 years ago (0.01)</td>
<td>Last burnt 37-41 years ago (-0.00)</td>
<td>Last burnt 3-6 years ago (-0.01)</td>
</tr>
</tbody>
</table>
To test the validity of the habitat suitability map based on 1999-2003 data, recently obtained records (2005-2006) were overlaid on the existing map (Fig. 2.3b). A total of 72 'presence records' were obtained during the 2005-2006 period. The distribution of records was significantly skewed towards higher habitat suitability classes with 45 of 72 (64%) Mallee Emu-wren records falling in the top 20% of habitat suitability envelopes and 60 of 72 (83%) of Mallee Emu-wren records falling within the top 50% of habitat suitability envelopes ($\chi^2 = 144.03 \ df = 9, p < 0.0005$) (Figs. 2.3b and 2.4).

![Figure 2.4](image)

**Figure 2.4** Observed distribution (black bars) of recent (2004-2007) Mallee Emu-wren records relative to habitat suitability classes. Expected distribution assumes Mallee Emu-wren records are evenly distributed across available habitat suitability classes and is shown as a broken trend line.

### 2.4.3 Group densities

Forty-seven groups of Mallee Emu-wrens (group size 1 to 5 individuals) detected during transect surveys in the Murray-Sunset and Hattah-Kulkyne NPs were used in distance analysis to determine group densities. No Mallee Emu-wrens were detected in Parilla Mallee, Sandstone Ridge Shrubland, or in mallee vegetation types that had been burned less than 16 years ago and these substrata were excluded from further analysis.
Three vegetation types (Woorinen Sands Mallee, Woorinen Mallee and Loamy Sands Mallee) and two fire age-classes (16-29 yr and >29 yr) were tested, individually and in combination, to explore their influence on the densities of Mallee Emu-wren (Table 2.6). Similar estimates for densities of groups were obtained regardless of the model form tested. We selected the model with the lowest AIC; half-normal with cosine (AIC = 163.91), goodness of fit: $\chi^2 = 2.56$, $df = 4$, $p = 0.63$ for pooled data.

**Table 2.6** Density of Mallee Emu-wren groups and individuals by stratum (EVC and/or fire age-class) calculated by DISTANCE analysis (Thomas et al., 2002). Three combinations of stratum tested (Test A, B, C) and pooled data using half-normal with cosine as the model. Upper and Lower 95% CI in brackets.

<table>
<thead>
<tr>
<th>Test</th>
<th>Substratum Tested (EVC/FAC)</th>
<th>Density of Groups ha$^{-1}$ (95% CI)</th>
<th>%CV</th>
<th>Density of Individuals ha$^{-1}$ (95% CI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>16-29</td>
<td>0.026 (0.017-0.04)</td>
<td>21.90</td>
<td>0.056 (0.037 - 0.085)</td>
</tr>
<tr>
<td></td>
<td>&gt;29</td>
<td>0.006 (0.002-0.016)</td>
<td>53.31</td>
<td>0.012 (0.005 - 0.035)</td>
</tr>
<tr>
<td>B</td>
<td>LSM</td>
<td>0.010 (0.006-0.018)</td>
<td>27.86</td>
<td>0.028 (0.013 - 0.038)</td>
</tr>
<tr>
<td></td>
<td>WSM</td>
<td>0.019 (0.01-0.034)</td>
<td>31.93</td>
<td>0.040 (0.022 - 0.073)</td>
</tr>
<tr>
<td></td>
<td>WS</td>
<td>0.005 (0.001-0.026)</td>
<td>100.39</td>
<td>0.011 (0.002 - 0.055)</td>
</tr>
<tr>
<td>C</td>
<td>LSM &gt;29</td>
<td>0.003 (0.001-0.011)</td>
<td>76.96</td>
<td>0.006 (0.002 - 0.024)</td>
</tr>
<tr>
<td></td>
<td>LSM 16-29</td>
<td>0.026 (0.015-0.044)</td>
<td>27.42</td>
<td>0.055 (0.032 - 0.093)</td>
</tr>
<tr>
<td></td>
<td>WSM &gt;29</td>
<td>0.011 (0.003-0.036)</td>
<td>69.22</td>
<td>0.022 (0.007 - 0.077)</td>
</tr>
<tr>
<td></td>
<td>WSM 16-29</td>
<td>0.032 (0.017-0.058)</td>
<td>31.62</td>
<td>0.067 (0.037 - 0.124)</td>
</tr>
<tr>
<td></td>
<td>WM &gt; 29</td>
<td>0.005 (0.001-0.038)</td>
<td>148.77</td>
<td>0.010 (0.001 - 0.080)</td>
</tr>
<tr>
<td></td>
<td>WM 16-29</td>
<td>0.007 (0.002-0.024)</td>
<td>70.12</td>
<td>0.015 (0.004 - 0.051)</td>
</tr>
<tr>
<td></td>
<td>Pooled</td>
<td>All stratum</td>
<td>0.013 (0.008-0.021)</td>
<td>23.62</td>
</tr>
</tbody>
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LSM = Loamy Sands Mallee  
WSM = Woorinen Sands Mallee  
WM = Woorinen Mallee  
FAC = Fire age-class  
EVC = Ecological Vegetation Class  
%CV = coefficient of variation

Pooled density was estimated to be 0.013 groups ha$^{-1}$. Exploration of density estimates for fire age-classes (Test A, Table 2.6) shows that the density of groups of Mallee Emu-wrens was considerably higher in the 16-29 fire age-class (0.026 groups ha$^{-1}$) compared
to the >29 fire age-class (0.006 groups ha\(^{-1}\)). Density estimates for EVCs show that Woorinen Mallee (0.005 groups ha\(^{-1}\)) is less favourable habitat than Lowan Sands Mallee (0.013 groups ha\(^{-1}\)) and Woorinen Sands Mallee (0.019 groups ha\(^{-1}\)). A final exploration splitting each of the three EVCs into two fire age-classes demonstrates that fire age-class is the overriding factor in determining densities. Each of the EVCs in the 16-29 fire age-class have higher densities of the Mallee Emu-wren than the >29 fire age-class, consistent with results from Test A which pooled the EVCs.

2.4.4 **Regional Population Size and Effective Population Size**

Using the area (km\(^{2}\)) calculated from digital maps, the number of groups of Mallee Emu-wrens and individuals was calculated for each EVC and fire age-class within six reserves (Table 2.4). The Murray-Sunset NP and adjacent State forests (i.e. Murray-Sunset reserve complex) contain the vast majority of the Mallee Emu-wren population in Victoria, with an estimated 15 709 individuals (range 7 939 – 35 702)(95%CI) or 92% of the global population. Hattah-Kulkyne NP supports a moderate population (526, range 238 - 1776) and the estimated carrying capacity for Annuello FFR is similar to Hattah-Kulkyne NP (586, range 253-1625). Given the skewed adult sex ratio, \(N_e\) is slightly lower than that for the total population (15 308 cf.16 822) (Table 2.4).

2.5 **Discussion**

2.5.1 **Distribution and declines**

Since the previous estimate made in 2000 (Garnett and Crowley 2000), the Mallee Emu-wren has contracted in distribution with only five of seven previously known reserve-scale populations surviving (including Annuello FFR). Habitat losses due to large-scale fires have directly caused the extinction of the Mallee Emu-wren from Billiat CP (Gates 2003) and the substantial decline of the Ngarkat CP population. Likewise, the rarity of Mallee Emu-wrens in the Big Desert/Wyperfeld reserve complex is likely to be attributed to recent fires. During 2002/03, about half the reserve was burnt (181 400 ha) (Department of Sustainability and Environment 2007) and large areas are now rendered unsuitable for the birds.

Of the five extant reserve-scale populations, the Murray-Sunset reserve complex contains the majority of the global population (~92%) and Hattah-Kulkyne NP also
has a significant population. Mallee Emu-wrens were observed within Annello FFR in 1998 and our projections of carrying capacity suggest a moderate sized population could persist here. Nevertheless, the lack of records during previous surveys (Robertson et al. 1989) suggests the population may be small, declining or have recently become extinct. The population status at Annello FFR requires clarification and surveys here could be used to further test the validity of the habitat suitability model.

The extinction of populations from Bronzewing and Wathe FFRs is consistent with the paradigm that small isolated populations are vulnerable to extinction through stochastic demographic (e.g. inbreeding depression) or environmental processes (Caughley 1994, Foley 1997, With and King 2001). Mallee Emu-wrens have locally patchy distributions within continuous vegetation (this study), suggestive of a metapopulation (Hanski and Simberloff 1997, Hanski 1998). Metapopulation theory predicts population extinction would be exacerbated in habitat specialists with patchy distributions (Simberloff 1995). At the landscape-scale, metapopulation dynamics are influenced by the complex interactions of the landscape mosaic and species’ dispersal ability (i.e. the permeability of the landscape matrix) (Wiens 1997, Cale 2003). The Mallee Emu-wren, with their characteristic poor flying ability would be predictably unable to disperse and recolonise at the reserve scale. We can therefore infer that the extinction of populations from these small isolated reserves was a result of adverse intrinsic population processes or environmental characteristics of the reserves (discussed further, below). Whether similar processes are occurring in Annello FFR remains speculative.

2.5.2 Habitat requirements, ENFA and habitat suitability maps

ENFA demonstrated a strong association between Mallee Emu-wren presence and Woorinen Sands Mallee (Tables 2.3 & 2.5, Factor 1). This is consistent with the Mallee Emu-wren being a known Triodia specialist in this region. Mallee Emu-wrens use mature Triodia for nesting, protection from aggressive birds and predators, and where it occurs in large swathes, use Triodia almost exclusively for foraging (S Brown unpublished data). The benchmark description of Woorinen Sands Mallee vegetation class includes a 15% cover of Triodia (Department of Sustainability and Environment 2004) (Table 2.1). In contrast, Lowan Sands Mallee is negatively associated with Mallee Emu-wrens (Table 2.5, Factor 1); Triodia is not listed as a benchmark criterion.
for this EVC and is largely absent. Note that although Mallee Emu-wrens occupy Loamy Sands Mallee (5% *Triodia* benchmark criterion) (see distance sampling findings) this EVC was excluded from ENFA and habitat suitability models as that ecogeographic variable was highly correlated with other variables that were included.

The positive association between Mallee Emu-wrens and areas last burnt 3-6 years ago was unexpected (Table 2.5). However this ecogeographic variable did not feature in any of the specialisation factors that were retained. Mallee Emu-wrens do not occupy a narrow niche within this fire age-class and the association, as suggested by the model, is unlikely to be of significance. A preference for older fire age-classes is consistent with *Triodia* maturing at around 15-30 years of age (Bradstock and Gill 1993) and is further substantiated by the distance sampling study that failed to detect any individuals in vegetation burnt less than 15 years ago.

2.5.3 Densities

The average densities of the Mallee Emu-wren are similar to those recorded for the Rufous-crowned Emu-wren (*Stipiturus ruficeps*) (0.008-0.021 cf. 0.011-0.012 birds ha\(^{-1}\)) at Lake Disappointment, Western Australia (Higgins et al. 2001), but considerably lower than those recorded for the Southern Emu-wren in southern Victoria (1.125-3.5 birds ha\(^{-1}\)) (Maguire 2004, Maguire 2006ab). Rufous-crowned Emu-wrens occur in spinifex grasslands of semi-arid inland Australia (Rowley and Russell 1997, Higgins et al. 2001); vegetation with similar structural attributes and rainfall of the south-eastern Australian mallee. In contrast, Southern Emu-wrens occupy dense coastal heathlands with higher annual rainfall and milder temperatures (Rowley and Russell 1997, Maguire 2004, Maguire 2006a and b). Maguire (2006b) has shown that higher insect biomass is correlated with higher quality territories and greater reproductive success in the Southern Emu-wren. The lower densities found for the Rufous-crowned Emu-wren and the Mallee Emu-wren are likely to be influenced by lower productivity within the semi-arid zones compared to the temperate coastal zones in which the Southern Emu-wren occurs.

Many small, insectivorous birds distinguish habitat on the basis of structural characteristics rather than floristics (Cody 1985, Wiens 1985). The variation in density of the Mallee Emu-wren among vegetation types and fire age-classes indicate that vegetation structure is a key influence in local distribution and abundance. The higher
densities associated with Woorinen Sands Mallee EVC (15% *Triodia*) compared to Loamy Sands Mallee (5% *Triodia*) (Table 2.1), reflect Mallee Emu-wren preference for dense swathes of *Triodia*. However, the time since last burned also influences the maturity, and hence volume, of *Triodia*, and therefore fire age-class is the overriding factor influencing densities within these two vegetation types.

Habitat selection theory predicts that organisms should preferentially select habitat that maximises their fitness and reproductive success (Fretwell and Lucas 1970). Our data suggests that as *Triodia* senesces and becomes less voluminous (>30 yrs), habitat quality for the Mallee Emu-wren declines, and this would have repercussions for reproductive output at the population level (Pulliam and Danielson 1991). Given temporal changes in patch quality, dispersal would be critical for metapopulation persistence, and largely driven by patch-disturbance dynamics caused by fires. Extinction in Bronzewing and Wathe FFRs may have been caused indirectly by inappropriate size and frequency of fire. Modelling demonstrates that stochasticity in patch dynamics increases the risk of extinction by increasing the risk that habitat will fluctuate to zero (Boughton and Malyadkar 2002). These smaller reserves may not contain a suite of spatially and temporally heterogenous age-class vegetation of sufficient size for a self sustaining population, enabling intrinsic adverse demographic processes to occur (Frankel and Soulé 1981, Hedrick and Kalinowski 2000). The implication is that the long-term viability of populations within other small reserves or isolated populations is vulnerable.

### 2.5.4 Climate change as a threatening process

Relatively small changes in rainfall and temperature are predicted to have dire consequences for the Mallee Emu-wren. Bioclimatic analysis predicts a >90% contraction in distribution of the Mallee Emu-wren with an increase in average yearly temperature of as little as 1°C, and extinction with a 3°C increase (Brereton et al. 1995). Population monitoring and evaluation of Emu-wren distribution in relation to rainfall corroborate this predictive modelling. Since 1997, the Murray Mallee region has experienced consecutive above-average annual temperatures (range 0.1-1.2°C), and in 2002 and 2006 it received about one-third of the average annual rainfall (Australian Bureau of Meteorology 2008). In 2007, higher than average temperatures (+1.2°C) combined with unseasonably low rainfall the previous year appeared to adversely affect the Mallee Emu-wren population at Hattah-Kulkyne NP. Monitoring
of a 135 ha patch found a halving in the local population density (0.25 birds ha\(^{-1}\) (2006) cf. 0.14 birds ha\(^{-1}\) (2007); S Brown, unpublished data), and a notable simultaneous decrease in abundance of small flying insects, on which Mallee Emu-wrens feed, was also observed (S Brown, pers. obs.).

Global warming is predicted to continue, causing an increase in the aridity of Australian semi-arid ecosystems and altering fire regimes (IPCC 2007). While wildfires are an intrinsic component of mallee ecosystems, at times extreme weather events will be conducive to large-scale fires that are impossible to control, rendering large tracts of vegetation unsuitable for the Mallee Emu-wren for a decade or more. Uncontrolled wildfire, particularly reserve-scale fires are one of the most immediate threats to Threatened mallee bird species (Woinarski and Recher 1997, Garnett and Crowley 2000). Larger, more regularly occurring fires are likely to homogenise and erode the mosaic of vegetation fire age-classes, making the vegetation structure less suitable to support a diversity of bird species. Currently, much of the Murray-Sunset NP contains vegetation of suitable fire age-class for Mallee Emu-wrens (Figure 2.2a). Nevertheless, a single major fire, or series of fires in this reserve is a very real risk, and such an event could significantly affect global population size.

2.5.5 Population estimate and effective population size

In this first attempt to empirically determine the global population size, we derived a population estimate about 68% higher than the 10 000 breeding birds assigned by Garnett and Crowley (2000) despite that fact that three previously known populations are likely to be extinct (i.e. Billiatt CP, Bronzewing and Wathe FFRs) and others have declined due to widespread wildfires. This discrepancy is not unexpected given Garnett and Crowley (2000) acknowledged the reliability of their estimates is low.

We consider our value for \(N_e\) to be an upper estimate. In the absence of life-history data it was not possible to incorporate parameters to determine a more reliable, and most likely lower, estimate of \(N_e\). Natural populations are complex, and traits such as adult sex ratios, variable mating systems, individual variance in offspring production and overlapping generations all influence \(N_e\) (see Nunney 1993, Anthony and Blumstein 2000). Further, we expect that the Mallee Emu-wren undergoes substantial fluctuations in mortality and recruitment in an environment that experiences prolonged cyclic-drought and fire periods; factors that lead to a large variance in
annual census and reproductive success, further reducing Ne (Vuchetich and Waite 1998). Unpublished data and anecdotal observations obtained from a colour-marked population show close similarities between the breeding biology and demographics of the Mallee Emu-wren to the Southern Emu-wren (Stipiturus malachurus). This includes a high turnover of the adult population, high mortality rates and population crashes (Maguire and Mulder 2004, Maguire, 2006b, S Brown unpublished data). We caution conservation managers to avoid erroneously equating population size with population viability.

2.5.6 Status under IUCN Red List

In May 2008, the results presented here contributed substantially to the reclassification of the Mallee Emu-wren from Vulnerable to Endangered (Birdlife International 2008). We have shown that the adverse impact of wildfire on populations, compounded by the effects of prolonged drought and historical habitat loss and fragmentation for agriculture, has been the pervasive factor in the global reduction of the Mallee Emu-wren. The decline to five reserve-scale populations since the conservation assessment in 2000 (Garnett and Crowley 2000), and the severe risk posed to extant populations from wildfire and climate warming, warrant reassessment of the conservation status of the Mallee Emu-wren on the IUCN Red List. Here we treated each reserve as a single location and population. This is because a single large wildfire can affect an entire reserve, and further, the genetic or demographic exchange between spatially isolated reserves or distant populations within continuous vegetation (eg. Ngarkat CP and Wyperfeld NP) is unlikely given the sedentary nature and poor flying ability of the Mallee Emu-wren. On the basis of our findings, the Mallee Emu-wren meets two threshold criterion for listing as Endangered. In accordance with IUCN Red List criteria for Endangered, the Mallee Emu-wren is; severely fragmented or known to exist in no more than 5 locations (EN B2a); is continuing (to) decline, observed, referred or projected in (i) extent of occurrence, (ii) area of occupancy, (iii) area, extent and/or quality of habitat, (iv) number of locations or subpopulations and (v) number of mature individuals (EN B2b(i,ii,iii,iv,v)) (IUCN 2001). Our data found the area of occupancy to be considerably less than the criterion for Vulnerable (20 000 km² VUL B1)(IUCN 2001) but not quite meeting the criteria for EN B2 (area of occupancy less than 500 km² (IUCN 2001)). Nevertheless, as we have highlighted, the risk to populations posed by wildfire is significant and it is possible
that in the near future a single extensive wildfire could reduce the area of occupancy to the ENB2 category. This observation highlights the limitations of some classification criteria. Although the area of occupancy may be large on a global scale, so too is the likely area that could be affected by a single disturbance (i.e. wildfire), hence the species’ vulnerability despite its large area of occupancy.

2.5.7 Implications for management

The Mallee Emu-wren is threatened by the interaction of climate change, fire regimes and adverse demographic processes through population isolation. Of these, large-scale wildfires pose the single most immediate threat. Nevertheless, the pervasive adverse affects of climate change and demographic stochasticity should not be underestimated. Climate change is a global management problem; however, at a local level, conservation managers can manage habitat to buffer populations. Given the poor dispersal ability of the Mallee Emu-wren, re-establishment of corridors containing structurally suitable habitat is required to maintain population connectivity between fragmented reserves. Similarly, where possible, fire-prescriptions within reserves should be planned and implemented to maintain habitat connectivity by encouraging re-growth of thick swathes of *Triodia* in areas that support Mallee Emu-wrens. Our knowledge of the fire ecology of *Triodia* is limited (but see Noble 1989, Bradstock 1989, Bradstock and Cohn 2002). One study has shown that seasonal timing of burns and post-fire climatic conditions strongly influence *Triodia* regeneration (Noble 1989). To improve management of this keystone species of the semi-arid zone and to understand its ecological role, more research is required on the influence of fire, climate and geophysical variables on its distribution.

As we have highlighted, several extant populations are precarious and/or have become isolated in recent decades. Population augmentation via translocation or breeding programs may need to be considered to ensure these populations persist until conditions are suitable for population expansion. Re-establishing populations in isolated reserves may also be a strategy for spreading the risk of losing the bulk of the global population in a single fire event. Programs should aim to maximise genetic diversity of local populations by preventing the occurrence of prolonged bottlenecks and susceptibility to genetic impoverishment, which may decrease individual fitness and population viability (Hedrick and Kalinowski 2000). Monitoring of populations and habitat condition should ideally be established to identify population trends so that management can respond with suitable actions.
CHAPTER 3

Habitat use by the Mallee Emu-wren *Stipiturus mallee* and Striated Grasswren *Amytornis striatus* (Aves: Maluridae); specialist use of *Triodia scariosa* in semi-arid mallee environments

Figure 3.1 Loamy Sands Mallee vegetation, Hattah-Kulkyne National Park, Victoria.
3.1 Abstract

Accurate assessment of habitat use for species of conservation concern is important for effective management. Correlative species-environment models based on coarse-grained environmental variables frequently fail to identify the underlying processes influencing observed patterns and thus may compromise effective management actions at local scales. Complementary fine-scale studies can elucidate underlying processes that influence a species' distribution at the local-scale. I examined fine-scale habitat variables that influence the local distribution of two threatened birds; the Mallee Emu-wren (*Stipiturus mallee*) and Striated Grasswren (*Amytornis striatus*) in fire-prone mallee vegetation in the Murray Mallee region of south-eastern Australia. Five candidate models were examined to identify variables that explain habitat use by these species. Both species were strongly associated with the hummock grass *Triodia scariosa*, although different aspects of *T. scariosa* structure explained the presence of each species at the fine-scale. The growth-phase and total volume of *T. scariosa* best explains habitat use by the globally Endangered Mallee Emu-wren, whilst the percent cover of *T. scariosa* best explains Striated Grasswren presence. Time-since-fire is thought to influence distribution of both species, although the modelling found this factor was not correlated with their incidence. I found that time-since-fire influenced the percent of cover and proportions of growth-phases of *T. scariosa* only up until sometime between 18 and 32 years-since-fire. This response has repercussions for what may constitute quality habitat for both species and should be considered for fire management. I conclude that the specific structure of *T. scariosa* is a key component of habitat for both species, and the differences in model responses may reflect subtle niche differences.
3.2 Introduction

Correlative species-environment models have enabled ecologists to delineate the habitat requirements of many species (Guisan and Thuiller 2005). When applied within a Geographical Information System (GIS), these models can be extrapolated to produce spatial predictions of suitable habitat (Guisan and Thuiller 2005, Peterson 2006, Rodríguez et al. 2007), and are well-suited for identifying species distributions over broad areas such as regions (Boitani et al. 2008, Santos et al. 2006). However, habitat and distribution models at broad-scales may fail to illuminate the underlying processes that drive local habitat use, because they frequently use variables such as latitude and temperature as surrogates for more causal factors (Austin 2002a).

Studies of the fine-scale habitat requirements of species, based on more direct variables, are a valuable complement to broad-scale models. Such studies are more likely to identify factors that infer habitat quality (e.g. Fernandez et al. 2003, Klar et al. 2008), and variables of biological significance responsible for patchiness of a species distribution (Austin 2002a, Fernandez et al. 2003, Klar et al. 2008). Studies at fine scales also have an important complementary role in the conservation of threatened species, when they assist in refining management solutions in ways not afforded by studies conducted at broad-scales.

The Mallee Emu-wren (*Stipiturus mallee*) and the Striated Grasswren (*Amytornis striatus*) are two species of conservation concern that occur in the arid and semi-arid zone of Australia (Fig.3.2) (Higgins et al. 2001). In south-eastern Australia, both species occupy dunefields of fire-prone vegetation, characterised by structurally dense shrub layers and low hummock grassland of spinifex (*Triodia* or *Plectrachne* spp.), with or without an overstorey of mallee eucalypts (Higgins et al. 2001, Rowley and Russell 1997). Both species are sedentary, with low fecundity and are regarded as habitat specialists (Rowley and Russell 1997, Higgins et al. 2001, Karubian 2001); attributes that make them particularly susceptible to environmental changes from habitat loss, large-scale wildfires (Pimm et al. 1988, Wiens 1997, Fahrig 2003).

Populations of the Mallee Emu-wren have declined precipitously in recent decades, attributed to widespread wildfires combined with drought and habitat fragmentation (Garnett and Crowley 2000, Smith 2004, Chapter2). This species is listed as globally Endangered (BirdLife International 2008). The Murray-Sunset and Hattah-Kulkyne
National Parks in Victoria are the stronghold, estimated to contain 92% of the global population (Chapter 2). Two small, precarious populations occur in mallee-heath vegetation in Ngarkat Conservation Park and Billiatt Conservation Park, South Australia (C. Hedger, pers. comm.)¹, and a single pair was recorded in mallee-*Triodia* vegetation in the south of its range in Wyperfeld National Park, Victoria (Chapter 2). A regional study of the Mallee Emu-wren in the Murray-Sunset and Hattah-Kulkyne National Parks, found that it primarily occurs in mallee-*Triodia* vegetation not burned for at least 15 years (Chapter 2). Nevertheless, many areas of seemingly suitable habitat remain unoccupied. Thus, the fire age-class and vegetation type may be indicative, but are unlikely to be a singular explanation for the patchy distribution of the Mallee Emu-wren. Greater understanding of fine-scale habitat use, within the species stronghold, is warranted.

The Striated Grasswren shows a preference for areas with a high density of *Triodia* (Karubian 2001) although little is known of their fine-scale habitat requirements. A regime of too-frequent fires, introduced vertebrate predators, and loss of habitat through stock grazing are thought to be major threats contributing to their decline (Garnett and Crowley 2000, Higgins et al. 2001, Rowley and Russell 1997). The Striated Grasswren is listed nationally as Near Threatened, although the species is now considered rare in south-eastern Australia (Higgins et al. 2001, Garnett and Crowley 2000).

In this chapter, I use data from a presence-absence survey, combined with a model selection procedure, to identify fine-scale vegetation and abiotic environmental variables that influence the local distribution of the Mallee Emu-wren and Striated Grasswren. The parameters identified by this approach can be used to determine areas of high quality habitat and to assess sites potentially suitable for reintroduction of the species. Finally, I assess the impact of fire on habitat suitability and make recommendations on fire management for effective conservation of these species within mallee-*Triodia* vegetation.

¹ Since Chapter 2 was published, a small group of Mallee Emu-wrens have been re-discovered in Billiatt Conservation Park.
3.3 Methods

3.3.1 Study area

The study area encompassed 90,000 ha within the Hattah-Kulkyne National Park (34°41'00"S, 142°16'00"E), south-eastern Australia (Fig. 3.2). Hattah-Kulkyne National Park is known to support the Striated Grasswren and has one of the larger populations of the Mallee Emu-wren (Higgins et al. 2001, Chapter 2).

The region has a semi-arid climate, with hot dry summers and mild winters. Mean annual rainfall is 334 mm, with most precipitation occurring during the period April to October (Australian Bureau of Meteorology, http://www.bom.gov.au). The landscape is dominated by narrow-crested, east-west dunes (Wasson 1989). The vegetation comprises fire-prone ‘mallee’ shrubland, consisting of multi-stemmed Eucalyptus spp. (3-10 m tall) with variable understorey associations. On the sandy soils of the dune slacks and crests, the understorey vegetation is dominated by the hummock grass Triodia scarisosa, hereafter Triodia and scattered sclerophyllous shrubs (Woorinen Sands Mallee and Loamy Sands Mallee) (Specht 1981a, Parkes and Cheal 1990).

Triodia is characterised by a distinctive growth-phase pattern. Small, immature plants are similar in structure to large grass hummocks; but as a plant matures it forms a large concentric ring of living tissue with matted dead material or bare ground in the centre (Fig. 3.3) (Specht 1981a). Triodia is thought to reach its peak growth-phase at around 15–30 years of age and may form rings several metres wide (Bradstock and Gill 1993).

3.3.2 Site selection and playback surveys for bird species

A map of Hattah-Kulkyne National Park was prepared using ArcView 3.2 (ESRI). Digital data for vegetation types (Ecological Vegetation Classes), and fire events were derived from the EVC_BSC100 and LASTBURNT data layers respectively (Department of Sustainability and Environment 2004). Sites from five fire age-classes and two Ecological Vegetation Classes (i.e. 10 classes) were selected to survey the presence or absence of the Mallee Emu-wren and Striated Grasswren. Sites were at least 500 m apart, a distance each species was unlikely to traverse between consecutive playback recording events. A total of 99 sites was selected within the study area.
Figure 3.2 The biogeographic range of the Mallee Emu-wren and Striated Grasswren (modified from Higgins et al., 2001) and the study area at Hattah-Kulkyne National Park, south-eastern Australia. White = agricultural land, stippling = three mallee vegetation types (Woorinen Sands Mallee, Loan Sands Mallee, Woorinen Mallee), solid grey = other vegetation types. Symbols denote the presence of Mallee Emu-wrens (□), Striated Grasswrens (●), and no birds recorded (○).

Two survey rounds were completed between August and December in each of 2006 and 2007. Playback surveys were conducted between dawn and 11.30 am unless weather was unsuitable (rain or winds greater than 10 knots). At each site, the observer listened for calls from the target species for 0.5 min. Then, a 1 min recording of the contact and alarm calls (©David Stewart/Nature Sound) of either the Mallee Emu-wren or Striated Grasswren was played through an MP3 player and amplified speaker system. This was followed by a 10 second listening period before the same process was repeated. Call playback for the second species then followed, using the same procedure. The order in which species’ calls were played was randomised. If individuals of either species were observed, the exact location of the first sighted bird for that species was noted for subsequent collection of vegetation data. Attempts were made to locate and observe all birds in a group as this provided data on numbers, sex and age of individuals present.
3.3.3 Site data

Data on fine-scale structural features and plant species composition were collected by using transect and quadrat methods (Sutherland 1996). Vegetation type (Ecological Vegetation Class) and estimated fire age-class were recorded at each site and compared with the GIS data to verify the accuracy of digital layers. A 30 m transect was placed to cross the location of the first-sighted bird, or was randomly positioned within a site if no birds were recorded.

The percent cover of *Triodia* and small shrubs (<3 m) were determined along each 30 m transect. All small shrubs were identified to species and the number of vegetation contacts between 0.1 m was recorded with a vertical pole. Measurements to 1 m were used as Mallee Emu-wrens and Striated Grasswrens are rarely observed to use higher level vegetation (S Brown pers. obs.). A representative sample of trees or large shrubs (>3 m) at each site was determined by identifying the individual plant nearest to each 10 m increment (i.e. 4 plants). Using the 30 m transect as an edge to create a 30 x 10 m quadrat, the number of trees and large shrubs (>3 m) were recorded to determine densities.

Each *Triodia* plant touching the 30 m transect line was assigned a growth-phase according to its diameter (cm) at the widest point, and whether it had an internal ring (Table 3.1, Fig. 3.3). The width and height of each plant was determined by measuring the extremity of the longest blades (excluding flower stalks) and the diameter of the internal ring was measured if present. The volume for each plant was calculated by treating it as a spherical cap, or for concentric rings, a half torus (i.e. $vol = \pi r^2 h$ and $(2\pi^2 R r^2)/2$ respectively). Where only a portion of a concentric ring was present (e.g. a semi-circular plant), volume calculations were adjusted accordingly. The total volume of *Triodia* at each site was calculated by summing the volume of individual plants.
Figure 3.3 Diagrammatic representation of the relative size and growth-phases of *Triodia*; a) immature plants (T1-T2), b) mature plants before collapse of the central tillers (T3), c) concentric rings resulting from collapse of the central tillers (T4). This latter growth-phase varies from <1 to many metres in width.

3.3.4 Model selection, fitting, evaluation and comparison

I used Generalized Linear Modelling to examine the relationship between the recorded presence or absence of the Mallee Emu-wren and Striated Grasswren and predictor variables, using the R 2.8.1 package (R Development Core Team, 2009). Because the dependent variable was binary, a binomial error distribution was assumed and logit link function used (Burnham and Anderson 2004). Ten predictor variables were selected to represent environmental and habitat attributes in the models (Table 3.1). These included percent cover and total volume of *Triodia* (PTrC and TotVol respectively) as well as two variables representing structural components of *Triodia* that influence habitat use, the T3 and T4 growth-phases of *Triodia* (Fig. 3.3). The growth-phases of *Triodia* were derived from a combination of the diameter of the *Triodia* plant and its structure (i.e. whether or not it was a concentric ring) (Table 3.1, Fig. 3.3). Density of trees or shrubs (>3 m) (Tha) and percent shrub cover (PSC) were also included as vegetation structural variables. The floristic composition of vegetation at survey sites was explored by cluster analysis and ordination, using non-metric multi-dimensional scaling (MDS) (PRIMER v6, Clarke and Gorley 2006). Cluster analysis was used to investigate whether sites could be classified into groups identifiable as distinct vegetation types (i.e. mapped Ecological Vegetation Classes for the area). Ordination values derived from MDS analysis of plant species composition
and abundance at sites were used as two variables representing floristic composition (FLAxis1 FLAxis2). Finally, a variable representing the time since last fire in years (TBurn) was included (Table 3.1). Predictor variables that did not meet assumptions of normality were transformed to approximate normality (Table 3.1).

Five models representing alternative hypotheses of factors potentially influencing the occurrence of the Mallee Emu-wren and Striated Grasswren were considered: 1) floristic composition of vegetation at the site, 2) time-since-fire, 3) overall habitat structure, 4) ground layer structure and 5) Triodia composition. Combinations of these sets of factors were also tested (Table 3.2).

I used the second-order Akaike’s information criterion (AICc) corrected for small sample size to select among models and model combinations (Burnham and Anderson 2004). Following Burnham and Anderson (2004), those models with Δi ≤ 2 were considered to be strongly competing models. However, as it is unlikely that a single model with the lowest AICc is the best model, I also used model averaging to determine the weighted average of variables across the set of models (Burnham and Anderson 2004). To further explore the relationship between the explanatory variables and recorded presence of the Mallee Emu-wren and Striated Grasswren, hierarchical partitioning was employed (hier.part package in R) (Mac Nally 1996, Chevan and Sutherland 1991). Explanatory variables in ecological studies are usually only nominally independent, and correlation among the explanatory variables makes it difficult to quantify the unique contributions of each explanatory variable to the response variable (Mac Nally 1996). Hierarchical partitioning alleviates the problems of multicollinearity among variables (MacNally 2000, 2002). Hierarchical partitioning provides relative estimates of the independent and joint explanatory capacities of each of the predictor variables separately, by considering all possible models (2ⁿ) in a multivariate regression setting (MacNally 1996, Chevan and Sutherland 1991).
Table 3.1 Ten environmental predictor variables, units of measurement and description used for logistic regression modelling of the distribution of the Mallee Emu-wren and Striated Grasswren.

<table>
<thead>
<tr>
<th>Predictor variable</th>
<th>Unit of measurement</th>
<th>Description</th>
<th>Transformation</th>
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<td>FLAxis1, FLAxis2</td>
<td>Floristic composition at site</td>
<td>Tree Species &gt;3m, Understorey species &lt;3m</td>
<td>Non-metric multi-dimensional scaling values, floristic axis values 1 and 2 (FLAxis1, FLAxis2)</td>
</tr>
<tr>
<td>TBurn</td>
<td>Time-since-fire</td>
<td>Time (years) since last burned</td>
<td>9, 18, 32, 55 and &gt;56 yr</td>
</tr>
<tr>
<td>PSC</td>
<td>Percent shrub cover</td>
<td>0-100 %</td>
<td>Proportional cover of shrubs and herbs along 30m</td>
</tr>
<tr>
<td>Tha</td>
<td>Tree density</td>
<td>Trees ha(^{-1})</td>
<td>Density of trees or shrubs (&gt;3 m) per hectare</td>
</tr>
<tr>
<td>DVShr1</td>
<td>Vertical density of shrubs</td>
<td>No of vegetation contacts to a vertical pole at 0-1 m</td>
<td>the number of vegetation contacts in a shrub recorded with a vertical pole at 0-1 m</td>
</tr>
<tr>
<td>TotVol</td>
<td>Total volume of Triodia</td>
<td>cm(^2)</td>
<td>Sum of volume of all Triodia plants along 30 m transect</td>
</tr>
<tr>
<td>PTrC</td>
<td>% Triodia cover</td>
<td>0-100 %</td>
<td>Proportional cover of Triodia along 30 m transect</td>
</tr>
<tr>
<td></td>
<td>Category of Triodia based on diameter and growth-phase characteristics#</td>
<td>0.25-0.49 m T1*, 0.5-0.99 m T2*, 1.0-2.0 m T3, 0.5-7.0 m T4</td>
<td>Small, emerging plant, Juvenile, no collapse at centre of plant, Mature, with or without start of collapse of centre, Mature, concentric ring configuration</td>
</tr>
</tbody>
</table>

† Log10 transformation was used for oneway ANOVA
* Not used in the modelling
# see figure 3.3 for growth-phase characteristics
Table 3.2 Five *a priori* models and their combinations representing alternative hypotheses of factors potentially influencing the occurrence of the Mallee Emu-wren and Striated Grasswren. FlAxis1 = Floristic Axis 1 values, FlAxis2= Floristic Axis 2 values, TBurn= time-since-burn, PTrC= percent *Triodia* cover, PSC =percent of total shrub cover, Tha= trees ha-1, DVShr1 = vertical density of shrubs 0-1m, TotVol =total *Triodia* volume, T3= number of *Triodia* plants assigned to growth-phase T3, T4 =number of *Triodia* plants assigned to growth-phase T4.

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Predictor variable</th>
<th>Model description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Floristic composition</td>
<td>FlAxis1 + FlAxis2</td>
<td>Floristic composition</td>
</tr>
<tr>
<td>Time-since-fire</td>
<td>TBurn</td>
<td>Time-since-fire</td>
</tr>
<tr>
<td>Overall habitat structure</td>
<td>PTrC + PSC + Tha</td>
<td>Percent <em>Triodia</em> cover + Percent shrub cover + Tree density</td>
</tr>
<tr>
<td>Ground layer structure</td>
<td>PTrC + PSC + DVShr1</td>
<td>Percent <em>Triodia</em> cover + Percent shrub cover + Vertical density of shrubs</td>
</tr>
<tr>
<td><em>Triodia</em> composition</td>
<td>TotVol + T3 + T4</td>
<td>Total volume of <em>Triodia</em> + T3 + T4 growth-phases</td>
</tr>
<tr>
<td>Model combinations</td>
<td></td>
<td></td>
</tr>
<tr>
<td>FlAxis1 + FlAxis2 + PTrC + PSC + Tha</td>
<td>Floristic composition + Percent <em>Triodia</em> cover + Percent shrub cover + Tree density</td>
<td></td>
</tr>
<tr>
<td>FlAxis1 + FlAxis2 + PTrC + PSC + DVShr1</td>
<td>Floristic composition + Percent <em>Triodia</em> cover + Percent shrub cover + Vertical density of shrubs</td>
<td></td>
</tr>
<tr>
<td>FlAxis1 + FlAxis2 + TotVol + T3 + T4</td>
<td>Floristic composition + Total volume of <em>Triodia</em> + T3 + T4 growth-phases</td>
<td></td>
</tr>
<tr>
<td>TBurn + PTrC + PSC + Tha</td>
<td>Time-since-fire + Percent <em>Triodia</em> cover + Percent shrub cover + Tree density</td>
<td></td>
</tr>
<tr>
<td>TBurn + PTrC + PSC + DVShr1</td>
<td>Time-since-fire + Percent <em>Triodia</em> cover + Percent shrub cover + Vertical density of shrubs</td>
<td></td>
</tr>
<tr>
<td>TBurn + TotVol + T3 + T4</td>
<td>Time-since-fire + Total volume of <em>Triodia</em> + T3 + T4 growth-phases</td>
<td></td>
</tr>
<tr>
<td>PTrC + PSC + Tha + DVShr1</td>
<td>Percent <em>Triodia</em> cover + Percent shrub cover + Tree density + Vertical density of shrubs</td>
<td></td>
</tr>
<tr>
<td>PTrC + PSC + Tha + TotVol + T3 + T4</td>
<td>Percent <em>Triodia</em> cover + Percent shrub cover + Tree density + Total volume of <em>Triodia</em> + T3 + T4 growth-phases</td>
<td></td>
</tr>
<tr>
<td>PTrC + PSC + DVShr1 + TotVol + T3 + T4</td>
<td>Percent <em>Triodia</em> cover + Percent shrub cover + Vertical density of shrubs + Total volume of <em>Triodia</em> + T3 + T4 growth-phases</td>
<td></td>
</tr>
</tbody>
</table>
3.4 Results

3.4.1 Distribution of the Mallee Emu-wren and Striated Grasswren

The Mallee Emu-wren and Striated Grasswren were detected at 22 and 15 sites, respectively, of the 99 sites surveyed, with both species recorded during the same playback survey on eight occasions. Both species were recorded across much of the western region of the Hattah-Kulkyne National Park (Fig. 3.2).

3.4.2 Floristic composition at sites

Fifty-three plant species were recorded at the 99 sites within the Hattah-Kulkyne landscape. The cluster and ordination analysis of sites did not discriminate between those mapped as Woorinen Sands Mallee or Lowan Sands Mallee, with sites assigned to both vegetation types containing a mixture of Eucalyptus spp, Callitris spp., sclerophyllous shrubs, Triodia and occasional succulents.

3.4.3 Growth form, cover and volume of Triodia in relation to time-since-fire

A total of 975 individual Triodia plants were measured. Comparisons of the mean dimensions (diameter, height and volume) of plants for each growth-phase (T1-T4) are given in Fig. 3.4. Growth-phases T1-T3 showed little within-group variation, whilst the mature growth-phase (T4), characterised by an internal ring, varied substantially in both diameter and volume. The diameter of T4 plants ranged from 0.5 - 8.0 m.

The percent cover of Triodia ranged from 0 - 67%, and the total volume of Triodia plants at a site ranged between 0 - 41.8 m³ (Fig. 3.5). The relative proportion of Triodia plants assigned to each growth-phase varied depending on time-since-fire at a site (Fig. 3.6). Sites burned 9 and 18 years previously had a relatively high proportion of early growth-phase plants (T1 and T2) with few T3, and no T4 plants. The remaining fire ages (32, 55 and >56 yr) had relatively fewer T1 plants with approximately equal proportion of T2, T3 and T4 plants (Fig. 3.6). The data imply that somewhere between 18 to 32 years-since-fire, a relatively stable proportion of growth-phases is established with equitable rates of senescing and newly emerging plants. The youngest vegetation in which the Mallee Emu-wren and Striated Grasswren were recorded was 18 years since fire, and this site contained 67% cover of Triodia. The Triodia cover at sites at which either species was recorded ranged from 15-67%.
Figure 3.4 Dimensions of *Triodia* plants in relation to four categories of growth-phase (T1-T4). The histograms show mean and standard deviation for Diameter (m), Height (m), Total volume (m³). Growth phase: T1-T2 = immature plants, T3 = mature plants, T4 = plants with concentric ring pattern.

Figure 3.5 Mean cover (%) and total volume (m³) of *Triodia* along each 30 m transect at survey sites in relation to time-since-fire.
Figure 3.6 The relative proportions of *Triodia* plants assigned to each growth-phase of *Triodia* (T1-T4) in relation to time-since-fire at survey sites.

3.4.4 Habitat models for the Mallee Emu-wren and Striated Grasswren

Alternative models of factors influencing the occurrence of the Mallee Emu-wren and Striated Grasswren are listed in rank order (by AICc weights, \( w_i \)) in Table 3.3. The proportion of deviance explained by these models for the Mallee Emu-wren ranged from 341%, with models 5, 1+5, 2+5, 3+5, 4+5 having the highest values (39-41%). The two strongest competing models include variables relating only to *Triodia* (volume and growth-phase), with or without the variable, time-since-fire (5, 2+5, Table 3.3). The three next strongest models (1+5, 3+5, 4+5) all included *Triodia* predictor variables.

Modelling for the Striated Grasswren identified four models as relatively strong candidates (3, 2+3, 2+4, 3+4, \( \Delta i \leq 2 \), Table 3.3). These models included predictor variables for ground layer structure, overall habitat structure and time-since-fire. The proportions of explained deviance for these models were lower than those obtained for the Mallee Emu-wren. They ranged from 26-29% for the strongest candidate models (i.e. 3, 2+3, 2+4, 3+4) to 3% for the poorest model.
Table 3.3 Model selection results for five a priori models and their combinations relating to factors influencing the occurrence of the Mallee Emu-wren and Striated Grasswren. Models are ranked by AICc weights (wi). K is the number of parameters in each model, AICc is the AIC for small sample size, Δi is the relative weight of model strength compared to the strongest model, and Rank is the relative rank of the models based on the wi. FLAxis1 = Floristic Axis 1 values, FLAxis2 = Floristic Axis 2 values, TBurn= time-since-burn, PTrC= percent Triodia cover, PSC=percent of total shrub cover, Tha= trees ha-1, DVShr1= vertical density of shrubs 0-1m, TotVol=total Triodia volume, T3= number of Triodia plants assigned to growth-phase T3, T4= number of Triodia plants assigned to growth-phase T4. Bold indicates strongly competing models, Δi ≤ 2.

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Variables</th>
<th>Model</th>
<th>K</th>
<th>AICc</th>
<th>Δi</th>
<th>wi</th>
<th>Rank</th>
<th>Model</th>
<th>K</th>
<th>AICc</th>
<th>Δi</th>
<th>wi</th>
<th>Rank</th>
</tr>
</thead>
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<td>Floristic composition</td>
<td>FLAxis1 + FLAxis2</td>
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<td>108.11</td>
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<td>35.40</td>
<td>15</td>
<td>88.03</td>
<td>0.000</td>
<td>17.56</td>
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<td></td>
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<tr>
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<td>80.67</td>
<td>0.002</td>
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<td>11</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Overall habitat structure</td>
<td>PTrC + PSC + Tha</td>
<td>3</td>
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<td>84.66</td>
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<td>0.226</td>
<td>0.37</td>
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<td></td>
</tr>
<tr>
<td>Ground layer structure</td>
<td>PTrC + PSC + DVShr1</td>
<td>4</td>
<td>5</td>
<td>88.35</td>
<td>0.000</td>
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<td>10</td>
<td>74.65</td>
<td>0.033</td>
<td>4.20</td>
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<td></td>
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<tr>
<td>Triodia composition</td>
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<td>5</td>
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<td>1</td>
<td>81.53</td>
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<tr>
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<td>FLAxis1 + FLAxis2 + PTrC + PSC + Tha</td>
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</tr>
<tr>
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<td>18.01</td>
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<td>78.56</td>
<td>0.005</td>
<td>8.12</td>
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</tr>
<tr>
<td></td>
<td>FLAxis1 + FLAxis2 + TotVol + T3 + T4</td>
<td>1+5</td>
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<td>3</td>
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<td>14.84</td>
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</tr>
<tr>
<td></td>
<td>TBurn + PTrC + PSC + Tha</td>
<td>2+3</td>
<td>6</td>
<td>86.52</td>
<td>0.001</td>
<td>13.81</td>
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<td>0.00</td>
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</tr>
<tr>
<td></td>
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<td>0.212</td>
<td>0.50</td>
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<td></td>
<td>TBurn + TotVol + T3 + T4</td>
<td>2+5</td>
<td>6</td>
<td>73.62</td>
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</tr>
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<td></td>
<td>PTrC + PSC + Tha + DVShr1</td>
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<td>9</td>
<td>70.99</td>
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<tr>
<td></td>
<td>PTrC + PSC + Tha + TotVol + T3 + T4</td>
<td>3+5</td>
<td>10</td>
<td>76.93</td>
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<td>0.012</td>
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<tr>
<td></td>
<td>PTrC + PSC + DVShr1 + TotVol + T3 + T4</td>
<td>4+5</td>
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<td>80.64</td>
<td>0.002</td>
<td>10.20</td>
<td>10</td>
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</tr>
</tbody>
</table>
The logistic regression coefficients derived from model averaging show a significant association between the presence of the Mallee Emu-wren and both the total volume (TotVol) and the mature T3 growth-phase of *Triodia* (Table 3.4). The presence of the Striated Grasswren was positively associated with the percent cover of *Triodia*. None of the remaining variables was significant for either species and many of the parameter estimates had large standard errors.

### 3.4.5 Variable contributions from hierarchical partitioning analysis

Hierarchical partitioning analyses identified variables relating to *Triodia* as primary explanatory variables for Mallee Emu-wren and Striated Grasswren presence (Figs. 3.7 a & b). For the Mallee Emu-wren, the *Triodia* predictor variables (i.e. total volume, T3 and percent cover) had greater independent explanatory power than other predictors included in the analysis, and together these three variables proportionately contributed 79% of total variance. However, most of the explained variation was related to joint effects of these variables (Fig 3.7a) which may be attributed to colinearity. For the Striated Grasswren, the percent cover of *Triodia* had marginally the greatest independent explanatory power than other predictor variables, with most of the explained variation for this variable related to joint effects. The vertical density of shrubs at 0-1m (DVShr1) and mature growth-phase of *Triodia* (T3) were the next most important variables (Fig. 7b). Comparison of results between the two species shows that the percent proportional contribution of the total volume of *Triodia* and T3 growth-phase for the Striated Grasswren is substantially lower than that for the Mallee Emu-wren. This suggests that the total volume and structure of the *Triodia* is of lesser importance to the Striated Grasswren.
Table 3.4 Summary of logistic regression coefficients from model averaging of factors influencing the occurrence of the Mallee Emu-wren and Striated Grasswren in the Hattah-Kulkyne area. Explanations of variable names are given in Table 3.1. *p ≤ 0.01

<table>
<thead>
<tr>
<th></th>
<th>Mallee Emu-wren</th>
<th></th>
<th></th>
<th></th>
<th>Striated Grasswren</th>
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<tbody>
<tr>
<td></td>
<td>Estimate</td>
<td>Std Error</td>
<td>z value</td>
<td>Pr(&gt;</td>
<td>z</td>
<td>)</td>
<td>Estimate</td>
<td>Std Error</td>
</tr>
<tr>
<td>Intercept</td>
<td>-6.799</td>
<td>1.961</td>
<td>-3.467</td>
<td>0.0005**</td>
<td>-2.323</td>
<td>4.731</td>
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<td>0.6207</td>
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<td>-0.375</td>
<td>0.7074</td>
<td>-0.006</td>
<td>0.137</td>
<td>0.047</td>
<td>0.9621</td>
</tr>
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<td>FLAxis2</td>
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<td>-0.357</td>
<td>0.7208</td>
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<td>0.118</td>
<td>-0.013</td>
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<td>-0.464</td>
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<td>0.022</td>
<td>0.037</td>
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<td>PTrC</td>
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<td>0.016</td>
<td>0.255</td>
<td>0.7984</td>
<td>**</td>
<td>0.072</td>
<td>**</td>
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<td>0.325</td>
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</tr>
<tr>
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<td>-0.944</td>
<td>0.668</td>
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</tr>
<tr>
<td>DVShr1</td>
<td>-0.000</td>
<td>0.024</td>
<td>-0.035</td>
<td>0.9721</td>
<td>-0.085</td>
<td>0.124</td>
<td>-0.686</td>
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<tr>
<td>TotVol</td>
<td>1.875</td>
<td>0.683</td>
<td>**</td>
<td>2.743</td>
<td>0.0061*</td>
<td>0.003</td>
<td>0.055</td>
<td>0.9533</td>
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<tr>
<td>T3</td>
<td>1.499</td>
<td>0.537</td>
<td>**</td>
<td>2.793</td>
<td>0.0052*</td>
<td>0.004</td>
<td>0.081</td>
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<td>T4</td>
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<td>0.7558</td>
<td>-0.004</td>
<td>0.067</td>
<td>-0.059</td>
<td>0.9531</td>
</tr>
</tbody>
</table>
**Figure 3.7 a & b** The independent and joint contributions (given as the percentage of the total explained variance) of the predictor variables estimated from hierarchical partitioning for; a) Mallee Emu-wren, and b) Striated Grasswren. Negative joint variance indicates that the other variables act as suppressors of the particular variable. Axis1= axis 1 values, Axis2= Axis 2 values, TBurn =time-since-burn, PTrC= percent Triodia cover, PSC= percent of shrub cover, Tha= trees ha\(^{-1}\), DVShr1= vertical density of shrubs 0-1m, TotVol= total volume of Triodia, T3= number of Triodia plants assigned growth-phase T3, T4= number of Triodia plants assigned growth-phase T4.
3.5 Discussion

Hummock grasslands of spinifex cover more than 25 percent of the Australian continent and are significant in terms of their contribution to biodiversity (Allan and Southgate 2002). This study is the first to quantitatively document the association of an avian species with specific structural attributes of *Triodia* spp. It describes how time-since-fire influences the proportion of later growth-phases and structural composition of *Triodia*, which in turn influences the distribution of the Mallee Emu-wren and Striated Grasswren at fine-scales within semi-arid mallee shrublands.

3.5.1 Factors affecting habitat use

All members of the genus *Stipitus* and *Amytornis* are associated with ground-layer vegetation (Rowley and Russell 1997, Higgins et al. 2001) and several have been shown to be associated with dense vegetation structure below 1 m, including the Mallee Emu-wren (Mercer 1988), the Southern Emu-wren *S. malurus* (Wilson and Paton 2004, Maguire 2006a) and the Thick-billed Grasswren *A. textilis* (Brooker 2000). In this study, modelling failed to find any clear association between the occurrence of either the Mallee Emu-wren or Striated Grasswren and shrub structure or composition (excluding *Triodia*), although both species are known to occur in vegetation dominated by mixed dense shrub and *Triodia* associations (Rowley and Russell 1997, Higgins et al. 2001, Smith 2004, Chapter 2). This discrepancy may, in part, be an artefact of sampling bias as Hattah-Kulkyne National Park is dominated by Ecological Vegetation Classes with higher *Triodia* and lower shrub cover compared to shrubby mallee-heath vegetation.

The marked association of the Mallee Emu-wren and Striated Grasswren with *Triodia* indicates that *Triodia* is a key factor influencing their fine-scale distribution. This is consistent with previous work that demonstrated the Mallee Emu-wren to be associated primarily with mallee-*Triodia* (Chapter 2) or mallee-heath with understorey associations of *Triodia* (Mercer 1998, Smith 2004). In mallee-heath, the Mallee Emu-wren occupied sites that had a taller and greater cover of *Triodia* than unoccupied sites (Mercer 1998, Smith 2004). Here, the association of the Mallee Emu-wren with the larger growth-phase of *Triodia* hummocks (T3) suggests this growth-phase is a critical resource for one or more life-history requirements (e.g. nesting). Likewise the Striated Grasswren displays a preference for dense *Triodia* (Karubian 2001, this study),
although it is known to occasionally nest in dense Banksia-heath in the absence of Triodia (Higgins et al. 2001), suggesting that it is not exclusively dependent on Triodia if other structurally suitable vegetation is present.

Other members of the genus Stipiturus and Amytornis that nest in, or are associated with, Triodia or Plectarchne spp. include the Rufous-crowned Emu-wren S. ruficeps, the Thick-billed Grasswren, the White-throated Grasswren A. woodwardi, the Carpentarian Grasswren A. dorotheae, and Dusky Grasswren A. purnelli (Noske 1992, Brooker 2000, Karubian 2001). The Mallee Emu-wren, Rufous-crowned Emu-wren and possibly the Carpentarian Grasswren appear to be the only species obligately dependent on Triodia or Plectarchne spp. (Rowley and Russell 1997). Triodia and Plectarchne spp. also are an important resource for many small marsupials, rodents and lizards of inland arid and semi-arid Australia, providing foraging substrates for prey, nesting sites, protective cover from predators and suitable microclimate (Pianka and Pianka 1976, Letnic 2002, Masters et al. 2003, Kelly et al. 2010).

Post-fire successional processes in semiarid mallee systems show rapid structural changes in the first three decades after fire, followed generally by a slower rate of change for various structural attributes (e.g. tree hollows) (Haslem et al. 2011). Triodia tracks this temporal pattern, reaching maximum cover 20-30 years post-fire followed by a minor decline and plateau up until at least 100 years (Haslem et al. 2011). Similarly, this study shows that the structure and proportion of growth-phases reaches an equilibrium between 18-32 years following fire. I found no evidence to suggest a decline in key attributes of Triodia that would prevent the Mallee Emu-wren or Striated Grasswren occupying older vegetation. Furthermore, the diameter of mallee eucalypts recorded from some sites that support the Mallee Emu-wren and Striated Grasswren indicate they are greater than 100 years old (Clarke et al. 2010), implying that relatively old habitat remains suitable for these species in Hattah-Kulkyne National Park.

The lack of strong association of the occurrence of Mallee Emu-wren and Striated Grasswren with the time-since-fire model indicates that fire per se is unlikely to exert a strong influence on these species’ fine-scale distribution in vegetation greater than 18 years since fire. This finding was surprising, as landscape-scale studies in semi-arid mallee shrublands have found that fire is a key element influencing the broader
distribution of these and other avian species (Clarke 2005, Chapter 2). It is probable that for these species large-scale stochastic processes (i.e. fire and drought) prevail over their ability to respond to habitat features at fine scales. The study area in Hattah-Kulkyne has a relatively diverse mosaic of fire age-classes occupying small areas, compared with other tracts of mallee vegetation where in the past decade individual fire events have exceeded 100 000 ha. These large-scale disturbances affect populations and habitats over large expanses, so that the ability to reoccupy areas that provide suitable habitat at fine-scales is diminished or no longer exists. In this study area, the smaller scale disturbances (i.e. small individual fire events) have meant that these species are able to respond to fine-scale habitat preferences where they occur.

3.5.2 Niche differences between the Mallee Emu-wren and Striated Grasswren

Model outcomes suggest that different variables define fine-scale habitat use by the Mallee Emu-wren and Striated Grasswren. In particular, the disparity between structural aspects of Triodia to which each species responds suggests that Striated Grasswrens and Mallee Emu-wrens exhibit niche differences at fine-scales. Niche theory (Hutchinson 1957) is the basic tenet for developing species-environment models. The underlying premise is that relations between the occurrence of a species and certain elements of its environment are predictable and the distribution of species has an adaptive significance (Rosensweig 1981). Differences between models for these species may reflect resource partitioning in foraging requirements, nest requirements (placement of nests in Triodia) or a requirement for cover when foraging. Both species nest in hummocks of Triodia, though the Striated Grasswren is reported to occasionally use other vegetation structure (Higgins et al. 2001). Striated Grasswrens forage on Triodia seeds, as well as insects (Rowley and Russell 1997, Karubian 2001, Higgins et al. 2001) including ants (Barker and Vestjens 1990, Higgins et al. 2001); whereas the Mallee Emu-wren appears to be exclusively insectivorous, and has not been observed to forage on ants (S. Brown, unpublished data). Extensive behavioural observations of the Mallee Emu-wren found that both species regularly encounter each other within the study area and aggressive behaviour towards each other was never observed (S. Brown, pers. obs.). Subtle niche differences between the Mallee Emu-wren and Striated Grasswren most likely signify a lack of interspecific competition for resources and may explain why the two species frequently cohabit.
3.5.3 Performance of models

Studies of fine-scale habitat occupation are more likely to detect functional relationships between species and their environment than are landscape-scale studies (Austin 2002a). This is particularly applicable to species that are highly sedentary and poor dispersers, where local rather than broad-scale variables influence local populations and patch occupancy (Whittaker et al. 2001). Concordance of fine-scale habitat modelling of the Mallee Emu-wren between mallee-heath (Smith 2004) and mallee-Triodia vegetation (this study) suggest that structural aspects of Triodia cover are a strong predictor of the occurrence of this species.

The proportion of explained variation in the habitat models was modest (≤ 40%), indicating that other factors also influence the distribution of these species at a fine-scales. Dispersal ability, social mechanisms, mechanistic constraints (physiological responses and constraints), resource fluctuations and competition are additional factors that may influence patch and local population dynamics (Guisan and Thuiller 2005, Campomizzi et al. 2008, Kearney and Porter 2009). The Mallee Emu-wren and Striated Grasswren do not appear to undertake long-distance movements (Rowley and Russell 1997, Higgins et al. 2001) and occur in fire-prone environments that are highly dynamic and heterogenous. It is probable that the population dynamics of these species are not in equilibrium. The interaction of one or more of these factors and the limited ability of these species to track resources through a heterogeneous landscape at a meso-scale (10-30 km) may in part explain local patch occupancy and modest model fit.

Predictive modelling is an iterative process, and the models discussed here can be used to guide future surveys for data collection and model refinement. These models can also be used as a preliminary guide for habitat modelling of the Rufous-crowned Emu-wren and species of Grasswren that occupy similar niches (Rowley and Russell 1997, Higgins et al. 2001).

3.5.4 Conservation implications

The results of this study have implications for fire management practices and conservation actions to secure these threatened species from local extinction events. Fire is recognised as the greatest threat to bird species of conservation concern in mallee ecosystems (Woinarski and Recher 1997, Garnett and Crowley 2000), and
widespread fires of high intensity have the potential to destroy significant populations and habitat of the Mallee Emu-wren and Striated Grasswren (Woinarski and Recher 1997, Baker-Gabb 2004, Chapter 2). Fire is widely used as a management tool in mallee ecosystems to prevent extensive areas being burned and homogenised, to protect biodiversity and built assets, and to maintain habitat for species dependent on particular seral stages (Bradstock and Cohn 2002, Sandell et al. 2006). However, gaps exist in knowledge of how species respond to fire, limiting the ability to effectively manage fire-prone landscapes for fauna (Driscoll et al. 2010). A requirement to integrate fire management for asset protection and biodiversity conservation is challenging because conflict between objectives may arise.

The response of *Triodia* to time-since-fire shown in this study concurs with that of Haslem et al. (2011) and suggest that ‘ecological’ burns that aim to benefit the Mallee Emu-wren and Striated Grasswren in mallee-*Triodia* need to be planned on a time cycle of 50 to at least 100 years. This relatively long period between fires is in marked contrast with avian responses to fire in coastal heathland vegetation in eastern Australia (Lindenmayer et al. 2008), and ground-story vegetation of forest habitats (Christensen et al. 1985). I suggest that an informed approach to strategic ‘management’ burns for these species in mallee-*Triodia* vegetation involves actions that aim to prevent uncontrollable wildfires from encroaching on areas supporting high percentage cover of *Triodia* and known populations of these bird species.

Management to reduce the incidence of large-scale fires should continue in a framework that also seeks to promote a high incidence of older seral stages suitable for the Mallee Emu-wren and Striated Grasswren at a spatial scale that enables these species to respond to fine-scale resources.

Another key management consideration is the maintenance of connectivity of structurally suitable habitat to aid dispersal. These species select habitat with high structural density at less than 1 m height (Mercer 1988, Smith 2004, this study). Both species move between closely placed *Triodia* hummocks and avoid small patches of open swales (Karubian 2001, S. Brown, pers. obs.). Poor flying ability and a dependence on dense *Triodia* and cover for movement are thought to restrict dispersal in the Striated Grasswren (Karubian 2001) and the White-throated Grasswren (Noske 1992). The absence of dense ground vegetation may also be a driving factor in the inability of the Southern Emu-wren to recolonise nearby suitable habitat (Wilson and
Paton 2004). Given this behavioural characteristic, I predict that the Mallee Emu-wren and Striated Grasswren will be unable or unwilling to traverse open areas such as wide linear prescription burns (e.g. 3 km wide, see Figure 2.3a), large burned areas and cleared agricultural areas, severely limiting their ability to disperse and recolonise nearby suitable habitat.

These models of habitat suitability may be useful for management across these species’ ranges to identify quality habitat for potential reintroduction or population augmentation, or to aid in vegetation management. For example, the Mallee Emu-wren has not been recorded in the nearby Annuello Flora and Flora Reserve (36 000 ha) (Robertson et al. 1989), though it is part of the same mallee ecosystem. Striated Grasswrens were recorded there in 2008 (S. Brown, pers. obs.). The reserve experienced large-scale wildfires in 1998 and much of the vegetation may soon be of suitable fire age-class for the Mallee Emu-wren to occupy. Assessment of this habitat for potential reintroduction is warranted as establishment of new populations through translocation will help ensure the Mallee Emu-wren against extinction in the probable event of further large-scale fires extirpating other local populations.

3.5.5 Conclusion

Studies of habitat preference at fine-scales can usefully complement broad-scale studies of species’ distribution by illuminating the underlying process that explains a species’ occurrence at local scales. I have shown a strong association between specific structural elements of Triodia and the occurrence of two avian species. Analysis of the relative proportions of growth-phases and cover of Triodia in relation to time-since-fire has helped elucidate the habitat selection process that mediates these species’ responses to fire. Further work that seeks to assess the causal factors for selection of particular growth-phases and cover of Triodia would contribute further to the understanding of the ecology of these threatened species.
CHAPTER 4

Microhabitat selection and foraging behaviour by the Mallee Emu-wren

Figure 4.1 Mallee-*Triodia* habitat (Woorinen Sands), Hattah-Kulkyne National Park, Victoria.
4.1 Abstract

For small vertebrates, micro-sites within habitat can represent very different environments in terms of foraging success, protection from predators, nesting sites and for thermal regulation. Understanding how individuals use resources at fine-scales is important for conservation management. I explored the biophysical variables and behavioural decisions that explain micro-habitat selection by a tiny ground-dwelling bird, the Mallee Emu-wren *Stipiturus mallee*. The Mallee Emu-wren is a globally-endangered, habitat specialist of the semi-arid zone of south-eastern Australia. It occupies dense understorey vegetation containing the hummock grass *Triodia scariosa*, which varies in its structural attributes with age. Free-ranging groups of Mallee Emu-wrens were observed in long-unburnt vegetation dominated by *T. scariosa*. I identified the structural attributes of *T. scariosa* preferred by Mallee Emu-wrens for foraging, when vocalising, and for use as a stepping stone for movement. Mallee Emu-wrens preferred *T. scariosa* hummocks of large volume and mature growth-phase for all activities, which is consistent with the use of dense cover as a predator avoidance strategy. When foraging, individuals preferred *T. scariosa* hummocks with a higher proportion of green leaves. Examination of the mallee microclimate found limited amelioration of temperatures within *T. scariosa* hummocks relative to open habitat.
4.2 Introduction

Understanding habitat selection at multiple scales is a primary focus of ecological research (Cody 1981, 1985, Wiens 1989b) and has important practical implications for conservation management (Serrano and Astrain 2005). Fine-scale selection (i.e. third- and fourth-order selection, Johnson 1980) relates to the selection of habitat components and choice of resource items by individuals (Johnson 1980, Orians and Wittenberger 1991). Theory postulates that natural selection should act on an individual's choice of habitat to maximize the probability of selecting habitat with the best available resources (Fretwell and Lucas 1970, Rosenzweig 1981, Pyke 1984). Therefore, understanding how individuals select resource items can help to elucidate the mechanistic basis of individual fitness and reproductive success, and link individual behaviour to higher level population dynamics (Fretwell and Lucas 1970, Clark and Shulter 1999, Buskirk and Millsapugh 2006, Johnson 2007).

Micro-sites within habitat can represent very different environments and provide resources that are important for foraging success, thermoregulation, predator avoidance and nest-site selection (Whelan 2001, Kanda et al. 2005, Antos et al. 2008, Godbout and Ouellet 2010). Interactions between the costs and benefits for different life-history activities (e.g. foraging, nesting, competition) influence resource selection and consequently influence micro-habitat and macro-habitat use (Cody 1981, Cuthill and Houston 1997, Brodin 2007). For example, animals need to consider the trade-offs between energetic gains from foraging, the risk of predation (Sih 1980, Lendrem 1983, Lima 1985) and thermal micro-site selection (Grubb and Greenwald 1982, Wachob 1996, Brodin 2007); or the gains derived from communication and display, against the risk of exposure (Campos et al. 2009).

This chapter presents a study on micro-selection of habitat by an endangered Australian species, the Mallee Emu-wren (Stipiturus mallee). The Mallee Emu-wren is a tiny (4-6.5 g) passerine endemic to the semi-arid zone of south-eastern Australia (Higgins et al., 2001, BirdLife International 2008, Chapter 2). The semi-arid zone is dominated by fire-prone shrublands, consisting of multi-stemmed Eucalyptus spp., often having an understorey association of hummock grass (Triodia scariosa, hereafter referred to as Triodia) (Specht 1981, Hill 1989, Parkes and Cheal 1990). Hummock grasses (Triodia and Plectrachne spp.) are slow growing, long-lived, dense, hummock-
forming perennials that mature in size at about 15-30 years following fire (Bradstock and Gill 1993, Chapter 3). They are comprised of evergreen blades, which are tightly rolled and hard, tapering to rigid, needle-like points (Lazarides, 1970). The Mallee Emu-wren depends on mature growth phases of hummock grasses (Fig. 3.3, Chapter 3) and is known to forage and nest within *Triodia* (Rowley and Russell 1987, Higgins et al. 2001). Hummock grasses provide many small vertebrates with micro-sites for foraging, protection from predation and thermal buffering from the harsh temperature extremes of the semi-arid and arid zones of Australia (Cogger 1974, Bos et al. 2002, Bos and Carthew 2003, Haythornthwaite 2005, Gordon et al. 2010). *Triodia* hummocks may provide similar resource benefits for the Mallee Emu-wren.

The aim of this study was to understand the biophysical variables and behavioural decisions that explain micro-scale habitat selection by Mallee Emu-wrens in long-unburnt vegetation dominated by *Triodia*. Long-unburnt mallee (>35 years) contains mixed age-classes of *Triodia* (Chapter 3), allowing a test of whether individuals select or avoid specific structural attributes (i.e. growth-stages of hummocks) for important life history activities including foraging, movement and display.

### 4.3 Materials and Method

#### 4.3.1 Study Site

A population of the Mallee Emu-wren was studied at a 900 ha site in Hattah-Kulkyne National Park (34°41’S, 142°16’E), in south-eastern Australia. The region has a semi-arid climate, with hot dry summers and mild winters. Mean annual rainfall is 334 mm with most precipitation occurring during the period April to October (Australian Bureau of Meteorology, 2010). The vegetation at the site is comprised of mallee woodland dominated by 4-5 m tall *Eucalyptus* spp. with an understorey dominated by mixed fire-age classes of the hummock grass *Triodia scariosa* and sparse scattered *Melaleuca* and *Callitris* shrubs.

#### 4.3.2 Microhabitat selection by the Mallee Emu-wren

Twenty-six sites, each 9 ha (300 m x 300 m), were randomly sampled from a grid within the 900 ha study area and were used to observe independent groups of Mallee Emu-wrens. Observations of colour-banded individuals showed that breeding pairs of Mallee Emu-wrens had a territory size of about 5 ha in this particular habitat (S.
Brown, unpublished data), and consequently 9 ha was considered sufficiently large such that no single group of birds was likely to be sampled more than once.

Observations and tracking of groups commenced either at dawn or late afternoon and usually ceased when birds were lost, or when settling down as dusk approached. Groups of Mallee Emu-wrens were located by playback recording of contact and alarm calls (©David Stewart/Nature Sound) played through an MP3 player and amplified speaker system. Once located, groups initially were followed from a distance of 25-30 m for 5-15 min until they became accustomed to the observer and settled into a constant rate of movement. Once settled, observations were made from 15-30 m, though generally a distance of 15-20 m was maintained. During short periods of 1-5 mins, the consecutive Triodia hummocks that were visited by a randomly selected individual within the group (disregarding the first hummock in the sequence) were colour flagged for later measurement, and the associated activity of the individual was recorded.

Mallee Emu-wrens were recorded using Triodia hummocks for three main activities; i) foraging, ii) vocalisation, and iii) as a stepping stone for movement (see Table 4.1 for description of activities). Other activities, including preening, attack by sympatric species and perching, were also recorded. When an individual was observed to occupy a Triodia hummock for >3 seconds, it was presumed to be for foraging. Typically, the individual was out of sight within the hummock. From extensive observations of Mallee Emu-wrens, I occasionally observed individuals foraging on the lower 1 m branches of eucalypts, Callitris spp. and on the ground, but such observations were very infrequent compared with the proportion of time spent within Triodia hummocks. From these observations, when Mallee Emu-wrens occupied Triodia hummocks, it was assumed to be primarily for foraging.

Triodia is characterised by a distinctive growth-phase pattern (Fig. 3.3, Chapter 3). Immature plants are similar in structure to large grass hummocks; but as a plant matures, it forms a large concentric ring (many metres wide) with matted dead material or bare ground in the centre (Specht 1981a). The study site contained Triodia hummocks of different growth-phases and, as such, it was assumed that Mallee Emu-wrens had equal access to different Triodia growth-phases. Each Triodia hummock visited by an individual was assigned a growth-phase according to its diameter at the
widest point and whether it had an internal ring (Fig. 3.3 Chapter 3, Table 4.2). Senescing *Triodia* hummocks can maintain their structural integrity, even with only a few tillers producing new green shoots. A value of the condition of each plant was determined by estimating the proportion of green shoots on tillers (0-100%) at 10% increments (Table 4.2).

**Table 4.1** Description of the behavioural activities of Mallee Emu-wrens recorded for this study.

<table>
<thead>
<tr>
<th>Activity</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Foraging</td>
<td>Observed foraging on upper stalks, or entering the <em>Triodia</em> hummock for &gt; 3 seconds (presumed to be foraging)</td>
</tr>
<tr>
<td>Vocalising</td>
<td>Perches on upper stalks of a hummock and vocalises</td>
</tr>
<tr>
<td>Stepping stone</td>
<td>Lands briefly on a <em>Triodia</em> hummock and then moves on to another location (i.e. did not enter the hummock, and was not observed foraging or vocalising)</td>
</tr>
</tbody>
</table>

**Table 4.2** Variables measured pertaining to *Triodia* hummocks in the study area. The growth-phases are based on the measurements described in Fig. 3.3, Chapter 3.

<table>
<thead>
<tr>
<th><em>Triodia</em></th>
<th>Measurement (diameter m)</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Growth-phase</td>
<td>T1 0.25-0.49 m</td>
<td>Small, emerging plant</td>
</tr>
<tr>
<td></td>
<td>T2 0.5-0.99 m</td>
<td>Juvenile, no collapse at centre of plant</td>
</tr>
<tr>
<td></td>
<td>T3 1.0-2.0 m</td>
<td>Mature, with or without start of collapse of centre</td>
</tr>
<tr>
<td></td>
<td>T4 0.5-7.0 m</td>
<td>Mature, concentric ring configuration</td>
</tr>
<tr>
<td>Volume</td>
<td>m³</td>
<td>A spherical cap or half torus</td>
</tr>
<tr>
<td>Diameter</td>
<td>m</td>
<td>Diameter of <em>Triodia</em></td>
</tr>
<tr>
<td>Condition</td>
<td>0-100</td>
<td>Percentage of green shoots on the plant</td>
</tr>
</tbody>
</table>
Measurements of *Triodia* hummocks also were made to represent the available population of plants in the study site. All *Triodia* hummocks touching a 30 m tape randomly placed at the site were measured for the same variables as described above. These were taken within 100 m of tracked birds, to ensure that territorial boundaries did not prohibit the availability of randomly selected *Triodia* hummocks.

4.3.3 Composition and mass of invertebrates

Emu-wrens are thought to be insectivorous (Schodde 1990, Higgins et al. 2001) and the closely allied Southern Emu-wren *S. maluridae* has been shown to preferentially feed its offspring with Lepidoptera, Diptera and larvae (Maguire 2006b). Different-sized *Triodia* hummocks were therefore selected for a survey of insect composition and mass to determine if Mallee Emu-wrens made selection decisions that may positively influence individual fitness and reproductive success. Mallee Emu-wrens have been observed to consume a similar range of invertebrates to that of Southern Emu-wrens, although notably ants and termites do not appear to be eaten (S Brown, pers. obs.). Thus, assessment of potential prey focused on sampling all invertebrates excluding ants and termites.

During early summer (December), invertebrates were collected by pitfall traps from *Triodia* hummocks representing three growth-phases. A 6 cm diameter, 100 ml plastic cup filled with car cooling fluid containing ethylene glycol (to minimise evaporation), was placed on the ground within each *Triodia* hummock. All hummocks selected were matched for slope, aspect, size and individual density. The growth-phases included; i) medium-sized *Triodia* hummocks (T2, n=8), ii) large *Triodia* hummocks (T3, n=8), iii) *Triodia* hummocks with a concentric ring (T4, n=8), and iv) under canopy vegetation (not in a *Triodia* hummock)(n=8). Cups were left open for 15 days and topped with additional fluid as required. Invertebrates were transferred to 70% alcohol for later sorting to family or genera. The total numbers of individual invertebrates and their length (mm) were calculated for each *Triodia* hummock. A sub-set of the medium-sized and large *Triodia* hummocks (each n=5), were those selected to measure the microclimate (see below).
4.3.4 Microclimate in mallee vegetation

Temperature data were collected from mallee micro-sites to determine whether micro-habitat conditions within *Triodia* were related to invertebrate productivity or potentially provided thermally favourable sites for the Mallee Emu-wren. Invertebrates are especially sensitive to temperature and humidity (Huey 1991; White 2008, Savilaakso et al. 2009) and the thermal consequences on invertebrate diversity and abundance may be conspicuous.

Twenty-two ibutton® temperature data loggers (MAXIM, Dallas Semiconductor: Thermochron, -40-85°C (±0.5°C accuracy)) were deployed from mid-August 2007 to late-December 2007 (Austral late winter to early summer) to measure the microclimate associated with *Triodia* hummocks. Temperature data loggers were placed in four kinds of micro-habitats: i) in large *Triodia* (T3 growth-phase, volume >0.25 m³), ii) in medium-size *Triodia* (T2 growth-phase, volume 0.15-0.25 m³), iii) in ambient conditions (under-canopy, south-facing at the base of a tree, but not in a *Triodia* hummock) and (iv) in open habitat (not under canopy vegetation or in a *Triodia* hummock). Eight replicate samples were selected for each of the *Triodia* growth-phases and three replicates for the ambient conditions and open habitat treatments.

Topography can influence habitat microclimate (Suggitt et al. 2011) and so to minimise the interaction of topography and the different densities of *Triodia* plants, all loggers were matched as closely as possible for canopy, slope, aspect and the density of *Triodia* hummocks. The data loggers were placed 5 cm above the ground surface and, where appropriate, in the centre of each individual plant. Data loggers placed in the open habitat were protected from direct insolation by a north-facing white hood. Temperature loggers placed in ambient conditions, were protected from direct insolation by the trunk of the tree. The temperature was simultaneously recorded by each ibutton® every two hours, providing 12 daily temperature readings for 123 consecutive days.

4.3.5 Statistical analysis

To test whether Mallee Emu-wrens selected *Triodia* hummocks randomly for one of the specified behaviours, a Welsh two-sample t-test (t-test for unequal variances) was employed. The independent variables compared for each behavioural activity were
Triodia hummock volume, diameter, and the proportion of green shoots on trillers. The volume of Triodia hummocks was log-transformed to meet the assumptions of normality. Chi-squared test was used to test the null hypothesis that Mallee Emu-wrens use the four Triodia growth-phases randomly for each of the specified behaviours.

To summarise the microclimate, three bioclimatic variables were derived from the temperature time-series data. The maximum (Tmax), minimum (Tmin) and range (Trange) of temperatures were determined for each day. These temperatures were selected to represent ecologically important or physiologically limiting variables commonly applied to a range of taxa in bioclimatic studies (Thuiller et al. 2006b, Preston et al. 2008). Daily mean values and 95% confidence intervals of the bioclimatic variables were calculated for the four kinds of micro-habitat and graphed. To display intra-day temperatures, mean values and 95% confidence intervals of two hourly intervals over 48 hours were calculated for each of the four kinds of microhabitats. These were calculated for days representing maximum and minimum temperatures recorded during the study period. All statistical analyses were carried out using the R package (R Core Development Team, 2006).

Due to the low number of invertebrates collected from sampling in Triodia hummocks and the degradation of some samples, it was not possible to conduct reliable statistical tests. Therefore, a qualitative description of the insect survey data is presented and discussed.

4.4 Results

4.4.1 Microhabitat selection by the Mallee Emu-wren

Nineteen independent groups of Mallee Emu-wrens were detected and observed, comprising 1 to 4 individuals, all of which were adult males or females. Twenty-six sets of observations were made, each representing a single bird visiting a consecutive sequence of between 2-41 Triodia hummocks (n=387 observations, n=434 activities recorded). Measurements of Triodia hummocks (n=305) were made from 18 randomly located transects to represent the relative proportions of Triodia growth-phases available to the birds (Table 4.3).
Table 4.3 The three major behavioural activities undertaken by the Mallee Emu-wren and the number of *Triodia* hummocks measured.

<table>
<thead>
<tr>
<th>Activity</th>
<th>Vocalising</th>
<th>Stepping stone</th>
<th>Foraging</th>
<th>No. <em>Triodia</em> hummocks</th>
</tr>
</thead>
<tbody>
<tr>
<td>Selected <em>Triodia</em></td>
<td>44</td>
<td>48</td>
<td>342</td>
<td>387</td>
</tr>
<tr>
<td>Available <em>Triodia</em></td>
<td></td>
<td></td>
<td></td>
<td>305</td>
</tr>
</tbody>
</table>

The range of activities undertaken by birds included foraging, vocalising, and using *Triodia* hummocks as a stepping stone for movement, for perching, for preening, and for protection from attacking Yellow plumed Honeyeaters *Lichenostomus ornatus*. On occasions, birds were observed using the same *Triodia* hummock for multiple activities such as foraging and vocalising.

Mallee Emu-wrens favoured the mature growth-phase *Triodia* (T3) over all other growth-phases and were never observed using the small emergent *Triodia* hummocks (T1) (Fig. 4.2). A comparison between the growth-phases of *Triodia* hummocks used by Mallee Emu-wrens and those randomly available in the environment showed that individuals were highly selective of particular growth-phases for foraging, vocalising and use as a stepping-stone (Chi-squared tests: $\chi^2 = 297.24, p<0.0001; \chi^2 = 62.71, p<0.0001; \chi^2 = 31.55, p<0.0001$, respectively).

Mallee Emu-wrens selected particular *Triodia* hummocks for different behavioural activities with respect to the volume of the hummock and the proportion of green shoots, but not with respect to the diameter (Table 4.4). The volume of individual *Triodia* hummocks influenced their use by Mallee Emu-wrens for foraging, vocalising and use as a stepping stone. Hummocks with greater volume were favoured over smaller hummocks for each of these three activities. *Triodia* hummocks with a higher proportion of green shoots were favoured for foraging (Table 4.4).
Figure 4.2 The proportion of *Triodia* hummocks of different growth-phases used by Mallee Emu-wrens for three behavioural activities; foraging, vocalising and use as a stepping stone for movement; and the proportions of each growth phase available in the environment.

Table 4.4 Results from Welsh two sample t-test (for non-equal variances) comparing the attributes of *Triodia* hummocks used for different behavioural activities with those available in their environment.

<table>
<thead>
<tr>
<th>Activity</th>
<th>Volume of <em>Triodia</em></th>
<th>Proportion of green shoots</th>
<th>Diameter of <em>Triodia</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Vocalising</td>
<td>$p \leq 0.0001$</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>Stepping stone</td>
<td>$p = 0.0016$</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>Foraging</td>
<td>$p \leq 0.0001$</td>
<td>$p = 0.0005$</td>
<td>n.s.</td>
</tr>
<tr>
<td>All behaviours</td>
<td>$p \leq 0.0001$</td>
<td>$p = 0.0004$</td>
<td>n.s.</td>
</tr>
</tbody>
</table>

4.4.2 Composition and mass of invertebrates

Twenty-one of the 40 samples of invertebrates collected in the cups were degraded and unusable because of the partial evaporation of the preservative in which they were stored in the unusually hot temperatures at the time of collection. Only 95 arthropods in total (excluding ants and termites) were collected in the remaining 19 cups. The data were too few to be able to make quantitative comparisons of the diversity or abundance of invertebrates between *Triodia* growth-phases. Despite the weaknesses of the data, they provide an insight to the composition of invertebrates occurring in *Triodia*. Four Orders of arthropods (Arachnida, Diplopoda, Insecta and Enthognatha), comprised of 11 Families were collected. The most common were Arachnida (19%) and
Insecta (73%). The latter were mainly Hemiptera (17%) and Diptera (13%). Notably, 85\% of specimens were only 1 or 2 mm in length.

4.4.3 Microclimate in mallee vegetation

A number of ibutton data loggers failed, so the number of replicates for each of the four micro-habitats varied. Temperature ranges within the four treatments over the period studied (August to December) were as follows; i) medium-sized Triodia -2.9 to 55.1°C (n=6), ii) large Triodia -3.4°C to 51.1°C (n=7), iii) ambient condition -3.4 to 48.6°C, (n=1) and iv) open habitat -3.4 to 54°C (n=2).

Triodia hummocks had very modest effects in ameliorating temperatures compared with those recorded in open habitat, with the strength of the effect varying depending on the bioclimatic variable and the time of the day (Figs. 4.3 & 4.4). Triodia principally moderated the temperature maxima (Fig. 4.3a) and the amplitude of temperature ranges (Fig. 4.3c). Specifically, open habitat showed consistently greater temperature maxima than the ambient condition and the temperature within Triodia hummocks (Fig.4.3a). Conversely, Triodia hummocks had greater temperature minima than open habitat, though this effect was subtle (Fig. 4.3b). The greatest daily range in temperature was for the open habitat, with the highest values generally during spring when night temperatures can be below zero and day time temperatures can be very warm (Fig. 4.3c). There was little variation between the medium-sized and the large Triodia hummocks (Figs. 4.3 & 4.4).

An examination of the intra-day temperatures (Figs. 4.4 a & b) showed that temperatures within Triodia hummocks closely track open habitat temperatures. The lag in Triodia hummock temperatures compared with ambient condition and open habitat temperatures is a result of the reduced flux of ingoing and outgoing radiation. Consequently, Triodia hummock temperatures are warmer than ambient conditions and open habitat during late evenings and early mornings. During early morning, temperatures in Triodia are less than five degrees Celsius warmer compared to open habitat temperatures (Figs. 4.3b and 4.4b). The coldest temperature recorded during the August to December period was -3.4°C in open habitat and in a large-sized Triodia hummock. However, temperature minima within an annual cycle can be considerably colder; a pilot trial of the ibuttons in the coolest month (July) recorded minima of -7.5°C in open habitat and -6.4°C in Triodia hummocks.
Figure 4.3a Daily maximum temperature across 123 days from August 23 to December 23. Mean temperatures and 95% confidence intervals are for large *Tridactylus n.* 7 (---), medium-size *Tridactylus n.* 6 (---), ambient conditions n=1 (---), and open habitat n=2 (---).
Figure 4.3b Daily minimum temperature across 123 days from August 23 to December 23. Mean temperatures and 95% confidence intervals for; large *Triodia* n=7 (---), medium-size *Triodia* n=6 (----), ambient conditions n=1 (-----) and open habitat n=2 (-----)
Figure 4.3c Daily temperature range across 123 days from August 23 to December 23. Mean temperature ranges and 95% confidence intervals for; large *Triodia* n=7 (●), medium-size *Triodia* n=6 (▲), ambient conditions n=1 (●) and open habitat n=2 (★).
Figure 4.4 a & b Intra-day temperature data over 48 hours for a) temperature maxima (November 18-19) and b) temperature minima (August 15-16) recorded through the study period. Means and 95% confidence intervals for; large *Triodia* n=7 (---), medium-size *Triodia* n=6 (---), ambient conditions n=1 (---) and open habitat n=2 (---).
4.5 Discussion

4.5.1 Selection of Triodia hummocks

Analysis of the structural attributes of almost 700 Triodia hummocks, of which 390 were associated with specific behaviours of Mallee Emu-wrens, highlighted several key attributes of Triodia hummocks important to this species. Mallee Emu-wrens prefer Triodia hummocks that are of a mature growth-phase and have a large volume; and for foraging, those that have the greatest proportion of green shoots (Table 4.4). This finding supports earlier work on fine-scale habitat selection that demonstrated that Mallee Emu-wrens prefer habitat containing high densities of mature growth-phases of Triodia of large volume (Chapter 3), but it suggests an additional element – the condition of the Triodia hummock plays a specific role in foraging. There are several possibilities, neither of which are mutually exclusive, that may explain why this selection strategy has evolved.

The preference for Triodia hummocks of a relatively large volume is consistent with carrying out activities within, or close to, cover as a predator avoidance strategy. Many small birds forage, communicate and carry out other vital life-history activities in micro-habitats that confer relatively greater concealment from predators (Grubb and Greenwald 1982, Carrascal and Alonso 2006, Campos et al. 2009), or whilst within close range of refugia (Lima 1985, Walther and Gosler 2001, Lee et al. 2005). The perceived risk of predation is such that foraging in micro-habitats that provide protection from predators is often at the expense of greater energetic gains that could be obtained elsewhere (Grubb and Greenwald 1982, Walther and Gosler 2001). Their tiny size and poor flying ability makes the Mallee Emu-wren particularly vulnerable to attack. For example, an individual Mallee Emu-wren was observed to be attacked up to 10 times per hour by aggressive Yellow-plumed Honeyeaters (S Brown, unpublished data). The importance of the cover of Triodia in determining habitat use (Chapter 3), suggests that protection from predators is a major concern for the Mallee Emu-wren. Triodia provides an effective form of protection because its dense and needle-like foliage is difficult for larger animals to penetrate. The importance of hummock grasses as protection against predators has also been suggested for other taxa (Cogger 1974, Haythornthwaite and Dickman 2000).
Chapter 4 Microhabitat selection

The greener *Triodia* hummocks preferred for foraging by the Mallee Emu-wren also suggest that in terms of costs and benefits, it is more energetically profitable to forage selectively for invertebrates within these plants. The growth of hummock grasses is dependent on the availability of soil moisture. Hummock grasses become dormant when soil moisture is exhausted (Lazarides 1970), thus *Triodia* hummocks with a higher proportion of green shoots most likely reflect micro-habitats of comparatively higher humidity. Invertebrates are particularly sensitive to micro-climatic conditions (Willmer 1982, Huey 1991) and occur in relatively greater abundance in micro-climates of higher humidity (Langlands et al. 2006, Savilaakso et al. 2009). Given this, presumably greener hummocks provide comparatively more favourable micro-niches for invertebrates than senescing hummocks in terms of susceptibility to desiccation, substrate to live on and available food.

Selection may operate strongly on the birds' ability to forage efficiently, in this instance by selecting *Triodia* hummocks that are more likely to support abundant invertebrates. Passerines have among the highest metabolic rates of any group of vertebrates (Dawson and Hulbert 1970, Nagy et al. 1999) and need to forage intensively to meet daily metabolic requirements (Gibb 1954). Small passerines have a high mass-specific rate of energy expenditure and a limited capacity to store energy (Gibbs 1954, Brodin 2007), and as such have elevated energetic requirements during cold periods and following overnight fasting (Buttemer 1985). At about 4-6.5 g, the Mallee Emu-wren is one of the world's smallest birds, placing them at the extreme spectrum of these physiological requirements. Moreover, the Mallee Emu-wren requires invertebrates as a source of water (Redford and Dorea 1984) to counterbalance evaporative water loss (Wolf and Wlasberg 1996a) during hot, dry spells that are characteristic of the semi-arid zone. So as to meet their metabolic requirements, the Mallee Emu-wren would predictably need to forage intensively. Observations of free-ranging Mallee Emu-wrens found that they forage for most of the day and a non-breeding individual may consume up to 69% of its body weight in 1.5 hours during early morning foraging (S Brown, unpublished data, inferred from a mass increase from 4.05 to 6.75 g). Indeed, aggressive engagement between territorial individuals is frequently interrupted by foraging (S Brown, pers. obs.) such that feeding takes priority over aggression. These observations are consistent with studies on the energetic requirements of several species of Maluridae that show they consume
about their own body weight of invertebrates daily, and double this when feeding young (Tidemann and Schodde 1989).

Given their high energetic requirement and the need to counterbalance evaporative water loss, a shortfall in food would place Mallee Emu-wrens at imminent risk of death from starvation or dehydration. Furthermore, the availability of invertebrates for food influences the fecundity of small insectivorous passerines (Pearce-Higgins and Yalden 2004, Lindstrom et al. 2005, Nagy and Holes 2005, Granbom and Smith 2006) and the growth rate, weight and survival of fledglings (Buse et al. 1999, Visser et al. 2006), resulting in significant effects on reproductive success (Jones 1987, Zannette et al. 2000). However, in the absence of individual foraging patterns and life-history information, in this study it is not possible to determine whether this selective choice has any bearing on reproductive success (Fisher 1958, Jones 2001) and hence whether this choice is in fact adaptive.

4.5.2 Thermal properties of Triodia

Mallee Emu-wrens may derive some thermal benefit from Triodia hummocks relative to more open habitat. Thermal factors such as solar radiation, wind and temperature can have significant impacts on the micro-habitat distribution of birds (Buttemer 1985, Grubb and Pravosudov 1994, Merola-Zwartjes 1998) as birds seek to optimise energy budgets (Walsberg 1985, Walsberg 1993, Wolf and Walsberg 1996a and b, Wolf et al. 1996). Living in an environment with extreme temperatures, Mallee Emu-wrens are likely to select micro-sites to maximise thermoregulatory considerations and minimise evaporative water loss (Walsberg 1985, 1986, Wolf et al. 1996, Merola-Zwartjes 1998). However, this study found limited amelioration of temperatures within Triodia hummocks compared with open habitat, providing little support for a hypothesis of strong thermal advantages. Nevertheless, benefits derived from foraging within the cover of Triodia hummocks may be the reduction in water loss through evapotranspiration in summer and, during cold periods, thermal benefits could be derived from being less exposed to wind (Wolf and Walsberg 1996b). Wind-chill greatly reduces the thermal properties of feathers and therefore increases the energetic requirements of birds (Buttemer 1985, Wolf and Walsberg 1996a and b). A tiny bird with poor insulation from feathers would be particularly vulnerable to convective heat loss by wind. Triodia hummocks are dense and, being located at
ground level, would provide considerable protection from the wind. The lag in temperature changes in *Triodia* compared to open habitat (Figs. 4.3 a & b), indicate properties consistent with reduced convective exchange of air.

### 4.5.3 Diversity and mass of invertebrates

This study confirms others (Land Conservation Council 1987, Greenslade and Greenslade 1989, Gordon et al. 2010) that demonstrate a wide range of invertebrates are associated with *Triodia* hummocks and thus are potentially available to Mallee Emu-wrens as potential prey. Invertebrates collected in *Triodia* hummocks included taxa favoured by nesting adult Southern Emu-wrens, such as Hemiptera, Diptera, Coleoptera, Lepidoptera and larvae (Maguire 2006b); and presumably these also form a major component of the diet of the Mallee Emu-wren. Notably, the size of most invertebrates collected was small (2 mm or less).

Unfortunately, the paucity of invertebrates precluded testing for a correlation between invertebrate productivity, bioclimatic variables and different growth-phases of *Triodia*, and hence any relationship with selection of *Triodia* hummocks by Mallee Emu-wrens.

### 4.5.4 Conclusion

The preference for specific attributes of *Triodia* hummocks by the Mallee Emu-wren is consistent with predator avoidance strategies (Grubb and Greenwald 1982, Sih 1980). *Triodia* hummocks are a critical resource for the Mallee Emu-wren; specifically, by providing a combination of protection from attack and predation, a substrate for the invertebrates on which they forage, nesting sites, and possibly some thermal advantages. Examination of the mallee microclimate found temperatures in microhabitats used by the Mallee Emu-wren can fluctuate as much as 60°C over an annual cycle and 40°C within a 24 hour period. The magnitude of these micro-habitat temperatures suggest that the Mallee Emu-wren and their prey are subject to acute physiological demands. Given their high metabolic requirements, the Mallee Emu-wren is particularly vulnerable to reduced productivity of invertebrates potentially associated with drought, and hence may be sensitive to increasing aridity associated with future climate warming.
Panmixia, genetic drift and bottlenecks characterise an endangered bird species in a dynamic, fire-prone ecosystem

Figure 5.1 Satellite imagery of the major reserves of north-east Victoria, showing fire footprints.
5.1 Abstract

Fire is a major cause of disturbance in many ecosystems world-wide, resulting in spatially and temporally dynamic landscapes. The effects of fire-induced landscape change on population recovery processes and the genetic patterns and structure among populations occupying such environments is poorly known. The Mallee Emu-wren Stipiturus mallee is a globally endangered passerine that occurs in fire-prone, semi-arid mallee shrublands in south-eastern Australia. This sedentary species has recently undergone a precipitous decline in distribution and numbers in recent decades due to large fires and prolonged drought. Genetic analyses of partial sequences of ND2 mtDNA and of twelve hypervariable nuclear loci were used to examine population structure and processes within this species. Populations of the Mallee Emu-wren exhibited a low to moderate level of genetic diversity, and evidence of genetic drift and bottlenecks. Fine-scale spatial autocorrelation analyses found non-random genetic structure at less than 2 km, most likely reflecting local kin associations. Bayesian clustering methods revealed weak genetic population structure across the species’ global range. These findings are inferred to be a consequence of both low to moderate genetic variability inherited from an evolutionary ancestor and contemporary metapopulation processes. Spatial and temporal patterns of fire in mallee ecosystems result in population bottlenecks, serial local extinctions and subsequent recolonisation, all of which interact to erode genetic diversity in this species. Movement among temporally and spatially shifting habitat, mediated by fire, appears to maintain long-term genetic connectivity. A plausible explanation for the observed genetic patterns is that recolonisation by founders, rather than in-situ survival is the prominent driver of population recovery and metapopulation processes for this species. These findings suggest that for species occupying highly dynamic landscapes, the spatial characteristics of refugia and the habitat mosaic may have profound demographic and genetic consequences.
5.2 Introduction


The effects of fire-induced landscape change on ecological and population processes are complex, and major gaps remain in our knowledge (Whelan 1995, Clarke 2008, Driscoll et al. 2010). Fire directly reduces population size (Brooker 1998, Whelan et al. 2002, Banks et al. 2011) resulting in bottlenecks which can lead to the loss of genetic variation, inbreeding and the accumulation of deleterious alleles resulting inbreeding depression (Charlesworth and Charlesworth 1999, Frankham 2005). Changes in the spatial pattern of habitat resulting from fire can also increase the isolation of populations (Chapter 2) and alter the movement of animals between patches (Porter 1999, McDonough and Loughry 2005, Stow et al. 2007). Following disturbance, subsequent population recovery will be influenced by the number and demographic parameters of survivors (Brooker 1998, Sanz-Aguilar et al 2011), post-disturbance pathways (Turner et al. 1998, Whelan 1995), species dispersal ability (Fauvelot et al. 2006), life-history traits of species (Whelan et al. 2002, Sanz-Aguilar et al. 2011), and the geographic scale and patchiness at which the fire occurred (Whelan 1995, Whelan et al. 2002, Banks et al. 2011). Understanding the consequences of disturbance by fire for population processes is profoundly important for species' management in fire-prone environments to develop appropriate fire regimes (Whelan 1995, Whelan et al. 2002, Driscoll et al. 2010, Sanz-Aguilar et al. 2011), to assess the susceptibility of populations to extinction (Norris 2004, Sanz-Aguilar et al. 2011) and to mitigate potentially adverse effects of post-fire disturbance activities (Banks et al. 2011).
In this chapter, I present analyses of the genetic diversity and structure of a globally endangered bird species, the Mallee Emu-wren *Stipiturus mallee*. The Mallee Emu-wren is a tiny (4-6.5 g) habitat-specialist, endemic to the semi-arid zone of south-east Australia (Fig 5.2) (Higgins et al. 2001, Birdlife International 2008, Chapters 2 & 3). The semi-arid zone of south-east Australia encompasses extensive tracts of fire-prone 'mallee' vegetation dominated by *Eucalyptus* spp. Multi-scale studies of this species' habitat requirements show that its distribution is strongly influenced by the post-fire age of vegetation, as a consequence of seral changes in the structure of ground-storey hummock grasses (*Triodia scariosa*) on which it depends (Chapters 2, 3 & 4). There are no studies on dispersal for this species, however it has tiny rounded wings and is adapted to scurrying through dense hummock grass. As a consequence, it is a notoriously poor flyer, suggesting they have limited dispersal capability (Schodde 1982b, Rowley and Russell 1997).

In recent decades, the Mallee Emu-wren has undergone a precipitous decline in population numbers. Large wildfires (>100 000 ha), exacerbated by prevailing drought, have caused the extinction of populations in parts of the south-west of its range (Gates 2003, Chapter 2) and fire is considered a significant threat to remaining populations. Geographic range contraction has occurred such that the Murray-Sunset and Hattah-Kulkyne National Parks in northern Victoria now support an estimated 92% of the global population (Chapter 2). Small, scattered and isolated populations occur in South Australia in Billiatt and Ngarkat Conservation Parks (Chris Hedger, pers. comm.) and only one pair of birds was recorded in the Big Desert/Wyperfeld reserve complex in Victoria in 2006 (Chapter 2)(Fig. 5.2).

Twelve hypervariable nuclear loci and partial DNA sequence from the ND2 gene of mitochondrial DNA were used to examine genetic diversity and structure of the Mallee Emu-wren. My first objective was to examine spatial genetic patterns among populations across the species' range to draw inferences about population structure and process. A second objective was to address a broader question; whether the dynamic characteristics of fire-prone mallee ecosystems have consequences for genetic processes in this species, which may affect its long-term persistence? If so, such a finding may have far reaching conservation implications for the management of other species that also occupy fire-prone ecosystems.
Figure 5.2 Map of sampling localities within the conservation reserve system of the Murray Mallee region, south-east Australia. Numbered ellipses indicate sites where Mallee Emu-wrens were sampled. 1 Hattah-Kulkyne National Park (NP), 2 Murray-Sunset NP (East), 3 Murray-Sunset NP (Central), 4 Murray Sunset NP (West), 5 Murray Sunset NP (South) and 6 Ngarkat Conservation Park. The historic distribution is represented by light grey stippling (Higgins et al. 2001). Solid grey represents the reserve system in Victoria and South Australia. FFR = Fauna and Flora Reserve. New South Wales (N.S.W.), South Australia (S.A.) and Victoria (Vic.)

5.3 Materials and Methods

5.3.1 Study area and sample collection

Blood and feather samples were collected from 72 individuals from six locations across the range of the Mallee Emu-wren in south-eastern Australia (bounded by 34°50'S-36°00'S, 140°00'N-142°50'N). These included four locations from the Murray-Sunset
Chapter 5  Genetic diversity and population structure

National Park (n=10, 10, 12, and 6) and also from Hattah-Kulkyne National Park (n= 28) and Ngarkat Conservation Park (n=6) (Fig. 5.2, Table 5.1).

Long-term ecological and genetic studies on other species of the family Maluridae have shown that males are philopatric, and related males (e.g. brothers) have a tendency to occupy neighbouring territories (Rowley and Russell 1987). A preliminary population study of the Mallee Emu-wren in which individuals were individually banded showed that males occupied overlapping breeding territories of about 5 ha (S Brown, unpublished data). On this basis, samples for population analysis, which typically consisted of samples from male/female pairs, were collected at minimum intervals of 500 m to prevent non-random sampling (i.e. sampling of related individuals).

Mallee Emu-wrens were captured either by trapping in micro-filament mist nets, or by throw nets (Appendix I) after being lured by playback recording of both contact and alarm calls (©David Stewart/Nature Sound). Between 10 and 100μl of blood was collected from the brachial vein, or a single pin feather was removed and stored in 70% molecular grade alcohol, for subsequent extraction of DNA and genetic analyses.

5.3.2  Gene selection and PCR

Whole genomic DNA was extracted from samples using a standard ethanol/chloroform extraction method (Sambrook et al. 2001). Samples were genotyped at 12 hyper-variable nuclear loci. Eleven microsatellites were amplified using primers developed for the Splendid Fairy-wren Malurus splendens (Webster et al. 2004), Superb Fairy-wren M. cyaneus (Double et al. 1997), Southern Emu-wren Stipiturus malurus (including a putative sex-linked marker, Smm4) (Maguire and Mulder 2008). A single locus was amplified from the Exon-Primed-Intron-Crossing (EPIC) region (Backström et al. 2008). Primers for the EPIC loci were re-designed so that the product could be run on Li-Cor systems. Four of the seven microsatellite primer pairs from the Southern Emu-wren were re-designed so that two panels of microsatellite products could be run on an ABI® capillary system (Table 5.2). A 603 to 786 bp region of ND2 mitochondrial gene was sequenced from a sub-sample of individuals (n=27), representing all locations across the species’ range. Primers used were designed from published ND2 sequences for the Mallee Emu-wren (Driskell and Christidis 2004, Donnellan et al. 2009) (Table 5.2).
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PCR reactions for microsatellites and product separation were performed in two different laboratories. PCR reactions for each marker were optimised using the following: 20-40 ng of sample DNA, 0.5 Units Go Taq DNA polymerase, 5 X buffer, 0.25 mM dNTPs, 0.5- 4.5 mM MgCl₂ (Promega/MBI Fementas) and 5-10 pmol of each primer pair in a total volume of 20 μl. ND2 gene products were purified using Epoch purification filters (Epochbiolabs) and sequenced using the Big Dye DyeDeoxy Terminator sequencing method (Applied Biosystems). Microsatellite products were run on an ABI® Capillary Analyser (Perkin Elmer) or a Li-Cor 4200 and 4300 Global IR2 two-dye DNA sequencer for separation and sizing. Putative homozygotes were amplified and genotyped twice to confirm their status. Positive and negative controls were used in all reactions.

The 5′ and 3′ strands of the ND2 sequences were matched using the Sequence Navigator™ package. DNA sequences were verified as being from the Mallee Emu-wren by comparing them with DNA sequences of the Mallee Emu-wren and Rufous-crowned Emu-wren S. ruficeps obtained from the world-wide deposit of DNA sequences, National Center for Biotechnology Information (NCBI) using the BLAST option search. Sequences were verified not to be mtDNA psuedogenes by translating the DNA sequence to protein products, checking for the presence of nonsense codons, and using the BLASTp option search in NCBI. The BLAST options provide the nearest match, given as a percentage. All sequences were aligned using CLUSTAL W (Thompson et al. 1994) and a 603 bp region was used for analysis.

5.3.3  ND2 diversity and phylogenetic analysis

Partial ND2 sequences from the Mallee Emu-wren which represented two different haplotypes were obtained for comparison with samples used in this study (Driskell and Christidis 2004, AY488328; Donnellan et al. 2009, EF621352). Four haplotypes of partial ND2 sequences from the Rufous-crowned Emu-wren and one from the Southern Emu-wren were included as outliers (Donnellan et al. 2009, EF621350-51, EF621353-56). Estimates of nucleotide diversity (π) were calculated following Nei (1998). To examine the phylogenetic relationship among haplotypes, maximum likelihood (ML) and maximum parsimony (MP) analyses of aligned sequences were performed in PAUP* V4.10b10 (Swofford 1999). Maximum likelihood and maximum parsimony analyses used heuristic searches with 1000 random addition sequences.
Maximum likelihood analysis was performed by using a step-wise addition model, estimating the transition to transversion ratios from the data.

5.3.4 Genetic diversity of microsatellites

Standard measures of genetic diversity for microsatellite markers were obtained in various programs, treating the six geographic locations as separate populations. **GENALEX** V6.0 (Peakall and Smouse 2006) was used to calculate observed (Ho) and unbiased expected heterozygosity (UHe). Allelic richness (AR) and inbreeding coefficient (FIS) was calculated in **FSTAT** 2.9.3.2 (Goudet 2001). Linkage equilibrium and conformance to Hardy-Weinberg expectations was tested using **GENEPOL** V4.0 (Raymond and Rousset 1995).

Genetic differentiation for each population pair was determined by two methods. First, levels of genic differentiation were assessed by Fishers exact test and the F-statistic estimator **F_{ST}** by using **GENEPOL** V4.0 (Raymond and Rousset 1995). However, **F_{ST}** may yield an underestimation or non-detection of genetic differentiation of highly variable loci (e.g. microsatellites) (Hedrick 2005, Jost 2008). Therefore, a second method also employed was a measure of actual differentiation **D**, corrected for small samples (**D_{act}**) (Jost 2008). **D** has been demonstrated to be a more sensitive measure of genetic differentiation, by partitioning allelic diversity into independent within- and between-subpopulation components (Jost 2008, Gerlach et al. 2010). **D** values range from zero to one, with zero indicating no differentiation and one representing maximum differentiation (Jost 2008). **D_{act}** was calculated using the DEMETICS package in R (R Development Core Team 2009).

5.3.5 Bottleneck analysis

Two methods were implemented in the program **BOTTLENECK** V1.2.03 (Piry et al. 1999) to ascertain whether historic declines in population size have occurred in the Mallee Emu-wren. The first test implemented is based on the heterozygosity excess test (Cornuet and Luikart 1996). Populations that have recently experienced a bottleneck lose relatively more allelic diversity than heterozygosity, relative to that expected if a population was at mutation-drift equilibrium (Cornuet and Luikart 1996). This hypothesis was assessed under a two-phase mutation model (TPM) in the program **BOTTLENECK** V1.2.03 (Piry et al. 1999). The TPM allows for mostly stepwise mutation (often assumed for microsatellites), but also a set proportion of multi-step
mutations. The proportion of stepwise mutations was set to 90% as recommended by Piry et al. (1999). Wilcoxon signed rank tests with 1000 iterations were used to determine the significance of heterozygosity excess. A second test available in BOTTLENECK is the allele frequency distribution test (Luikart and Cornuet 1998). This test examines the frequencies of all alleles in a population and compares this to the distribution expected at mutation-drift equilibrium, when rare alleles are numerous. At equilibrium the rarest allele class is expected to be more frequent than the second rarest class. A shift away from an L-shaped allele frequency distribution to one with fewer alleles in low frequency categories (a mode-shift), reflects instances where the rarest alleles have been rapidly lost in a population bottleneck (Luikart and Cornuet 1998, Luikart et al. 1998).

5.3.6 Population structure

Two Bayesian software packages were used to examine genetic population structure across the species’ global range, STRUCTURE 2.3.3 (Pritchard et al. 2000, Falush et al. 2003) and TESS 2.0 (François et al. 2006, Chen et al. 2007). Each of these methods estimates genetic structure based on different assumptions of theoretical inheritance and from multi-locus genotypes without assuming pre-defined populations.

STRUCTURE 2.3.3 (Pritchard et al. 2003, Falush et al. 2003) is a Bayesian clustering method that identifies the most likely number of genetically distinct clusters \((K)\) and probabilistically assigns individuals to them. The STRUCTURE analysis involves computing the posterior probability of \(K\), from multiple replicates of each value of \(K\) (Pritchard et al. 2000, Falush et al. 2003). The possible number of genetic clusters \((K)\) is set by the user. STRUCTURE was run using the admixture model (i.e. where a proportion of an individual genome has originated from population \(K\)) with correlated allele frequencies, and \(K\) values 1 to 10. Twenty replicate runs were performed for each \(K\) value. Each run was \(3 \times 10^5\) Markov Chain Monte Carlo (MCMC) repetitions following a burn-in period of \(10^5\) repetitions.

The second method implemented, TESS 2.0, is a spatial Bayesian clustering algorithm that includes information on individual geographical coordinates (François et al. 2006, Chen et al. 2007). TESS assumes \(K_{max}\) clusters and computes posterior estimates of membership coefficients or admixture proportions by updating spatially explicit prior distributions (François et al. 2006, Chen et al. 2007). This program has been shown to
be more powerful than non-spatial algorithms, especially in weakly differentiated populations (Chen et al. 2007, Durand et al. 2008). TESS was run using the CAR admixture model with spatial interaction parameter set at 0.6. One hundred replicate runs of 100 000 sweeps (disregarding the first 30 000) sweeps were performed for $K$ values 2 to 9. The Deviance Information Criterion (DIC) was used to select the model that best fitted the genetic data (Speigelhalter et al. 2002). DIC values averaged over 100 independent iterations were plotted against $K$, and $K$-values for which DIC first reached a plateau were selected. The 10 runs with the lowest DIC values for the selected $K$-values were retained and their admixture estimates were averaged using CLUMPP V 1.1.2 (Jakobsson and Rosenberg 2007), applying the greedy algorithm with random input order and 1000 permutations to align the runs and calculate $G’$ statistics. Results were visualised using DISTRUCTION 1.1 (Rosenberg 2004).

In addition to the Bayesian clustering methods, fine-scale spatial genetic structure was also investigated using multi-locus spatial autocorrelation analyses in GENALEX V6.41 (Peakall and Smouse 2006). The autocorrelation coefficient, $r$, estimates the genetic similarity between individuals within defined geographic distance classes. Individuals with missing data for a locus were assigned the most common genotype for that locus. Distance classes were set at 1 km, 2 km, 5 km, 10 km, 15 km, 20 km, 50 km, 150 km and 206 km. In addition, patterns of spatial autocorrelation were compared between males and females to test for sex-specific differences in autocorrelation. A sub-set of 27 individuals (females n=11, males n=16) sampled within 2 000 ha area of Hattah-Kulkyne National Park was tested following the method outlined in Smouse et al. (2008) using the same distance classes to 25 km. The calculated autocorrelation coefficients, $r$, were plotted as a function of distance class to produce spatial genetic auto-correlograms. Tests for significance were performed using two methods: random permutation and bootstrapping estimates of $r$, with the number of permutations and bootstraps set to 999 (Peakall et al. 2003).

The program GENECLASS 2 (Piry et al. 2004) was used to identify first generation likely migrants. The likelihood that the sampling site of an individual was its population of origin ($L_{homo}$) was determined using the Bayesian method of Rannala and Mountain (1997) with Monte-Carlo resampling algorithm (Paetkau et al. 2004). The simulation was run using 10 000 simulated individuals with a type I error set at 0.01.
Sex-biased dispersal for a sub-set of 24 individuals (females n=11, males n=13) sampled within a 2 000 ha area of Hattah-Kulkyne National Park was assessed for all loci using GENALEX V6.1 (Peakall and Smouse 2006). The program calculates an Assignment Index correction (AIC) for each individual and the mean of each sex. In this model, AIC values average zero for the total population, whilst negative values will characterise individuals with a higher probability of being immigrants (Peakall and Smouse 2006).

5.4 Results

5.4.1 ND2 diversity and phylogenetic analysis

No variation was found in the sequence of the ND2 gene for 27 individuals representing a sub-sample of the six populations, including one individual from the more isolated Ngarkat Conservation Park population (Fig. 5.2). The haplotype of the Mallee Emu-wren sequenced in this study is different to that of the same species originating from Hattah-Kulkyne National Park (Driskell and Christidis 2004), and to the haplotype described by Donnellan et al. (2009) originating from Ngarkat Conservation Park and Comet Bore, South Australia. Alignment of the three haplotypes showed that 10 of the 601 nucleotides were variable. Uncorrected sequence divergence for these three Mallee Emu-wren haplotypes (excluding the Rufous-crowned Emu-wren) was 0.06, suggesting little phylogenetic diversity within the Mallee Emu-wren.

The ND2 sequences for all three species of Emu-wren provided 61 parsimony-informative sites and 8 parsimony-uninformative sites. Analysis of the phylogenetic structure of the ND2 haplotypes of the Mallee Emu-wren and its relationship with the Rufous-crowned Emu-wren showed that both species are paraphyletic with respect to the Southern Emu-wren. A single tree was found for the maximum likelihood (ML) analysis (Fig 5.3), (log-likelihood = - 1165.45, ti/tv ratio = 4.95, kappa=9.95). Two equally parsimonious trees were found for the maximum parsimony (MP) analysis (not shown) with near identical topologies to the maximum likelihood tree.
Figure 5.3 Maximum Likelihood (ML) tree for the three species of Emu-wrens. SEW = Southern Emu-wren, RECEW (haplotypes T, U, V, W) = Rufous-crowned Emu-wren, MEW (haplotype S) = Mallee Emu-wren (Donnellan et al. 2009); MEW AY28 = Mallee Emu-wren (Driskell and Christidis 2004), and MEW B = this study.

5.4.2 Genetic diversity of microsatellites

The microsatellite marker Smm4 was confirmed to be sex-linked (i.e. females were hemizygotes) and therefore excluded from all subsequent analyses. $F_{is}$ values were positive and significant ($p=0.05$) for Hattah-Kulkyne National Park, with two loci (Smm1, Smm3) deviating significantly from Hardy-Weinberg expectations (homozygote excess). One locus (Mcy4) showed significant homozygote excess in the Murray Sunset (Central) sample (Table 5.1). Homozygote excess at a small number of loci may indicate the presence of null alleles; alleles that are not expressed or their product not detected (Pemberton et al. 1995). However, the detection of homozygote excess for more than one locus in the same population suggested that null alleles were probably not the cause. Furthermore, homozygote excess was not detected consistently across sampling locations. Homozygote excess observed for Hattah-
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Kulkyne National Park is most likely the result of the Wahlund effect, whereby deficit of heterozygotes in a population is a result of sub-population structure (e.g. presence of multiple breeding groups) (Wahlund 1928). Linkage disequilibria were not detected for any loci pairs, so physical linkage was unlikely.

Allelic diversity ($N_a$) was highly variable among loci, ranging from 2 to 32 alleles (Table 5.2). In general, the genetic diversity across all populations was moderate, based on microsatellite allelic richness (AR, range 2.92-3.83) and expected heterozygosity (UHe, range 0.43-0.52) (Table 5.1). With the exception of the Murray-Sunset (West) population, populations were monomorphic for a number of loci (Table 5.1), indicating fixation of alleles.

The two measures of population differentiation found two-thirds of the population pairs showed significant, but low, genetic differentiation. Results were consistent for most pairwise comparisons between the two methods (Table 5.3). Significant pairwise $F_{ST}$ values were low, ranging from 0.011-0.044. As expected, significant $D_{est}$ values were marginally higher, ranging from 0.077 - 0.179 (Table 5.3). The Ngarkat Conservation Park population showed the greatest level of population differentiation for both measures.
Table 5.1 Sample size (n), allelic richness (AR), observed (Ho) and expected heterozygosity (UHe) and inbreeding coefficient ($F_{IS}$) for 72 individuals of the Mallee Emu-wren from six locations across the species' global range. * $p=0.05$

<table>
<thead>
<tr>
<th>Population</th>
<th>n</th>
<th>AR</th>
<th>Ho</th>
<th>UHe</th>
<th>$F_{IS}$</th>
<th>H-W disequilibrium</th>
<th>Monomorphic loci</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hattah-Kulkyne NP</td>
<td>28</td>
<td>3.57</td>
<td>0.41</td>
<td>0.46</td>
<td>0.124*</td>
<td>Smm1, Smm3</td>
<td>Msp6, Smm6, Smm7</td>
</tr>
<tr>
<td>Murray Sunset NP (East)</td>
<td>10</td>
<td>3.06</td>
<td>0.46</td>
<td>0.45</td>
<td>-0.038</td>
<td>Mcy7</td>
<td>Msp6, Smm6, Smm7</td>
</tr>
<tr>
<td>Murray Sunset NP (Central)</td>
<td>10</td>
<td>3.83</td>
<td>0.44</td>
<td>0.49</td>
<td>0.095</td>
<td>Mcy7</td>
<td>Smm6, Smm7</td>
</tr>
<tr>
<td>Murray Sunset NP (West)</td>
<td>12</td>
<td>3.80</td>
<td>0.53</td>
<td>0.52</td>
<td>-0.022</td>
<td>Mcym4</td>
<td>Mcym4</td>
</tr>
<tr>
<td>Murray Sunset NP (South)</td>
<td>6</td>
<td>3.50</td>
<td>0.43</td>
<td>0.47</td>
<td>0.094</td>
<td>Mcym4</td>
<td>Mcym4</td>
</tr>
<tr>
<td>Ngarkat Conservation Park</td>
<td>6</td>
<td>2.92</td>
<td>0.43</td>
<td>0.43</td>
<td>-0.094</td>
<td>Mcym4</td>
<td>Msp6, Smm6, Smm7</td>
</tr>
</tbody>
</table>
### Table 5.2: Nuclear loci and ND2 primer pairs used in this study and their characteristics. \( bp \) = allele size range, \( N_a \) = number of alleles.

<table>
<thead>
<tr>
<th>Locus</th>
<th>Reference</th>
<th>Accession No.</th>
<th>Primer Pair</th>
<th>( bp # )</th>
<th>( N_a )</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Microsatellites</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Smm1†</td>
<td>Maguire et al. 2006</td>
<td>DQ160181</td>
<td>5' TGGGAAATGCTCTATTCTCTGG 3' ACTCCAATGGACCTACCAAGC</td>
<td>274-330</td>
<td>15</td>
</tr>
<tr>
<td>Smm2</td>
<td></td>
<td>DQ160185</td>
<td>5' CCAAGACTGCAGCATCCTGCG 3' CACAGAGGAGCGTACACAGCG</td>
<td>203-398</td>
<td>26</td>
</tr>
<tr>
<td>Smm3</td>
<td></td>
<td>DQ160186</td>
<td>5' CATATGAAATGACGTGACGTGG 3' CATGACAGTGGAGTCTGG</td>
<td>299-497</td>
<td>32</td>
</tr>
<tr>
<td>Smm4†</td>
<td></td>
<td>DQ160179</td>
<td>5' TAAATGCTAGGCGGCTTGTCC 3' TCTGCTGTTAGGTCCCTA</td>
<td>161-187</td>
<td>4</td>
</tr>
<tr>
<td>Smm5†</td>
<td></td>
<td>DQ160184</td>
<td>5' TCAGGGAGAAAGAAGCAAGGA 3' CCGCTAGGTGCACCGATGTGTT</td>
<td>309-351</td>
<td>3</td>
</tr>
<tr>
<td>Smm6†</td>
<td></td>
<td>DQ160182</td>
<td>5' AAGCCTGCGATCCCAAGG 3' AAGTGGGTTGAATGCTGGTGG</td>
<td>441-443</td>
<td>2</td>
</tr>
<tr>
<td>Smm7†</td>
<td></td>
<td>DQ160182</td>
<td>5' AAGCCTGCGATCCCAAGG 3' AAGTGGGTTGAATGCTGGTGG</td>
<td>187-189</td>
<td>2</td>
</tr>
<tr>
<td>Mcy7</td>
<td>Double et al. 1997</td>
<td>U82391</td>
<td>5' CTGGGTGTCTGGGTAGTTTGAGA 3' GCCCTACACGCCTGCTGAT</td>
<td>86-88</td>
<td>2</td>
</tr>
<tr>
<td>Mcy4</td>
<td></td>
<td>U82388</td>
<td>5' AATAAGATCTAGTGCTCTGCTG 3' TACAAATTGGTGATCACTCCTGGT</td>
<td>158-180</td>
<td>10</td>
</tr>
<tr>
<td>Msp4</td>
<td></td>
<td>AY320050</td>
<td>5' GAGGAGGAGCGGAGAAGCAAGAC 3' GCCAGCAGCCAGGCTCAGT</td>
<td>167-174</td>
<td>3</td>
</tr>
<tr>
<td>Msp6</td>
<td></td>
<td>AY320051</td>
<td>5' GAGGTTTTAATTGCCATTAGCAG 3' GCCAGCAGCCAGGCTCAGT</td>
<td>237-241</td>
<td>2</td>
</tr>
<tr>
<td>Msp10</td>
<td></td>
<td>AY320051</td>
<td>5' CGCGCTTTATAGGAGGAGAAGCC 3' GAGCAGCCAGCAGGCTCAGT</td>
<td>143-173</td>
<td>9</td>
</tr>
<tr>
<td><strong>EPIC</strong></td>
<td>Backström et al. (2008)</td>
<td>P23913</td>
<td>5' TGGAACTCCTGCTATGGCCAG 3' ATGGTTTCAATCTCAGAAGC</td>
<td>292-294</td>
<td>2</td>
</tr>
<tr>
<td><strong>ND2 mtDNA</strong></td>
<td>Driskell and Christidis 2004</td>
<td>AY488328</td>
<td>5' AATTAGGACCTGTTCTCTCA 3' TCTTACACTGGCTCAGGGCC</td>
<td>783</td>
<td>1</td>
</tr>
<tr>
<td>H6313</td>
<td></td>
<td></td>
<td>5' TGGGAGCTGCTTCTCTCA 3' TCTTACACTGGCTCAGGGCC</td>
<td>783</td>
<td>1</td>
</tr>
<tr>
<td>SmND2AF</td>
<td>This study</td>
<td></td>
<td>5' TGGTATGATGACTGCGCTGAGT 3' AGATGGAGGAGGAGGAGGAGG</td>
<td>774</td>
<td>1</td>
</tr>
<tr>
<td>SmND2AR</td>
<td></td>
<td></td>
<td>5' TGGTATGATGACTGCGCTGAGT 3' AGATGGAGGAGGAGGAGGAGG</td>
<td>760</td>
<td>1</td>
</tr>
</tbody>
</table>

*Primers designed from genebank submission sequence (Driskell and Christidis 2004)
† Primers re-designed from genebank submission sequence clones (Maguire et al. 2006)
‡ Primers modified from Backström et al. (2008), Sasha Pavalova (unpublished data)

# Microsatellite sizes detected in the Mallee Emu-wren
@ Sex-linked loci (Maguire et al. 2006)
Table 5.3. Measures of pair-wise population differentiation for six populations of the Mallee Emu-wren based on; i) $F_{ST}$ (below the diagonal) and ii) actual differentiation $D_{est.}$ (above the diagonal). * $p<0.05$

<table>
<thead>
<tr>
<th>Population</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hattah-Kulkyne NP</td>
<td>0.101*</td>
<td>0.044</td>
<td>0.077*</td>
<td>0.035</td>
<td>0.122*</td>
<td></td>
</tr>
<tr>
<td>Murray-Sunset NP (East)</td>
<td>0.037*</td>
<td>0.081*</td>
<td>0.105*</td>
<td>0.103*</td>
<td>0.092*</td>
<td></td>
</tr>
<tr>
<td>Murray-Sunset NP (Central)</td>
<td>0.011*</td>
<td>0.014*</td>
<td>0.004</td>
<td>0.020</td>
<td>0.104*</td>
<td></td>
</tr>
<tr>
<td>Murray Sunset NP (West)</td>
<td>0.020*</td>
<td>0.025*</td>
<td>0.000</td>
<td>0.000</td>
<td>0.132*</td>
<td></td>
</tr>
<tr>
<td>Murray Sunset NP (South)</td>
<td>0.002</td>
<td>0.030*</td>
<td>0.000</td>
<td>0.000</td>
<td>0.179*</td>
<td></td>
</tr>
<tr>
<td>Ngarkat CP</td>
<td>0.027*</td>
<td>0.032*</td>
<td>0.018</td>
<td>0.041*</td>
<td>0.044*</td>
<td></td>
</tr>
</tbody>
</table>

5.4.3 Population bottlenecks

Significant ($p<0.05$) heterozygosity excess was detected for the Murray-Sunset National Park (East) and Ngarkat Conservation Park populations under the TPM model, indicating evidence of recent bottlenecks in these populations (Table 5.4). The Murray-Sunset (East) population showed further evidence of a bottleneck under the allele frequency distribution test.

Table 5.4. Results from the BOTTLENECK test of microsatellite from the six populations. Wilcoxon test values ($p$ values) for the two-phase mutation (TPM) model, and the allele frequency distribution test. Bold indicates significance at $p<0.05$.

<table>
<thead>
<tr>
<th>Population</th>
<th>TPM</th>
<th>Allele frequency distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hattah-Kulkyne NP</td>
<td>0.213</td>
<td>L-shaped</td>
</tr>
<tr>
<td>Murray Sunset NP (East)</td>
<td><strong>0.002</strong></td>
<td>Mode-shift</td>
</tr>
<tr>
<td>Murray Sunset NP (Central)</td>
<td>0.188</td>
<td>L-shaped</td>
</tr>
<tr>
<td>Murray Sunset NP (West)</td>
<td>0.601</td>
<td>L-shaped</td>
</tr>
<tr>
<td>Murray Sunset NP (South)</td>
<td>0.285</td>
<td>L-shaped</td>
</tr>
<tr>
<td>Ngarkat Conservation Park</td>
<td><strong>0.004</strong></td>
<td>L-shaped</td>
</tr>
</tbody>
</table>

L-shaped and mode-shift are defined in the Methods text.
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5.4.4  Population structure

The STRUCTURE analyses estimated the likelihood of the posterior probability as $K = 1$ (Fig. 5.4), indicating no genetic structure across the global range of the Mallee Emu-wren. The TESS analyses showed DIC values for $K = 6$ stabilised, indicating a maximum of 6 clusters, $K_{\text{max}} = 6$, was likely (Fig. 5.5). However, the DIC sometimes selects models in which $K_{\text{max}}$ is greater than $K$ (Durand et al 2009) and DIC does not always lead to choosing the best model fit (Brooks 2002).

![Figure 5.4](image1)

**Figure 5.4** The estimated posterior probability of $K$ from the STRUCTURE analysis using the method of Pritchard et al. (2000, 2003). The mean Ln probability of the data ($\text{LnP}(X \mid K)$) ($\pm$ SDEV) against $K$. Maximum $\text{LnP}(X \mid K)$ is at $K=1$.

![Figure 5.5](image2)

**Figure 5.5** The Deviance Information Criterion (DIC) as a function of $K_{\text{max}}$ for the Mallee Emu-wren. Arrow corresponds with the estimated number of clusters $K=2$, based on boxplot analysis.
Boxplots showed the TESS analyses assigned individuals proportionately to one of two clusters (represented by green and yellow proportions), rather than 6, indicating that $K_{\text{max}} = 2$ (Fig. 5.6). Spatial admixture analyses as determined by TESS, for $K_{\text{max}} = 2$ (Fig. 5.7), showed that the Ngarkat Conservation Park population had a lower probability of belonging to the remaining populations. However, the assigned probabilities indicate the magnitude of the observed genetic structure was slight. There is also evidence for weak east-west structure in the Murray-Sunset and Hattah-Kulkyne reserve complex. Collectively, the analyses of the data using STRUCTURE and TESS showed at the most, weak genetic structure across the global range of the Mallee Emu-wren.

**Figure 5.6** TESS boxplots for $K_{\text{max}} = 6$ (top) and $K_{\text{max}} = 2$ (bottom) based on 12 loci for 72 individuals. NCP= Ngarkat Conservation Park, MSW=Murray-Sunset (West), MSC= Murray-Sunset (Central), MSS=Murray-Sunset (South), MSE=Murray-Sunset (East).
Figure 5.7 Spatially predictive explicit map of admixture coefficients as determined by TESS for 2 clusters, $K_{max}=2$. The colour scale represents the posterior probability of individuals having membership to a single genetic cluster. Black circles represent sampled individuals with known geographic locations (n=72). Numbered ellipses indicate the populations; 1= Hattah-Kulkyne, 2= Murray-Sunset (East) 3= Murray-Sunset (Central), 4= Murray-Sunset (West), 5= Murray-Sunset (South) and 6= Ngarkat Conservation Park.

The spatial autocorrelation results for all 72 individuals showed positive and significant ($r=0.082, p=0.001$) spatial autocorrelation among individuals separated by less than 2 km (Fig 5.8), indicating that proximal pairs are on average more related than are spatially random pairs; $r$ values decreased gradually with separation distance, becoming significantly negative at 50 km (Fig 5.8). No sex-biased spatial autocorrelation was detected. The frequency distribution of AIC values among males and females differed significantly ($p=0.026$). Females showed higher probability of being immigrants (AIC -0.429, SE 0.225) than males (AIC 0.363, SE 0.257), indicating that in the Mallee Emu-wren, females are more likely to disperse than males. GENECLASS analysis identified a male in the Murray-Sunset (West) population, and a female in the Murray-Sunset (Central) population as likely immigrants.
Figure 5.8  Spatial autocorrelation correlogram for the Mallee Emu-wren for all individuals across the species’ global range (n=72). Error bars represent 95% confidence intervals for the point estimate of the autocorrelation coefficient, $r$, in each distance bin, as determined by bootstrapping resampling. The red lines represent the upper and lower 95% confidence intervals as determine by permutation. Statistical significance ($p = 0.001$) is indicated with an asterisk.

5.5  Discussion

Samples were obtained from 72 individual Mallee Emu-wrens from six separate geographical locations to examine global population structure and processes in this species. The results of the genetic analyses of mtDNA and hypervariable nuclear loci were concordant, showing uniform, low to moderate genetic diversity across the global range of the species. Analyses of the nuclear loci found evidence of genetic drift and bottlenecks. The low level of population differentiation and weak evidence for genetic structure indicates that the Mallee Emu-wren is possibly panmictic, contrary to expectation given their patchy distribution as a habitat specialist (Chapters 2, 3 & 4) and their presumed poor dispersal ability.

5.5.1  Genic diversity and phylogeny

The level of ND2 nucleotide diversity found in the Mallee Emu-wren was considerably lower than that of closely related temperate species, the Southern Emu-wren (Donnellan et al. 2009) and the Splendid Fairy-wren (Kearns et al. 2009), but is similar to that of other arid-zone species of Maluridae including the Red-backed Fairy wren
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*Malurus melanocephalus* (Lee and Edwards 2008) and the Short-tailed Grasswren *Amytornis merrotsyi* (Christidis et al. 2008). The low haplotypic diversity within ND2 gene (3 haplotypes) suggests that the Mallee Emu-wren has descended from a small number of maternal lineages. Consistent with mtDNA diversity, the level of expected heterozygosity for the nuclear loci was also found to be low compared with that of the Superb Fairy-wren (Double et al. 2005), the Splendid Fairy-wren (Webster et al. 2004) and the Southern Emu-wren (Maguire and Mulder 2008). The concordance between allelic diversity and haplotype diversity suggests that low to moderate polymorphism in extant Mallee Emu-wrens is inherited from ancestral founders.

Phylogenetic analyses of published Emu-wren ND2 sequences from Emu-wrens (Driskell and Christidis 2004, Donnellan et al. 2009) and data from this study corroborate a close relationship between the Mallee Emu-wren and Rufous-crowned Emu-wren (Donnellan et al. 2009). However, the inclusion of an additional haplotype sequenced in this study shows they are paraphyletic, suggesting that divergence between these species is very recent. Mitochondrial paraphyly, in which individuals of one species or population have mtDNA that is more closely related to that of another than their own, is commonly detected in Australian birds (Joseph et al. 2006, Joseph and Omland 2009). Paraphyly is attributed to complex speciation events as a result of climatic oscillations during the Pleistocene (Byrne 2008, Byrne et al. 2008). This finding raises the question as to whether the Mallee Emu-wren and Rufous-crowned Emu-wren are separate species. Exploration of the systematic relationship between the Rufous-crowned Emu-wren and Mallee Emu-wren is beyond the scope of this thesis and this knowledge gap is discussed further in Appendix IV.

5.5.2  Fine-scale genetic structure

Fairy-wrens and Emu-wrens exhibit male natal philopatry, female-biased dispersal and distance-restricted dispersal (Russell and Rowley 1997, Double et al. 2005, Maguire 2006b, Maguire and Mulder 2008), characteristics which are expected to generate fine-scale non-random genetic patterns. The correlograms showed positive and significant autocorrelation over distances of less than 2 km (Fig. 5.8), probably reflecting local kin associations (Double et al. 2005). The $r$ values became consistently negative and significant at about 50 km, indicating the point at which more distant pairs are on average, less related than are random pairs (Smouse et al. 2008), suggesting a weak isolation-by-distance effect. At fine-scales, female-biased dispersal is expected to
generate positive local genetic structure among males and little or no genetic structure among females (Double et al. 2005) however, no difference between the sexes was found in this species. The sampling intensity was low, and may have had inadequate power to detect these patterns.

Offspring that disperse from their natal territory are likely to introduce new alleles into an area (Double et al. 2005). Assignment tests detected immigrants (one male and one female) and female-biased dispersal, findings consistent with the known social structure and dispersal characteristics of other species of Maluridae (female-biased dispersal, with infrequent male dispersal) (Rowley and Russell 1997, Double et al. 2005, Maguire 2006b). The populations in which probable immigrants were detected are 2 to 10 km from other known groups of Mallee Emu-wrens (S Brown, unpublished data, Appendix II) which may have been the source of these individuals.

5.5.3 Population bottlenecks

The survey of microsatellite variation suggests that the populations of Ngarkat and the Murray-Sunset (East) have been affected by recent bottlenecks. Indeed the Ngarkat population has declined severely following a series of fires, including a large fire (>100 000 ha) in 1998 (Gates 2003) that has resulted in scattered groups of Mallee Emu-wrens totalling fewer than 50 breeding pairs (Chris Hedger pers. obs.). With the exception of the Murray-Sunset (West), populations were found to have several monomorphic loci or homozygote excess, suggesting that these populations may have also experienced inbreeding, either through founders or a population bottleneck. Bottleneck and inbreeding populations are important to identify for conservation management because they are subject to the effects of genetic drift and the increase in homozygosity of deleterious alleles (genetic load) can lead to inbreeding depression (Charlesworth and Charlesworth 1999, Reed and Frankham 2003). In turn, the loss of genetic variation and increased genetic load can limit adaptive potential and compromise species persistence in the long term (Hedrick and Fredrickson 2010).

5.5.4 Global genetic structure and landscape-scale processes

The evidence for population bottlenecks in two spatially separated populations, and genetic drift and fixation of alleles across most populations, suggests that contemporary landscape-scale processes are influencing the metapopulation structure of the Mallee Emu-wren. Environmental variability is a feature of arid and semi-arid
zones of Australia. Pulsed rainfall, prolonged drought periods and frequent fires result in marked population fluctuations in vertebrates (Letnic et al. 2005, Kelly et al. 2010, Letnic and Dickson 2010) including the Mallee Emu-wren (Chapter 2, Appendix II). These environmental fluctuations create the conditions for serial population bottlenecks and founder events as local populations contract and decline, expanding once again when favourable conditions occur (Letnic and Dickman 2010). Such population fluctuations tend to reduce genetic diversity, erode heterozygosity and increase inbreeding (Whitlock and Barton 1997, Vucetish and Waite 1998).

Spatial and temporal changes to habitat resulting from fire can be predicted to have different effects on population recovery processes. The spatial distribution of residual survivors is important to understanding the process of population recovery and its genetic consequences. Population recovery may occur by re-colonisation by individuals originating beyond the boundary of the fire footprint, or there may be in-situ recovery from residual survivors within the fire footprint (Whelan et al. 2002, Banks et al. 2011). These contrasting processes could result in different genetic signatures in recovering populations. Colonisation of empty habitat patches may result in a genetic bottleneck through founders, and younger populations should be less genetically diverse than older ones (Hagg et al. 2005). In contrast, population recovery from in-situ survivors is less likely to lose a proportion of the original genetic diversity, except where significant bottlenecks occur (England et al. 2003). In actuality these two processes are not mutually exclusive, but more likely the two extremes of a continuum.

Fire-mediated extinction and founder events are a plausible explanation for the bottlenecks, moderate genetic diversity and genetic drift observed in populations of the Mallee Emu-wren. Fire is a major driver of structure and function of mallee ecosystems (Bradstock and Cohn 2002, Haslem et al. 2011, Avitable et al. in press) and has a strong influence on the distribution of many species (Whelan et al. 2002). Fires in mallee shrublands vary in their scale, frequency and intensity. Most fires are small, less than 100 ha in size (Avitable et al. in press). Fuel in mallee ecosystems is discontinuous, and as such many fires leave unburnt patches at fine-scales (Bradstock and Gill 1993, Haslem et al. 2011, Avitable et al. in press). These unburnt patches can provide temporary refugia for surviving Mallee Emu-wrens and other animals, enabling in-situ population recovery. However landscape-scale wildfires exceeding 100,000 ha also occur within the region every 10-20 years (Noble and Vines 1993,
Bradstock and Cohn 2002). These wildfires create vast homogenous areas initially devoid of vegetation structure as ground, shrub and low canopy strata are all consumed (Haslem et al. 2011) (Fig. 5.9). These areas of denuded vegetation immediately post-fire are unable to support Mallee Emu-wrens and many other species. In the Murray-Sunset and Hattah-Kulkyne reserve complex, vegetation does not reach a suitable age for this species to occupy until at least 15-18 years following fire (Chapters 2 & 3). It is reasonable to conclude that under these circumstances population recovery occurs exclusively from recolonisation by founders. Extirpation of populations and re-colonisation by founders mostly (but not invariably) lead to the loss of genetic diversity and/or increased genetic differentiation (Slatkin 1977, Pannell and Charlesworth 2000, Haag et al. 2005). The loss of genetic diversity following intense large wildfires has been reported for various taxa in other ecosystems (Cleary 2006, Fauvelot et al. 2006, Collevatti et al. 2007).

Figure 5.9 Sand-dune landscape following an intense landscape-scale fire.

Disturbance by fire can also alter gene flow (Cleary et al. 2006, Fauvelot et al. 2006, Collevatti et al. 2007, Stow et al. 2007, Spear and Stofer 2010) and lead to increased genetic variance and genetic differentiation among populations (Ujari et al. 2008, Schery et al. 2010). For a sedentary species with presumed poor dispersal capabilities,
such as the Mallee Emu-wren, rapid differentiation between isolated populations would be predicted, enhanced by drift-induced divergence (Wright 1942, Baker and Moeed 1987, Bouzat et al. 1998, Johnson et al. 2004). Loss of gene flow because of restricted dispersal can re-distribute genetic variability among spatially structured populations over the course of only a few generations (Harrison and Hastings 1996). In this study the weak genetic structure and low genetic differentiation among populations of the Mallee Emu-wren have most likely arisen because recent subdivision, caused by the loss of habitat from fires and vegetation clearing, has disrupted gene flow between populations. As expected for a species with poor dispersal capacity, the greatest genetic dissimilarity was found between populations most spatially distant (e.g. Ngarkat Conservation Park and the northern reserve complex populations) (Table 5.3, Fig. 5.7). Nevertheless, weak genetic structure was also detected among populations of the Murray-Sunset/Hattah-Kulkyne reserve complex (Fig. 5.7), suggesting that vegetation unsuitable as habitat (due to post-fire age) may have also restricted gene flow over considerably shorter distances. The paradox to genetic subdivision caused by fire over the short-term (several to many generations) is that spatio-temporal tracking of suitable habitat by the Mallee Emu-wren (sensu a shifting habitat mosaic, Wimberly 2006), mediated by fire, appears to maintain genetic connectivity and prevents substantial genetic differentiation evolving among populations in this presumably sedentary species.

The size and frequency of fires can result in small isolated groups of Mallee Emu-wrens, such as those currently found in Ngarkat and Billiatt Conservation Parks. Landscape-scale fires prohibit opportunities for genetic augmentation by immigrating individuals, possibly for many generations, until Mallee Emu-wrens recolonise empty patches. Such isolated populations or groups are particularly vulnerable to stochastic events (genetic or environmental) and population extinction (Reed 2008). I found evidence that the loss of genetic variability has already occurred within the Ngarkat Conservation Park population (Tables 5.1 & 5.4) and this process may also explain the high proportion of monomorphic loci among remaining populations.

Metapopulation dynamic theory (Kallimanis et al, 2003, Wilcox et al. 2006, Vuilleumier et al. 2007) suggests that species occupying dynamic landscapes are prone to fluctuating metapopulation dynamics and are at risk of extinction where large-scale recurrent disturbance (e.g. fire and drought) occur over relatively short time-frames.
Disturbance by fire in the Ngarkat, Big Desert and Wyperfeld reserves (southern reserves) occurs at a frequency about twice that experienced within Murray-Sunset reserve complex (northern reserves) (Pausas and Bradstock 2007). Consequently populations of the Mallee Emu-wren within the southern part of the species' range are likely to be at a greater risk of extinction (Kallimanis et al. 2003, Wilcox et al. 2006, Vuilleumier et al. 2007). Frequent fires have been partially responsible for their decline in this region (Chapter 2, Gates 2003). The relationship between the frequency of disturbance by fire and levels of genetic and taxonomic diversity among different locations requires further exploration, particularly in light of the predicted increased frequency of fire with climate warming (Steffen et al. 2009).

5.5.5 Population viability

Low genetic variability, compounded by the potential for serial population bottlenecks, has consequences for individual fitness and population viability (Crnokrak and Roff 1999, Reed and Frankham 2003, Reed 2005). A prolonged bottleneck can rapidly erode the remaining genetic diversity and increase inbreeding in populations of less than a few thousand individuals (O'Grady et al. 2006). Thus, all populations of the Mallee Emu-wren are at risk of extinction from these processes. Further, genetically depauperate populations have been shown to have disproportionately lower fecundity in more stressful environments (Ambruster and Reed 2005). Again, the Mallee Emu-wren may be particularly vulnerable. These generalisations are, however, not universal (Milot et al. 2007, Hable et al. 2009, Johnson et al. 2009) and the Mallee Emu-wren may be resilient to such threats. Arguably the Mallee Emu-wren has been subject to strong evolutionary selection. Given the persistence of this species despite harsh environmental conditions (Chapter 4), it is possible that deleterious alleles have been purged, reducing genetic load and retaining adaptive potential for environmental stressors such as climate change. Selective sweeps; the reduction or elimination of variation linked to a mutation with strong positive selection, can also be responsible for greatly reduced variability (Maynard-Smith and Haigh 1974). Thus, the relatively low genetic variability detected here may not necessarily equate to low fitness.
5.5.6 Implications for species occupying dynamic ecosystems

These findings suggest that the spatial and temporal characteristics of dynamic ecosystems and subsequent population recovery processes can have profound effects on the temporal genetic changes within species and patterns of gene flow. First, the spatial characteristics of refugia (or lack thereof) may play a significant role in the genetic patterns of subsequent population recovery. The potential for the loss of genetic diversity emphasizes the need to identify the primary mechanism driving population recovery in ecosystems subject to disturbance (i.e. recolonisation or in-situ persistence or a combination of both). The scarcity of refugia following large wildfires in mallee ecosystems (small burrows may be an exception, providing refugia for some animals) results in a system that closely resembles the classic metapopulation paradigm (Hanski 1998). Where recolonisation by founders is a major driver of metapopulation dynamics, populations or species are at risk from adverse genetic effects associated with serial population reductions (Charlesworth and Charlesworth 1999, Bouzat 2010, Hedrick and Fredrickson 2010). Those most at risk are restricted range species that are habitat specialists and dependent on late seral stage vegetation (Benshemesh 1992, 2000, Clarke et al. 2005).

Second, the shifting habitat mosaic (Wimberly 2006) appears to maintain genetic connectivity and prevent genetic differentiation among populations, even in a poorly dispersing species. The challenge for conservation management is to consider the multi-faceted aspects of patch dynamics, the intrinsic characteristics of species (e.g. fecundity, mating systems and dispersal) and how they interact to affect the biota. The frequency, spatial configuration and temporal pattern of disturbance events and the proportion of patches that are lost (patch demography) will all greatly affect genetic connectivity and metapopulation persistence (Wilcox et al. 2006).

5.5.7 Conclusion

This study has helped better understand micro-evolutionary processes in an ecosystem subject to disturbance by fire. In the case of the Mallee Emu-wren the observed moderate level of genetic variability is most likely a consequence of both low to moderate genetic variability inherited from their evolutionary ancestor and contemporary metapopulation processes driven by fire and drought. Movements among temporally and spatially shifting habitats resulting from fire appear to
maintain genetic connectivity in this specialist sedentary species. Nevertheless, the high environmental variability caused by fire, rainfall and drought in semi-arid ecosystems is likely to have resulted in serial extinction, founder events and population bottlenecks which have resulted in genetic drift and contributed to the erosion of genetic diversity in this specialist species. These findings suggest that the spatial characteristics of refugia and spatio-temporal pattern of the habitat mosaic characteristic of highly dynamic landscapes may have profound demographic and genetic consequences for species.
CHAPTER 6

Discussion: synthesis, implications, management and future research directions

Figure 6.1  Male and female pair of Mallee Emu-wrens in Triodia.
6.1 Thesis overview

The precipitous decline of the Mallee Emu-wren in recent decades caused by landscape-scale fires and prolonged drought prompted this study into aspects of its distribution, habitat requirements, and population size and genetic structure. The aim of this final chapter is to synthesize the key findings of the study (Table 6.1). First I briefly summarise the main findings. Second I discuss these findings in relation to dynamic landscapes and the risk posed to endemic species. Third, I discuss the implications for the management of the Mallee Emu-wren focusing on fire and genetic management. Last, I briefly list knowledge gaps and provide suggestions for future research.

6.1.1 Summary of key findings

The findings of this study make a significant contribution to understanding the distribution, habitat requirements and population size and structure of the Mallee Emu-wren (Table 6.1). The Mallee Emu-wren is a habitat specialist threatened by a combination of several pervasive processes identified in this thesis; i) habitat loss and population decline due to landscape-scale fires and inappropriate fire regimes, and ii) adverse genetic and demographic consequences within small and isolated populations or groups. These three threats are directly or indirectly exacerbated by global warming. The work presented in this thesis provides a basis to inform conservation actions specific to the Mallee Emu-wren (see section 6.3); components of which are relevant to other sedentary and specialist bird species of the mallee such as the Striated Grasswren (Chapter 3) and also other species occupying dynamic ecosystems.

Habitat use and selection by the Mallee Emu-wren was measured at three spatial scales; the landscape-scale, local scale and at the scale of resource selection by individual birds. Because Mallee Emu-wrens occur in a fire-prone dynamic ecosystem, temporal scales were implicitly included.

The results of multi-scale habitat modelling confirmed that the Mallee Emu-wren is a habitat specialist (Rowley and Russell 1997, Higgins et al. 2001). Ecological niche factor analysis and habitat suitability modelling of the occurrence of the species in the Murray-Sunset and Hattah-Kulkyne National Parks found that the Mallee Emu-wren occupies vegetation greater than 15 years since last burnt and that mallee-Triodia
vegetation associations supported the greatest density (Table 6.1). Specifically, Woorinen Sands Mallee and Loamy Sands Mallee were found to be key Ecological Vegetation Classes for this species, and the 16-29 year fire age-class contained the greatest densities (Chapter 2).

At finer scales, the Mallee Emu-wren was shown to prefer vegetation that contained high levels of Triodia cover with a relatively higher proportion of individual Triodia plants of mature growth-phase and high volume (Chapter 3). Furthermore, Mallee Emu-wrens specifically select healthy, mature growth-phase Triodia hummocks that have relatively large volume for foraging (Chapter 4). The structural attributes of Triodia that the Mallee Emu-wren prefer are strongly dependent on time-since-fire (Chapter 3, Haslem et al. 2011), directly linking this key resource requirement to the temporal element of scale – the fire regime of mallee ecosystems.

The status of Mallee Emu-wren populations across its global range varied considerably. The Murray-Sunset and Hattah-Kulkyne National Parks are the species’ stronghold and were estimated to support about 92% of the global population. The large southern reserve complex (Ngarkat, Big Desert and Wyperfeld reserves) supports a few, very small isolated populations. In addition to these scattered populations, a small group (about 3 birds) was recently located in Billiatt Conservation Park, South Australia (Chris Hedger pers. comm.). The long-term persistence of these small populations is precarious, as they are susceptible to environmental (Fahrig and Merriam 1994, With and King 2001), demographic (Pimm et al. 1988, McCarthy et al. 1994), Allee effects (Stephens et al. 1999, Stephens and Sutherland 1999, Berec et al. 2007) and genetic stochastic processes (Lacy 1987, 1993, Reed 2010).

Applying a landscape-scale perspective to the habitat requirements of the Mallee Emu-wren is important as key factors acting on the dynamics of populations can often be found at this level (Orians and Wittemberger 1991, Rosenweig 1991). Landscape-scale fires (> 100 000 ha) that occur in the region (typically in different locations) on a decadal to bi-decadal basis are major drivers of mallee ecosystems (Noble and Vines 1993, Bradstock and Cohn 2002, Haslem et al. 2011, Avitabile et al. in press). A feature of intense fires within mallee ecosystems is the total destruction and subsequent regeneration of vegetation (Haslem et al. 2011) leaving little, if any, refugia for the Mallee Emu-wren and other species following the fire. Large areas of
unsuitable aged vegetation (<15-18 years since fire) are likely to disrupt metapopulation dynamics leading to increased isolation of populations, inbreeding and the risk of adverse consequences from genetic drift.

Genetic analyses found the Mallee Emu-wren to have relatively moderate to low genetic diversity, low genetic differentiation and evidence of genetic drift and bottlenecks (Table 6.1). I inferred from these findings that the observed level of variability is a consequence of both low to moderate genetic variability inherited from their evolutionary ancestor and the effects of contemporary metapopulation processes. Spatial and temporal patterns of fire in mallee ecosystems result in population bottlenecks, serial local extinctions and subsequent recolonisation, all of which interact to erode genetic diversity in this species. Movement among temporally and spatially shifting habitat, mediated by fire, appears to maintain long-term genetic connectivity. I conclude that recolonisation by founders, rather than in-situ survival is the prominent driver of population recovery and metapopulation processes for this species (Chapters 4 & 5).

Each data chapter has provided an insight into the precarious status of the Mallee Emu-wren in the face of climate change. Populations are at a great risk of local extinction because of the risk of increased frequency and magnitude of wildfires associated with global warming (Chapters 2 and 5). Increased aridity predicted for north-western Victoria under global warming may also adversely affect population numbers indirectly, by reducing the availability and abundance of invertebrates on which they depend (Chapter 4).
<table>
<thead>
<tr>
<th>Theme</th>
<th>Objectives</th>
<th>Key Findings</th>
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<tr>
<td>Global distribution and population size</td>
<td>• determine population distribution and estimates of population size in Victoria</td>
<td>• The Murray-Sunset and Hattah-Kulkyne National Parks support about 92% of the global population. Only one pair was recorded in the large southern reserve complex (Wyperfeld/Big Desert conservation reserves). No Mallee Emu-wrens were recorded in the medium-size reserves (e.g. Wathie and Bronzewing Fauna and Flora Reserves). The total population size was estimated to be 16,821, although confidence intervals were large (range 8,431-39,104).</td>
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<td>• determine the density of the Mallee Emu-wren in different vegetation types and fire-age classes</td>
<td>• The Mallee Emu-wren prefers Woorinen Sands Mallee to Loamy Sands Mallee and has very low density in Woorinen Mallee vegetation type. Overall, densities were highest in the 16-29 year fire-age class, which supports mature <em>Triodia</em>. The 0-15 year fire-age class did not support the Mallee Emu-wren.</td>
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<td>• evaluate the risk of fire and climate change as threatening processes</td>
<td>• Landscape-scale wildfires of increasing frequency are considered a serious threat to the long-term persistence of the Mallee Emu-wren. Drought caused by climate change is a threat to long-term population persistence and is likely to exacerbate the recovery of populations affected by fire.</td>
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<td>• assess the global conservation status in accordance with IUCN Red List criteria</td>
<td>• The high probability of landscape-scale fires extirpating a substantial proportion of the global population warranted re-assessment of conservation status from Vulnerable to Endangered in accordance with IUCN Red List criteria.</td>
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<td>Local-scale habitat selection</td>
<td>• identify fine-scale vegetation and abiotic environmental variables that influence the distribution of the Mallee Emu-wren and Striated Grasswren</td>
<td>• The Mallee Emu-wren and Striated Grasswren were associated with high levels of cover of <em>Triodia</em>. The mature growth-phase (T3) and volume of <em>Triodia</em> hummocks explained Mallee Emu-wren occurrence, whilst the percent cover of <em>Triodia</em> cover explained Striated Grasswren occurrence at sites.</td>
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<td>• identify parameters that indicate areas of high quality habitat</td>
<td>• The mosaic of small area of different fire age-classes in Hattah-Kulkyne National Park relative to the western Murray-Sunset National Park may enable these species to respond to habitat requirements at fine-scale.</td>
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<td>• assess the impact of fire on habitat suitability</td>
<td>• The structural attributes of <em>Triodia</em> are strongly dependent on time-since-fire. Those structural attributes preferred by the Mallee Emu-wren and Striated Grasswren are associated with mature growth-phases of <em>Triodia</em>.</td>
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<td>Theme</td>
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<td><strong>Behaviour and substrate selection</strong></td>
<td>- determine whether Mallee Emu-wrens select specific growth-phases of <em>Triodia</em> for a range of behavioural activities</td>
<td>- Mallee Emu-wrens select specific growth-phases of <em>Triodia</em> for behavioural activities (foraging, display and movement). They avoid immature <em>Triodia</em>, and preferentially select the large healthy plants, presumably for foraging.</td>
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<td><strong>Mallee microclimate</strong></td>
<td>- explore the microclimate of mallee-<em>Triodia</em> vegetation</td>
<td>- <em>Triodia</em> hummocks have a limited capacity to buffer environmental temperatures compared with open habitat temperatures.</td>
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<td><strong>Global population structure</strong></td>
<td>- examine genetic patterns and structure among populations</td>
<td>- The Mallee Emu-wren exhibits low to moderate level of genetic diversity, and evidence of genetic drift and bottlenecks.</td>
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<td>- make inferences about population structure and processes in fire-prone ecosystem</td>
<td>- Spatial autocorrelation analyses revealed non-random genetic structure at fine-scales, most likely reflecting kin associations.</td>
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<td>- Low population differentiation and weak genetic population structure exhibited across the species’ global range was inferred to be a result of population subdivision caused by fire.</td>
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<td>- The observed genetic patterns in the Mallee Emu-wren were inferred to be a result from a series of bottlenecks and founder events caused by environmental stochasticity (cyclic drought and fire). A shifting habitat mosaic, mediated by fire appears to have maintained gene flow across the species’ global range.</td>
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6.2 Dynamic ecosystems and population processes

Mechanical agents of terrestrial disturbances such as fire, flood, silviculture, and cyclones, add a spatio-temporal component to environmental heterogeneity. They alter patch suitability for species (e.g. Chapters 2 & 3) and therefore have major consequences for species diversity (Sousa 1984, Karr and Freemark 1985, Brawn et al. 2001), and population and metapopulation processes (Vrijenhoek 1985, Porter 1999, Kallimanis et al. 2005, Vuilleumier et al. 2007, Chapter 5). Several elements of dynamic ecosystems have the potential to alter species distributions and population dynamics drastically, thus diminishing their long-term persistence.

Changes in disturbance regimes (intensity, severity, frequency, extent and season), whether natural or anthropomorphic in origin, can significantly alter community structure and population dynamics (Pickett and White 1985, Rundel et al. 1998, Brawn et al. 2001, Holmgren et al 2006). Managed intervention in natural disturbances occurs world-wide (e.g. flood levees, suppression or application of fire, silviculture) and has resulted in substantial changes in ecosystems with associated changes in the abundance and distribution of many species. For example, the suppression of fire in tall prairie across North American grasslands has led to the decline of many avian (Brawn et al. 2001, Hutto 2008) and plant species (Leach and Givnish 1996). In contrast the increased application of fire in tropical ecosystems has drastically transformed areas of forest into scrub and grasslands (Cochrane 2003).

Moreover, climate change is predicted to contribute to more extreme weather events in the future (IPCC 2001). More frequent occurrence of these extremes will indirectly alter climate-mediated disturbance regimes including those of fire, flooding and storms, ultimately altering the habitat of many species and consequently their distribution and abundance.

The spatial characteristics and frequency of disturbance regimes can have profoundly different effects on metapopulation persistence (Kallimanis et al. 2003, Wilcox et al. 2006, Vuilleumier et al. 2007). Spatially and temporally autocorrelated disturbances (e.g. large floods and fire, and prolonged drought) are ecologically important because their impacts are large in extent and may even persist for many hundreds of years (Turner and Dale 1998). Spatially correlated disturbance increases the risk of metapopulation extinction (Kallimanis et al. 2003) and may disrupt population
processes by creating isolated populations (Chapters 2 & 5). Dispersal-limited species, or those with restricted ranges such as the Mallee Emu-wren and Striated Grasswren, are at particularly at risk (Kallimanis et al. 2003).

Some species have intrinsic attributes that combine with living in highly dynamic environments to make them inherently at risk of extinction from environmental, demographic and genetic stochastic processes (Reed 2008). Species with low vagility are more likely to be directly killed by agents of disturbance such as fire and flood because they are unable to escape to refugia. They are also less likely to locate suitable patches of habitat successfully, if patches are beyond the dispersal capabilities of individuals (Chapters 2, 3 & 5). Species with low fecundity may take many years for populations to recover fully and, if dependent on late seral stage vegetation, are particularly susceptible to frequent disturbance events (e.g. Leadbeater possum Gymnobelideus leadbeateri, Lindenmayer and Possingham 1995, California spotted owls Strix occidentalis occidentalis, Bond et al. 2009).

Species living within dynamic environments may also be subject to repeated population bottlenecks and founder events, processes which result in the loss of genetic diversity and increase genetic drift (Vrijenhoek 1985, Vucetich and Waite 1998, Reed 2008, Chapter 5) and may lead to the accumulation of deleterious alleles, inbreeding depression and the reduction of population viability (Charlesworth and Charlesworth 1999, Bouzat et al. 2010, Hedrick and Fredrickson 2010). The extent in the loss of genetic diversity depends on the magnitude of the event (i.e. the proportion of individuals of a population lost) and the intrinsic rate of post-disturbance recovery of affected populations (Vrijenhoek 1985). Species with low fecundity and which depend on late seral stage vegetation are particularly susceptible to deleterious genetic processes because the long duration for populations to recover further increases the rate of loss of alleles due to genetic drift (Vrijenhoek 1985). For species with low fecundity occupying semi-arid and arid zones (e.g. Black-eared Miner, Higgins et al. 2002), the effects of sustained drought on food supplies may further impede population recovery and exacerbate genetic drift.
6.3 Management of populations of the Mallee Emu-wren

This study has identified three pervasive processes that threaten the Mallee Emu-wren;

i) population decline and habitat loss due to landscape-scale fires and altered fire regimes,

ii) adverse genetic and demographic consequences within small and isolated populations.

These threats are likely to be directly or indirectly exacerbated by increased aridity in the species' current geographical range caused by climate warming (Hennessy et al. 2005, Steffen et al. 2009). Although climate warming is a global management problem, I discuss below potential actions that can mitigate these threatening processes. These considerations are not mutually exclusive, and management actions should involve consideration of their wider repercussions on the global distribution of the Mallee Emu-wren and sympatric species.

6.3.1 Fire management

The risk of landscape-scale wildfires destroying a large proportion of the Mallee Emu-wren population was stressed in Chapter 2, and in part, was the basis for the re-listing of this species from Vulnerable to Endangered under the IUCN Red List criterion (IUCN 2001). If a single wildfire were to occur in the Murray-Sunset National Park equal to that experienced in 2003 in the Ngarkat and Big Desert complex (>181 400 ha, Department of Sustainability and Environment 2007) a significant proportion of the global Mallee Emu-wren population would be destroyed. Recognising the catastrophe that such a fire would pose to the Murray-Sunset reserve complex, the state government agency responsible for public land (Department of Sustainability and Environment) has burned wide strips, aligned north-south through the reserve (about 3 x 28 km, see Figure 2.3a, Chapter 2) to impede the spread of large wildfires (Sandell et al. 2006).

Some of the key sites that support Mallee Emu-wrens (Chapter 2, 5 and Appendix II) are at greater risk of being destroyed by wildfires than others because of a) their position relative to ignition sites and the prevailing direction of fire, b) the type of surrounding land (e.g. agricultural land, claypans or mallee shrublands) and c) the age
of the vegetation. I suggest that strategic management of this species requires actions to prevent uncontrolled wildfires encroaching on known populations (Chapter 3). In South Australia, fine-scale burns have been strategically placed to protect groups of Mallee Emu-wren from wildfire (i.e. south-west of extant Mallee Emu-wren groups). Such strategic burns or other control mechanisms could play a role as part of a larger landscape management plan to protect key populations. On-ground managers (e.g. local rangers and fire crews) need to be aware of location of the key populations, so that their protection can be considered in decision-making processes in the immediate response to wildfires. In addition, fire breaks and back-burning operations should not be conducted within, or close to existing populations.

Ecological burns (i.e. burns to enhance habitat quality) may be warranted at sites where *Triodia* has senesced to a point that it no longer supports Mallee Emu-wrens. Although the maximum age for suitable habitat is unclear (it may vary at local scales depending on rainfall and soil type), data presented in this study suggest that in the northern reserve complexes (Murray-Sunset and Hattah-Kulkynye), ecological burning to conserve local populations of the Mallee Emu-wren should be at intervals of no less than 50 years, and perhaps more than 100 years (Chapter 3). I estimate these figures based on allowing 20 years for *Triodia* to reach a mature growth-phase plus a minimum of 30 years for Mallee Emu-wrens to reproduce (30 overlapping generations) and establish a population following recolonisation. I suggest 30 years post recolonisation as it may take many years for Mallee Emu-wrens to recolonise empty patches, particularly if succeeding years of below-average rainfall impede reproductive output and subsequent population expansion. The rate at which individuals track and recolonise suitable-aged habitat is unclear, but anecdotal evidence from Ngarkat Conservation Park, South Australia suggests that recolonisation occurs via emigration from closely adjacent habitat (Chris Hedge, pers. comm.). Current monitoring of the progression of recolonisation by the Mallee Emu-wren into a 1999 fire footprint in Ngarkat Conservation Park will in the future provide a better estimate of the time taken to colonise and for the population to recover.

A critical aspect of the global management of the Mallee Emu-wren is the appropriate management of patches to ensure long-term genetic connectivity and metapopulation persistence. Metapopulation theory and modelling show that metapopulation persistence depends on individual dispersal ability (Hanski 1999, Hanski and
Ovaskainen 2000, Johst et al. 2002), as well as the spatial aggregation of suitable habitat and the frequency of disturbance (Fahrig 1992, Broughton and Malvadkar 2002, Johst and Drechsler 2003, Vuilleumier et al. 2007). For a species with poor dispersal ability, metapopulation theory and successional patch dynamic theory (Broughton and Malvadkar 2002, Kallimanis et al. 2003) would advocate reducing the spatial correlation of disturbances (i.e. multiple smaller fires, rather than single extensive fires) in a manner that enhances ongoing temporal provision of habitat that is spatially connected (Vuilleumier et al. 2007).

This study has not addressed the size (grain) of a patch required to support viable sub-populations of the Mallee Emu-wren; that is, a sub-population that is of an adequate number and genetic diversity to minimise the risk of extinction from stochastic (environmental and genetic) processes. Manipulation of patch demography (i.e. fire age) could be used to enhance species abundance and population connectivity at the landscape scale (Johnson 2000). Although this level of sophistication in fire management is crucial, it is difficult to implement, especially in dynamic systems that support multiple species at risk that are dependent on different stages of successional habitat (Broughton and Malvadkar 2002, Kelley et al. 2011, Nimmo et al. in litt).

The findings presented here need to be integrated into the broader context of biodiversity conservation across the southern Murray Mallee region, by considering sympatric species of plants and animals, and other landscape-scale processes (e.g. invasive species, habitat fragmentation and climate change). Findings from major research projects (e.g. the Mallee Fire and Biodiversity Project, Deakin and La Trobe Universities) that undertake a holistic, regional or landscape-scale approach are making progress towards meeting this end.

6.3.2 Reintroduction and population augmentation

Both ecological factors and genetic considerations are essential to ensure the persistence of threatened species. Genetic diversity within populations generally has shown to be positively correlated with species persistence and robust ecosystems (Armbruster and Reed 2005). Exceptions occur (Milot et al. 2007, Hable et al. 2009, Johnson et al. 2009) and the underlying mechanism by which genetic diversity influences extinction risk remains yet to be fully resolved (Reed 2010, Bouzat 2010). Nevertheless, an understanding of the small population paradigm (Caughley 1994)
and genetic stochasticity (Reed et al. 2007) has led to an overarching goal of preventing the loss of genetic variability for species conservation (Hedrick and Miller 1992, Reed 2008).

Genetic factors important in conservation can be divided into those with immediate effects, such as inbreeding and genetic drift; and longer term effects such as genetic load and adaptive potential (Bouzat 2010, Hedrick and Fredrickson 2010). Among the problems that conservation managers may have to face in the immediate term are small, isolated populations subject to increased homozygosity that may lead to the accumulation of deleterious alleles, inbreeding depression and a reduction in population viability (Charlesworth and Charlesworth 1999, Jamieson et al. 2007, O’Grady et al. 2006). Numerous studies have shown a strong case for the importance of genetic variability in maintaining population viability (Jamieson et al. 2007, Reed 2010), and genetic augmentation has been shown to improve population viability in highly inbred populations (Hedrick and Fedrickson 2010).

The comparatively low to moderate level of genetic variability within the global population of the Mallee Emu-wren (as found in this study) justifies monitoring of the size and distribution of local populations so that early intervention strategies may be implemented. An increased risk of large wildfires for this region (Hennesy et al. 2005, Steffen et al. 2009) is likely to result in further population fragmentation into small isolated populations, such as those in Ngarkat and Billiatt Conservation Parks and Wyperfeld Conservation Park (Chapter 5). The isolation, small size and low genetic variability of populations in Ngarkat (n=–50) and Billiatt (n=–3) place them at immediate risk of inbreeding depression (Frankham 2005) and warrant urgent consideration for genetic management. For the latter population, unless immediate population augmentation is undertaken, this population is likely to become extinct due to demographic stochasticity. The development of a pre-emptive strategic approach to population augmentation and monitoring in response to potential cataclysmic stochastic events (e.g. prolonged drought or a major fire in the Murray-Sunset NP) will increase the success of future intervention programs.

A proposal to augment the Mallee Emu-wren populations in South Australia genetically and to re-introduce a population into Annuello Fauna and Flora Reserve requires a strategic framework that considers a priori targeted questions (Table 6.2),
monitoring requirements (Ewen and Armstrong 2007, Armstrong and Seddon 2008) and risk assessment (e.g. considering outbreeding depression against the risk of inbreeding depression, Frankham 2005). In this case, questions and issues to consider are focused at the population and metapopulation level (Armstrong and Seddon 2008). A re-introduction program at Annuello Fauna and Flora Reserve could provide an opportunity to implement an adaptive management approach to metapopulation management by incorporating the testing and refining the fine-scale habitat models developed in this thesis (Chapter 3) and post-release monitoring. Detailing a framework is beyond the scope of this discussion, although a summary of some major issues for consideration are presented in Table 6.2.

Table 6.2. Key questions for reintroduction and genetic augmentation of a species. (Modified from Armstrong and Seddon 2008)

<table>
<thead>
<tr>
<th>Population level</th>
<th>Metapopulation level</th>
<th>Ecosystem level</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Establishment:</strong> How is establishment probability affected by the size and composition of the release group?</td>
<td>Where should the translocated population be sourced from?</td>
<td>Is the target species and its parasites native to the ecosystem?</td>
</tr>
<tr>
<td>How are post-release survival and dispersal affected by pre- and post-release management?</td>
<td>How heavily should the source population be harvested?</td>
<td>How will the ecosystem be affected by the target species and its parasites?</td>
</tr>
<tr>
<td><strong>Persistence:</strong> What habitat conditions are required for persistence?</td>
<td>What is the optimal allocation of translocated individuals?</td>
<td>How does the order of re-introductions affect the ultimate species composition?</td>
</tr>
<tr>
<td>How will genetic makeup affect persistence?</td>
<td>Should translocation be used to compensate for isolation?</td>
<td></td>
</tr>
</tbody>
</table>

6.4 Future research

6.4.1 Knowledge gaps in the distribution, ecology and biology of the Mallee Emu-wren

This study has contributed substantially to knowledge of the habitat requirements and ecology of the Mallee Emu-wren and will inform future management of this species. However major gaps exist in the knowledge of the species' distribution and ecology, including:
• distribution and status of the Mallee Emu-wren in the Wyperfeld National Park and Big Desert Wilderness areas (southern reserve complex)
• dispersal patterns and processes (e.g. sex, age and distances)
• metapopulation processes
• foraging ecology
• social structure and reproductive ecology
• productivity in response to rainfall

6.4.2 Population and metapopulation processes in dynamic landscapes

There is a paucity of empirical research that examines demographic and population processes in dynamic landscapes (Brawn et al. 2001, Driscoll et al. 2010). This topic is in urgent need of further work given the magnitude of the adverse impacts on ecosystems that can occur from inappropriate management practices and from changes in disturbance regimes arising from climate warming.
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APPENDIX I

A method for capturing ground-dwelling birds in grassland habitat

Netting technique used to capture Mallee Emu-wrens, Murray-Sunset National Park.
Abstract

Capturing birds is an essential component of many ecological studies of avian populations; particularly where studies require the marking of individuals (i.e. banding studies) or the collection of molecular samples. Mist nets are a widely used method for capturing birds, but are difficult to use under certain circumstances and can be unsuitable if birds are small enough to pass through available mesh sizes. The Mallee Emu-wren (*Stipiturus mallee*) is a tiny, inconspicuous passerine, morphologically adapted to living in dense tussock-grasses and heaths. As a consequence, they are effective at manoeuvring through complex three-dimensional structures, reducing the efficiency of mist netting. Here, I describe a custom-made throw net and capture technique that capitalizes on the species' behaviour to improve the efficiency of capture success. The required effort and success of mist nets is compared with that of the throw nets. The throw nets are easily constructed from inexpensive materials and the technique is sufficiently versatile that it could be applied to the capture of other ground-dwelling grassland birds or other small terrestrial vertebrates.

Introduction

Research into aspects of avian biology frequently involves techniques that require the capture of individuals. Capture is a necessary activity for understanding demographics, behaviour, movement and the collection of morphological measurements or samples for molecular study. Mist netting has long been a successful tool employed for capturing passerines. Mist nets are typically used in gaps within vegetation (e.g. open areas or paths) to passively capture moving birds, or to target particular species aided by playback recording (Bub 1978). Mist netting has limitations when the habitat is not tractable to nets being erected (e.g. continuous thick scrub, swamps or water), the target species occurs in low densities over large areas and when it does not respond to playback recording beyond an individual bird's territory.

The Mallee Emu-wren (*Stipiturus mallee*) is a tiny (4-6 g) passerine endemic to the Murray Mallee region of south-eastern Australia. They have short, rounded wings and filamentous rectrices with reduced barbs; adaptations that facilitate efficient movement through dense vegetation (Rowley and Russell 1997, Schodde 1982, Higgins et al. 2001). They inhabit two principal vegetation associations. In the north of the species' range they occur in open mallee (3-10 m tall, multi-stemmed *Eucalyptus*

*Triodia* is a long-lived, evergreen, tussock-forming perennial. It consists of hard, circular, leaf-blades tapering to needle-like points (Lazarides, 1970, 1997). The leaf-blades of an individual plant are densely arranged so that only very small vertebrates are able to pass through the plant without difficulty. Mature plants form large tussocks to about 1.5 m high. With age, these tussocks develop into enlarged rings with open centres, as central trillers die and new growth is produced at the outer margins (Lazarides 1970). These characteristic rings may form up to two or more metres wide (Specht 1981). *Triodia* is the favoured habitat of the Mallee Emu-wren and they are known to nest in the centre of mature plants (Higgins et al. 2001).

During the breeding season (August to December) pairs of Mallee Emu-wrens occupy about 5 ha territories. These territories appear not to be defended during the non-breeding season, when groups of 6-10 individuals typically forage together over much larger areas (S Brown, unpublished data). Mallee Emu-wrens typically forage in dense *Triodia* or low level shrubs (Higgins et al. 2001), mostly hopping, and occasionally flying, between plants, rarely venturing into open areas. They are poor fliers, rarely seen to fly at heights greater than 1 m unless chasing a conspecific within their territory (S Brown, pers. obs.). Mallee Emu-wrens have a weak, high pitched call that is audible during windless conditions at about 50-60 m. They respond to playback recording during both breeding and non-breeding seasons (S Brown, pers. obs.).

The capture of Mallee Emu-wrens is difficult for several reasons. The habitat of the Mallee Emu-wren consists of a structurally complex ground flora, a shrubby understorey, scattered low level twigs and broken branches from fallen *Eucalypt* stems. In the absence of narrow tracks, the density of the vegetation requires that mist nets are erected with multiple bends, weaving around *Triodia* and small shrubs. This is time consuming and, given the relatively low density of birds (0.013 – 0.25 ha⁻¹)
(Brown et al., 2009), the probability of encountering birds in the immediate area can be low. Attempts to capture Mallee Emu-wrens using conventional 25 mm mist nets are difficult as the birds easily pass through the net mesh. Field observations attribute this to their ability to manoeuvre through dense leaf-blades of *Triodia* (S Brown pers. obs.). When encountering 25 mm mesh, individuals simply open their short rounded wings above their back and pass through the nets. The use of two parallel mist nets doubled over (i.e. four layers of netting) and flushing the birds into the nets also proved ineffective. The use of doubled over 35 mm monofilament nets captured birds more efficiently, but it was not always practical to carry equipment into remote areas, whilst searching for birds in low densities over a large region. Once birds were located, the time taken to set multiple nets at ground level between vegetation often meant the birds had moved on to other areas before the net setting could be completed.

With these limitations in mind, a throw net of black mosquito netting weighted with lead beading, large enough to cover individual *Triodia* tussocks was developed. These nets were simple to make and sturdy enough to withstand catching on branches, with the added advantage that several nets were easily carried in the field.

**Methods**

**Study Area**

From April 2006 to July 2008, Mallee Emu-wrens were studied in remote conservation reserves within the Murray Mallee region (34°30’S–35°15’S; 141°00’N–143°00’N), in south-eastern Australia. Mallee Emu-wrens were searched for, and captured, in mallee-*Triodia* associations in the north of their geographic distribution, and in mallee-heath associations in the south-west of their distribution, in South Australia.

**Design of throw nets**

Standard black nylon mosquito netting and lead beading (conventionally used to weight curtains), available from material suppliers, are used to make nets. Netting was sewn together to create a single 3 m x 2 m or larger sheet; the size required to adequately cover large *Triodia* plants. Fifteen centimetres in from the edge, a continuous run of lead beading was sewn onto the mosquito netting in the manner of upholstery piping (Fig. 1a). The lead beading ensured that the mosquito netting was weighted on the ground to prevent birds from escaping under the netting. The
components for each net cost approximately AUD$60 ($15 for netting and $45 for lead beading).

Using throw nets

Groups of Mallee Emu-wrens were located and, if necessary, enticed to more favourable vegetation nearby by using playback recording of contact and alarm calls (©David Stewart/Nature Sound) played through an MP3 player (iRiver T30MX) and amplified speaker system (JBL OnTour). Most individuals became accustomed to the presence of humans after 10-15 mins, but generally remained at least 10-20 m distant. Whilst the observer used the playback recording intermittently to maintain a visual fix on the group’s location, Mallee Emu-wrens continued foraging in the Triodia with frequent contact calls and singing from low shrubs or upper Triodia leaf-blades. When individuals were seen to enter deep into a large Triodia plant that was not obstructed by shrubs or fallen Eucalypt stems, the throw net(s) were quickly dropped over the plant, trapping the bird. It was essential that the Triodia was large enough (minimum of 1.5 m diameter) that the bird felt more secure by remaining within the Triodia when the observer approached than flying out, otherwise birds flew out before the opportunity to drop the net was completed. This technique was most effective when two observers approached the bird and dropped nets from opposing directions. The net edge was quickly laid to prevent birds escaping through small gaps between the netting and the ground, and then pockets of loose netting were created to trap the bird (Fig. 1 b). Once the netting was in place, a short pole was used to flush the bird from the Triodia into the loose netting.

Standard and monofilament mist nets

Mist nets were erected along narrow tracks or occasionally in open gaps in the vegetation. Initially, 25 mm standard mist nets were used, singly set, then doubled over. Monofilament nets (Bleitz, but no longer available) with a 35 mm mesh size were subsequently trialled doubled over. All nets were secured to the ground at about 30 cm intervals to prevent birds passing under the nets. Playback recording was used to attract Mallee Emu-wrens to the nets. When birds became trapped in the nets, the netting was immediately thrown over the mist net and bird. Birds rarely became tangled in the netting for more than a few seconds and the additional throw net
prevented the birds’ escape. On a few occasions, individuals were caught in the mist net by their feathers and required extraction using conventional techniques.

Comparison of efficiency of the two techniques

The effort (hours), capture and observed escape rates (designated as ‘misses’) were recorded to determine the most efficient method to capture Mallee Emu-wrens. A miss was recorded when: 1) a bird passed directly through a mist net, or was briefly entangled and then escaped, or 2) a bird escaped from a *Triodia* plant whilst the observer was in the process of placing the throw net over the plant, during the securing of the net or whilst flushing the bird.

![Diagram of net design and use](image)

**Figure 1.** Diagrammatical representation of a) the design of nets, and b) their use in trapping a Mallee Emu-wren in *Triodia*

Results

Effort and effectiveness of capture

The low density of Mallee Emu-wrens and the lack of data on local population distribution meant that many hours were spent searching for birds. Throw nets were used where the search for birds was required over large areas (> 100 ha) and access to tracks were absent or limited. This increased the opportunity to locate high quality habitat in localised areas where birds may occur. When birds were encountered near tracks, and there was immediate access to equipment, mist nets were erected along narrow tracks or occasionally in open vegetation. On several occasions, by the time nets were set, groups of Mallee Emu-wrens had moved on.
In areas that contained low, dense mallee-heath (i.e. in the south of the species' range), it was not possible to set mist nets unless a track was nearby. In this habitat, unusually large Triodia occurred and all birds were trapped in a combination of small shrubs and Triodia. In order to successfully capture birds in this vegetation, several field personnel and the use of 4 or 5 nets was required.

Standard 25 mm mist nets were inefficient in capturing Mallee Emu-wrens, even when doubled over and the pockets were set loosely (Table 1). This was attributed to the coarseness of the netting that failed to catch their feathers. The larger mesh size, but significantly finer monofilament nets (35 mm mesh), often held individuals for several seconds, providing the opportunity to retrieve the bird before it escaped (Table 1).

Table 1. The number of hours devoted to different capture techniques, capture rates per hour effort of male and female Mallee Emu-wrens and recorded misses.

<table>
<thead>
<tr>
<th>Method</th>
<th>No. of hours</th>
<th>Missed</th>
<th>Male</th>
<th>Female</th>
<th>Capture rate/hr</th>
<th>Misses rate/hr</th>
</tr>
</thead>
<tbody>
<tr>
<td>Throw nets</td>
<td>112</td>
<td>50</td>
<td>28</td>
<td>24</td>
<td>0.46</td>
<td>0.46</td>
</tr>
<tr>
<td>35 mm monofilament nets, doubled</td>
<td>35</td>
<td>34</td>
<td>7</td>
<td>2</td>
<td>0.37</td>
<td>0.97</td>
</tr>
<tr>
<td>25 mm nets, doubled</td>
<td>13</td>
<td>9</td>
<td>1</td>
<td>1</td>
<td>0.15</td>
<td>0.69</td>
</tr>
</tbody>
</table>

Behaviour of Mallee Emu-wrens

Generally, the approach to capturing Mallee Emu-wrens was to search until a group was encountered. Once located, birds were followed from 25-30 m distance until they became accustomed to the presence of humans. Once accustomed, observers could usually follow the birds from 15-20 m without disturbing their foraging behaviour. Birds were either followed until the opportunity arose to capture one in a large Triodia, or they were enticed to areas that contained larger Triodia by intermittent use of playback recording. Usually a combination of approaches was used. Very large Triodia plants were not ideal for capturing birds as they did not flush out of the plants easily. On several occasions, these capture attempts were abandoned after 15 mins so as not
to stress the bird. In instances where birds escaped, this occurred because the nets were not completely secured against the substrate.

The presence of humans and the playing of Mallee Emu-wren calls elicited a variety of behavioural responses in the birds, depending on the structure of the habitat which the birds occupied. For example, in habitat that consisted of low density Triodia plants with 1-1.5 m tall Callitris shrubs, Mallee Emu-wrens preferred to investigate the source of the playback recording from the dense foliage of Callitris shrubs. On these occasions, by erecting a 35 mm mist net between stands of Callitris, birds were captured as they flew between the shrubs. On one occasion, four of five individuals from a group were captured; though a female was not captured despite passing through the net eight times. Frequently, a bird could be caught by using a throw net whilst it was foraging in a large Triodia plant adjacent to the mist net and playback recording equipment.

**Discussion**

By using knowledge of the species’ behaviour, both the encounter and capture rates of Mallee Emu-wrens were improved. The availability of the two techniques (mist netting and throw nets) facilitated more efficient capture of birds depending on the structure of the habitat. An advantage of throw nets was that it made it possible to search remote areas several kilometres from tracks without carrying heavy cumbersome equipment (i.e. poles and sand pegs). It provided flexibility because the light-weight throw nets were always on hand when chance encounters with Mallee Emu-wrens were made.

The rate of misses for the standard 25 mm mist nets was less than that recorded for the 35 mm monofilament mist nets despite recording a higher capture rate for the 35 mm mist nets. This can be attributed to an effort bias because 25 mm mist nets were used infrequently after the early phase of the project. The 35 mm monofilament nets were more likely to entangle the birds' feathers restraining them briefly and providing an opportunity to capture them. The disadvantage of monofilament nets is that they can cause harm to birds by cutting into soft parts when they are entangled, though this was not a problem with these tiny birds.
The method described here could be applied to other ground-dwelling grassland birds or organisms that live in similar structural habitat and have similar behavioural traits. On one occasion, a Mallee Ningauli (Ningauli yvonneae); a marsupial that inhabits Triodia was captured when its presence was mistaken for the similar-sized Mallee Emu-wren. Other species that inhabit Triodia (e.g. venomous snakes) may pose a hazard using this technique and should be considered.

Acknowledgements

I wish to acknowledge the volunteers that assisted in the capture of Mallee Emu-wrens, though too large to list here. However, I particularly thank Ash Herrod for suggesting the use of black mosquito netting instead of white, and his generous assistance on many field trips. I also thank Martin Schulz for providing 35 mm monofilament nets. Thank-you to Andrew Bennett and Rohan Clarke for comments on the manuscript. This research was funded by Parks Victoria, Holsworth Wildlife Foundation and the Winifred Violet Scott Trust. The research was carried out in accordance with research permits A34/2005 (Deakin University Ethics Committee) and the Department of Sustainability and Environment, permit No. 10003389 and the South Australia Department of Environment and Heritage, permit No.G24995.

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Survey of the Mallee Emu-wren *Stipiturus mallee* within Murray Sunset National Park and Hattah-Kulkyne National Park in October 2009

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Mallee Catchment Management Authority
February 2010

![Juvenile female Mallee Emu-wren. Photo Simon Watson](image_url)

This work was commissioned by the Mallee Catchment Management Authority with support from Parks Victoria, Australia. The views expressed in this report are those of the author and do not necessarily reflect the views of the Mallee Catchment Management Authority or Parks Victoria, Australia.
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1 Executive Summary

Since 1996 the Murray-Mallee region has experienced consecutive years of higher than average temperatures, with two-thirds of years experiencing lower than average rainfall. Given this, it is anticipated that the population size of the endangered Mallee Emu-wren *Stipiturus mallee* may have experienced a decline. The aim of this survey was to provide information on the current status of the Mallee Emu-wren within the Murray-Sunset and Hattah-Kulkyne National Parks and gather information on population trends. The project also aims to identify the need for future management actions for the Mallee Emu-wren based on population trends using current data versus data from 2001-2007.

Areas within the Murray-Sunset and Hattah-Kulkyne National Parks were surveyed for Mallee Emu-wrens and other threatened birds during October 2009. Deakin University staff experienced in surveys of mallee birds covered 149 km of transects, spanning 20 field person-days, using playback calls for threatened species at 298 points.

Twenty-two groups of Mallee Emu-wrens, consisting of between 1-4 individuals, were detected. Density estimates of this species for Ecological Vegetation Classes and fire age-classes were explored using DISTANCE analysis and compared to previous estimates. Densities of the Mallee Emu-wren were slightly higher than previous estimates; however, the broad confidence intervals mean that it is not possible to conclude whether there has been a change in the population trend.

Two main factors thought to influence the population size of the Mallee Emu-wren are the extent of suitable habitat and climate fluctuations. Key Ecological Vegetation Classes were found to be Loamy Sands Mallee and Woorinen Sands Mallee, with Mallee Emu-wrens preferring Woorinen Sands Mallee. Within these Ecological Vegetation Classes, Mallee Emu-wrens were found only in fire age-classes greater than 16 years since last burned. Mallee Emu-wren density was greater in fire age-classes 16-29 years compared with >29 year fire age-classes. The number of hectares of suitable habitat has not altered significantly since 2006.

The distribution of the Mallee Emu-wren (and other threatened birds) revealed by this survey suggest there are localised 'hotspots' for threatened mallee birds including the Mallee Emu-wren; that is, locations where there are a cluster of records of one or more species.

Recommendations from this report include:
A) that managers of the Murray-Sunset National Park and Hattah-Kulkyne National Park are made aware of avian hotspots and 1) these are considered in prescription fire planning and 2) they are given priority in biodiversity asset protection in the event of a wild-fire.

B) a more refined technique for DISTANCE sampling be developed for detecting population trends in the Mallee Emu-wren and other similar bird species.
2 Objectives

This research sought to achieve the following objectives:

- provide information on the current status of the Mallee Emu-wren within the Murray-Sunset and Hattah-Kulkyne National Parks;
  - employ transects and call-playback to survey for the Mallee Emu-wren and other threatened birds in the Murray-Sunset and Hattah-Kulkyne National Parks;
  - record habitat at each transect and document fire history and Ecological Vegetation Classes;
  - determine population densities of the Mallee Emu-wren in Ecological Vegetation Classes and fire age-classes;
- identify the need for future management actions for the Mallee Emu-wren based on population trends using current data versus 2001-2006 data.

3 Introduction

In Australia, 17.3% of avian taxa are considered Threatened or Near Threatened (BirdLife International 2008; Garnett and Crowley 2000). Twenty-six species have become extinct, but most disconcerting is that the rate of taxa qualifying for higher categories of threat status is increasing (Brooke et al. 2008). More than 80% of threatened bird species in Australia are identified as being affected by a combination of habitat loss, fragmentation and degradation (Garnett and Crowley 2000), with nearly half also affected by altered fire regimes (Woinarski and Recher 1997; Gill et al. 1999; Garnett and Crowley 2000). In recent years, accumulating evidence suggests climate change is also having a detrimental effect on many organisms, and even entire ecosystem processes (Chambers et al. 2005; Wormworth and Mallon 2006). In particular, studies of birds have shown that climate change is altering distributions, abundance, movement patterns, phenology, community composition, physiology, morphology and behaviour (Woinarski and Recher 1997; Garnett and Crowley 2000; Crick 2004).

Fire-prone ‘mallee’ vegetation (semi-arid eucalypt shrublands 3-10 m tall, in which individual trees are multi-stemmed) supports a high proportion of avian species of conservation concern (Woinarski and Recher 1997; Garnett and Crowley 2000; Higgins et al. 2001; Baker-Gabb 2004; Clarke 2005a). Those most threatened are mallee endemics, or near endemics, that characteristically are highly site tenacious, have low fecundity, and specialist habitat requirements (Schodde 1989; Benshemesh 2000; Garnett and Crowley 2000; Baker-Gabb 2004, Clarke 2005a). This includes the Mallee Emu-wren *Stipiturus mallee*.

The Mallee Emu-wren is a small (4-6g), endemic passerine that occurs in a limited part of the Murray Mallee region of south-eastern Australia. Little is known of the life history, breeding biology or ecology of this secretive species. It is thought to be highly sedentary, with low fecundity, and is a habitat specialist with a patchy distribution (Schodde 1982; Menkhorst and Bennett 1990; Higgins et al. 2001; Rowley and Russell 1997); attributes limiting the ability to disperse and re-colonise, and making the species vulnerable to environmental changes (Schodde 1982; With and King 2001).
Early 20th Century records indicate Mallee Emu-wren once occupied a region extending from Annuello Fauna Reserve in the east of Victoria (Higgins et al. 2001) to eastern South Australia bounded by Billiatt Conservation Park, Nadda, Pambinga and Pinnaroo and Comet Bore (Ngarkat Conservation Park) (Garnett 1992; Carpenter and Mathews 1986; Hatch 1977; Eckert 1977; McGilp 1943; Howe and Burgess 1942), and from the northern Sunset Country to south of the Big Desert at Yanac (Chisholm 1946; Howe and Burgess 1942; Howe 1933). Wide scale habitat clearance in the 1920s-60s (Harris 1990), fragmented the vegetation and population into two large regional areas and several isolated reserves (Figure 1). Mallee Emu-wren populations have been extirpated from those areas under agricultural cultivation and have disappeared from several of the small to medium sized conservation reserves (Brown et al. 2009). The decline from Wathe and Bronzewing Fauna and Flora Reserves may be because of unsuitable fire history or demographic process or a combination of both. A series of landscape-scale wildfires in 2003 and 2005, compounded by prolonged drought, have severely affected most of the south-western populations in the large reserves (i.e. Billiatt, Ngarkat and Big Desert conservation areas). The decline in Wyperfeld National Park is unknown, but we can speculate that fire regimes and/or drought are influencing population numbers and distribution. Analysis of survey data collected between 2001 and 2006 has shown that the Murray-Sunset and Hattah-Kulkyne National Parks contain the majority of the global population of the Mallee Emu-wren (Brown et al. 2009). Although the estimated number of Mallee Emu-wrens was found to be relatively high for a threatened species (16,821: range 8,431-39,104), the likelihood of wide-scale fires extirpating entire populations within all reserves was considered to be high. Analysis of population numbers, individuals and threats warranted re-assessment of the status of the Mallee Emu-wren under IUCN Red List criteria (IUCN 2001) and in May 2008 it was re-assessed as globally Endangered (Birdlife International 2008).

Figure 1. Distribution of the Mallee Emu-wren within the Murray Mallee. Dark grey = reserve system, pale grey hatching = approximate historical extent, FFR = Fauna and Flora Reserve
The distribution of the Mallee Emu-wren spans two major landforms within the Murray Mallee region; namely the Woorinen Formation that comprises short, narrow-crested, linear east-west dunefields, and the Lowan Sands that comprise of steep parabolic, transverse and irregular dunefields. Lowan Sands intrude into the Woorinen Formation in the southern half of the Sunset Country (i.e. Murray-Sunset and Hattah-Kulkyne National Parks) (Wasson 1989). Vegetation communities within these landforms are floristically and structurally variable reflecting the complex origins of the soils and overlying sands, topology of the dunefield systems, and disturbance history - notably fire regimes (Wasson 1989; Cheal and Parkes 1989; Menkhorst and Bennett 1990). The vegetation communities of the Woorinen Formation, pertinent to the Mallee Emu-wren, are generally dominated by open, 3-10 m high mallee Eucalypt spp. Small trees and shrubs associated with these communities include Acacia spp, Dodonaea spp, Exocarpos spp, Melaleuca spp and Callitris verrucosa (Cheal and Parks 1989)(Figure 2). In the drier, sandy soils commonly associated with the dune slacks or crests, the herbaceous layer is often dominated by continuous cover of Triodia irritans (hereafter referred to as Triodia) (Figure 3). Triodia is a sclerophyllous grass which forms large hummocks up to 1-2 m in diameter. Triodia is characterised by a distinctive growth-phase pattern. Small, immature plants are similar in structure to large grass hummocks, however as a plant matures - growing outward, it forms a large concentric ring (Sprecht 1981). Triodia is thought to reach its peak growth-phase at around 15-30 years of age (Bradstock and Gill 1993). The Mallee Emu-wren is associated with Triodia and they forage and nest within the hummocks (Schodde 1982; Robertson et al.1989; Higgins et al. 2001). The vegetation communities in the Lowan Sands, in the southern range of the Mallee Emu-wren, are the mallee-heath and heath-like communities (Mercer 1998; Menkhorst and Bennett 1990; Cheal and Parks 1989). They have a structurally dense, sclerophyllous shrub-layer and scattered Triodia and occasionally lack a mallee eucalypt overstorey.

Figure 2. Habitat of a Mallee Emu-wren site at the western sector of the Murray-Sunset National Park. The understorey comprised of a mix of small shrubs and large Triodia plants favoured by Mallee Emu-wrens.
Figure 3. Habitat of a Mallee Emu-wren site along the Nowingi Track at Hattah-Kulkyne National Park. Note the dense swathes of mature Triodia.

A landscape-scale study of habitat requirements in the Murray-Sunset and Hattah-Kulkyne National Parks, found that the Mallee Emu-wren occupies vegetation greater than 15 years since the last burn and that mallee-Triodia vegetation associations support the greatest density. Woorinen Sands Mallee and Loamy Sands Mallee were found to be key Ecological Vegetation Classes for the Mallee Emu-wren, and the 16-29 year fire age-class contained the greatest densities (Brown et al. 2009).

Since 1996, the Murray-Mallee region has experienced higher than average temperatures for consecutive years since 1996, with more than two-thirds of the past 10 years experiencing lower than average rainfall (Bureau of Meteorology 2010). Given the lower rainfall patterns, it is anticipated that the population size of the Mallee Emu-wren may have experienced a decline. This study sought to gather information on the trend in population numbers within the species stronghold. Earlier work by Brown et al. (2009) is used as a baseline value against which population trends may be measured.

4 Outcomes
The intended outcome of this project is to ensure that the Mallee Emu-wren can survive, flourish and retain its potential for evolutionary development in the wild, as per the Draft Flora and Fauna Guarantee Action Statement.
5 Methods

Digital Data Layers

Digital maps for the Murray Mallee reserves in Victoria were prepared using ArcMap 9.2 (ESRI). Digital data for vegetation types (Ecological Vegetation Classes (EVCs)) and fire footprints were layered and delineated. Ecological Vegetation Classes were derived from the EVC_BSC100 data layer. Fire footprints were prepared from satellite images available from 1972 onwards (Mallee Fire and Biodiversity Project, La Trobe and Deakin Universities), Fire_Fire100_2008 and Fire_Fire100_2009 (Department of Sustainability and Environment 2010).

Records of the Mallee Emu-wren

Records for Mallee Emu-wrens were collected during transect surveys in October 2009. About 70% of transects were identical to those surveyed in previous years. Given the nature of the mallee topography and vegetation, several vegetation types were traversed (Table 1). Systematic transects of 500 m length were traversed on foot by experienced observers. Transects were continuous, with the end of each transect equating to the start of the next transect (Appendix 3). Searches commenced at dawn and continued until about 1300 hrs unless conditions were deemed unsuitable (windy, wet or too hot for the observers). At the start of each 500 m transect, a single 60 sec sound recording track of the Mallee Emu-wren contact and alarm calls (©David Stewart/Nature Sound) was played through an MP3 player and amplified speaker system. Call playback was followed by a 30 second listening period.

Detailed information was gathered for each group of Mallee Emu-wrens encountered. This included the number of individuals present, their sex, the vegetation type they occupied and notes on breeding activity. When birds where located whilst traversing transects, both the bird and the observers co-ordinates were recorded on a Garmin GPS. The perpendicular distance from the fixed transect line was calculated (m) and used for subsequent analysis.

Records for the years 2001-2006 were used for yearly comparison. Data for the years 2001-2006 were collected in a similar manner with minor differences (see Brown et al. (2009) for details).

Density of the Mallee Emu-wren

The program DISTANCE (Thomas et al. 2002) was used for all data exploration and distance-sampling analyses. Mallee Emu-wrens forage in breeding pairs or family groups during the breeding season and individuals within a group generally forage in close proximity (<15 m) to one another (S Brown, personal observations). Consequently, no attempt was made to ascertain the centre of the group; the first sighted bird was used to determine the perpendicular distance for that group. Data points from all surveys (2001-2009) were used to create a distance detection function for the Mallee Emu-wren, and this function was used in subsequent analyses. Following Buckland et al. (1993), we dealt with outliers by truncating the data set to exclude records beyond 50 m distance. Visual inspection of the histograms of sighting distances excluded uniform or negative exponential distributions as suitable models.
for the detection curve. The detectability function for the Mallee Emu-wren was compared within Ecological Vegetation Classes types and globally using pooled data from all years and applied at the stratum level (i.e. Ecological Vegetation Classes and fire age-classes).

Four models (half-normal with cosine expansion, half-normal with simple polynomial expansion, half-hazard with cosine expansion, half-hazard with simple polynomial expansion) were considered for analysis. The model with the lowest Akaike’s Information Criterion (AICc) was automatically selected. Group densities of the Mallee Emu-wren (groups/ha) were determined by Ecological Vegetation Class, fire age-class, year and in combination.

Estimation of Population Size within the Murray-Sunset and Hattah-Kulkyne National Parks

The total number of groups of Mallee Emu-wrens for each reserve was determined by multiplying the average density for each Ecological Vegetation Class and fire age-class by the corresponding area (km²) within each reserve. The population size for the entire Murray-Sunset and Hattah-Kulkyne National Parks was extrapolated by the number of birds in a breeding group (2.0 birds/group).

Table 1. Composition and benchmarks (% cover) for major Ecological Vegetation Classes (EVCs) in the Murray-Sunset National Park and Hattah-Kulkyne National Park, that were included in this study.

<table>
<thead>
<tr>
<th>EVC</th>
<th>Broad Description</th>
<th>Key Understorey Composition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Woorinen Mallee</td>
<td>Mallee woodland to 12m tall</td>
<td>Sub-shrubs</td>
</tr>
<tr>
<td></td>
<td>Open chenopod understorey</td>
<td>Herbs</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Grasses</td>
</tr>
<tr>
<td>Woorinen Sands Mallee</td>
<td>Mallee shrubland to 7m tall</td>
<td>Hummock grass <em>(Triodia spp.)</em> 15% cover</td>
</tr>
<tr>
<td></td>
<td>Hummock dominated understorey</td>
<td>Medium shrub</td>
</tr>
<tr>
<td>Lowan Sands Mallee</td>
<td>Low woodland mallee to 7m tall</td>
<td>Healthy understorey</td>
</tr>
<tr>
<td>Loamy Sands Mallee</td>
<td>Low mallee shrubland to 5m tall Scattered shrubs above a</td>
<td>Hummock grass <em>(Triodia spp.)</em> 5% cover</td>
</tr>
<tr>
<td></td>
<td>hummock grass layer</td>
<td>Medium shrub</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Small shrub</td>
</tr>
<tr>
<td>Red Swale Mallee</td>
<td>Dense to whipstick mallee to 6m tall</td>
<td>Medium shrub</td>
</tr>
<tr>
<td></td>
<td>Sparse understorey</td>
<td>Small shrub</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Soil crust</td>
</tr>
<tr>
<td>Chenopod Mallee</td>
<td>Open to very open mallee woodland to 12m tall</td>
<td>Saltbush</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Semi-succulent understorey</td>
</tr>
<tr>
<td>Parilla Mallee</td>
<td>Open mallee to 10m</td>
<td>Highly variable floristic understorey and/or</td>
</tr>
<tr>
<td></td>
<td></td>
<td>well-developed woody shrub</td>
</tr>
<tr>
<td>Sandstone Ridge Mallee</td>
<td>Low open mallee (3m) with tall shrubby understorey or</td>
<td>Medium shrub 40% cover</td>
</tr>
<tr>
<td></td>
<td>shrubland with emergent mallee</td>
<td></td>
</tr>
</tbody>
</table>
6 Results

Records of the Mallee Emu-wren

Between the 4-8th of October 2009, a total of 143 km of transects were traversed at five geographic locations within the Murray-Sunset and Hattah-Kulkyne National Parks. Twenty-two groups of Mallee Emu-wrens were observed by transect and playback (19 in Murray-Sunset National Park and 3 in Hattah-Kulkyne National Park) with Mallee Emu-wrens observed at all five locations (Figure 4) (Appendix I). At the two most northerly transects along the South Bore Track, relatively high numbers of other threatened birds were also recorded. Of particular note, 27 Red-lobed Whistlers (*Pachycephala rufogularis*), 6 Striated Grasswrens (*Amytornis striatus*), 4 Gilberts Whistlers (*Pachycephala inornata*) and 4 groups of the Mallee Emu-wren were recorded within about 20 ha (data not shown).

Observed group sizes of Mallee Emu-wrens varied from 1-4 individuals (average = 2.7). The composition of observed groups was as follows: a lone adult (n=1), a breeding pair where the female was observed with a bent tail indicating nesting (n=2), family groups consisting of a breeding pair and 2 chicks (n=2), groups of two (unknown composition but behaviour suggests likely to be adult pairs)(n=9), single chick (n=1) and unknown composition (n=4) (Appendix I).
Figure 4. Extent of fire age-classes for Woorinen Sands Mallee and Loamy Sands Mallee and Mallee Emu-wren records collected during September 2009 and all other years.
Estimates of Group Density

Nineteen of the 22 groups of Mallee Emu-wrens (group size 1 to 4 individuals) detected during the transect surveys were used in DISTANCE analysis to determine group densities. Three groups were excluded from the detection function analysis as they were beyond 50 m. No Mallee Emu-wrens were detected in Parilla Mallee, Sandstone Ridge Shrubland, Woorinen Mallee or mallee that had been burned less than 16 years ago and these substrata were excluded from further analysis. Two Ecological Vegetation Classes (Woorinen Sands Mallee and Loamy Sands Mallee) and two fire age-classes (16-29 yrs and >29 yrs) were tested, individually and in combination, to explore their influence on the density of the Mallee Emu-wren.

The detection function produced by DISTANCE was explored by year, by Ecological Vegetation Class, and pooled. All models obtained for the detectability function fitted well. The detectability function differed little between the previous study by Brown et al. (2009), (2001-2006 pooled) and this survey in 2009, or between Ecological Vegetation Classes, and so a pooled detectability function (n = 68 observed groups) was considered appropriate, and was applied globally and at the stratum level. Similar estimates for densities of groups were obtained for all exploration tests regardless of the form of the model tested. The models ‘Half-normal + cosine’ or ‘Half-normal + simple polynomial series expansion’ had the equally lowest AICc value. Half-normal + cosine was used for all subsequent analysis.

Comparison of the density of groups of the Mallee Emu-wren for each year is shown in Figure 5a. From 2001 to 2003, the results suggest a possible slight decline in Mallee Emu-wren numbers with an apparent increase in 2006 - 2009, but the confidence intervals for the density estimates are very broad. This means that it is not possible to reliably conclude that there has been a change in density since 2001-2009. The average mean maximum temperature and rainfall is given for each year (Figure 5a) (Walpeup Research Station, Bureau of Meteorology, 2010). Since 1996, each year has had above average temperature, ranging from values that are 1-5% greater than the long-term average. With the exception of 2007, each year has experienced below average rainfall - most years by more than 10%.

Using pooled data (i.e. all years), exploration of density estimates for fire age-classes show that the density of groups of Mallee Emu-wrens was considerably higher in the 16-29 fire age-class (0.0075 groups/ha)(CI 0.001-0.005) compared to the >29 fire age-class (0.0022 groups/ha)(CI 0.005-0.011) (Figure 5b, Table3). Density estimates for Ecological Vegetation Classes show that Lowan Sands Mallee (0.0031 groups/ha)(CI 0.0019-0.0053) is slightly less favourable habitat than Woorinen Sands Mallee (0.005 groups/ha)(CI 0.003-0.008). A final exploration, by splitting each of the two Ecological Vegetation Classes into two fire age-classes, demonstrated that fire age-class is the overriding factor in determining densities. For each of the Ecological Vegetation Classes, the 16-29 fire age-class had higher densities of the Mallee Emu-wren than the >29 fire age-class. These results were consistent when analysed by year (Table 3).

Regional Population Size

Using the area (km²) calculated from digital maps, the number of groups of Mallee Emu-wren and individuals was calculated for each Ecological Vegetation Class and fire age-class within three reserves (Table 4). GIS analysis of the distribution of key
vegetation types and fire age-classes show that since 2006 the total areas have altered little. The total area of the 16-29 year fire age-class has declined by about 9%, due largely to maturation of the fire age-class rather than habitat lost by fire; whilst the >29 year fire age-class has declined by about 4%. The Murray-Sunset National Park and adjacent state forests (i.e. Murray-Sunset reserve complex) contain the vast majority of the Mallee Emu-wren population in Victoria, with an estimated 12,449 individuals (range 3,738 – 42,995) or about 84% of the global population. Hattah-Kulkyne National Park supports a moderate-sized population (1,054, range 337-3,497).

Table 3. Densities (ha) of Groups of Mallee Emu-wrens for; i) years 2001, 2002, 2003, 2006, 2009 across all Ecological Vegetation Classes (EVCs) and, ii) by Loamy Sands Mallee (LMS) and Woorinen Sands Mallee (WSM) and fire age-class (FAC)

<table>
<thead>
<tr>
<th>Year</th>
<th>EVC</th>
<th>FAC</th>
<th>Density (CI) ha</th>
<th>CV</th>
<th>n#</th>
<th>n*</th>
<th>Transect effort km</th>
</tr>
</thead>
<tbody>
<tr>
<td>2001</td>
<td>LSM</td>
<td>&gt;29</td>
<td>0.006 (0.002 - 0.02)</td>
<td>60</td>
<td>14</td>
<td>N/A</td>
<td>160</td>
</tr>
<tr>
<td></td>
<td>16-29</td>
<td></td>
<td>0.0009 (0.0001-0.006)</td>
<td>133</td>
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<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>WSM</td>
<td>&gt;29</td>
<td>0.01 (0.003 - 0.03)</td>
<td>56</td>
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<td></td>
<td>16-29</td>
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<td>0.0009 (0.0001-0.006)</td>
<td>133</td>
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<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>Total</strong></td>
<td></td>
<td><strong>0.003 (0.001 - 0.007)</strong></td>
<td><strong>41</strong></td>
<td>14</td>
<td>N/A</td>
<td><strong>160</strong></td>
</tr>
<tr>
<td>2002</td>
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<td>0.0008 (0.0004)</td>
<td>107</td>
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<td>40</td>
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<tr>
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<td>0.004 (0.006 - 0.03)</td>
<td>127</td>
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<tr>
<td></td>
<td>16-29</td>
<td></td>
<td>0.006 (0.002 - 0.02)</td>
<td>64</td>
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<tr>
<td></td>
<td><strong>Total</strong></td>
<td></td>
<td><strong>0.004 (0.001 - 0.01)</strong></td>
<td><strong>52</strong></td>
<td>14</td>
<td>N/A</td>
<td><strong>160</strong></td>
</tr>
<tr>
<td>2003</td>
<td>LSM</td>
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<td>0.0009 (0.0005)</td>
<td>100</td>
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<td>16-29</td>
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<tr>
<td></td>
<td><strong>Total</strong></td>
<td></td>
<td><strong>0.0003 (0.000 - 0.001)</strong></td>
<td><strong>101</strong></td>
<td>1</td>
<td>N/A</td>
<td><strong>160</strong></td>
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<td>2006</td>
<td>LSM</td>
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<td>0.002 (0.003 - 0.008)</td>
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<td></td>
<td>16-29</td>
<td></td>
<td>0.009 (0.005 - 0.02)</td>
<td>34</td>
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</tr>
<tr>
<td></td>
<td>WSM</td>
<td>&gt;29</td>
<td>0.029 (0.01 - 0.089)</td>
<td>61</td>
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<td>42</td>
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</tr>
<tr>
<td></td>
<td><strong>Total</strong></td>
<td></td>
<td><strong>0.005 (0.003 - 0.008)</strong></td>
<td><strong>30</strong></td>
<td>20</td>
<td>4</td>
<td><strong>160</strong></td>
</tr>
<tr>
<td>2009</td>
<td>LSM</td>
<td>&gt;29</td>
<td>0.01 (0.003 - 0.05)</td>
<td>84</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>16-29</td>
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<td>74</td>
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<tr>
<td></td>
<td>WSM</td>
<td>&gt;29</td>
<td>0.02 (0.009 - 0.05)</td>
<td>44</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>16-29</td>
<td></td>
<td>0.048 (0.014 - 0.17)</td>
<td>70</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>Total</strong></td>
<td></td>
<td><strong>0.026 (0.014 - 0.05)</strong></td>
<td><strong>34</strong></td>
<td>19</td>
<td>3</td>
<td><strong>143</strong></td>
</tr>
</tbody>
</table>

n# = used in distance analysis  
n* = responded to play-back recording  
LMS = Loamy Sands  
WSM = Woorinen Sands Mallee  
EVC = Ecological Vegetation Class  
FAC = Fire age-class  
CI = 95% confidence interval  
CV = % coefficient of variation  
N/A = not available
Figure 5. Density of Mallee Emu-wren groups by a) year, b) fire age-class, ecological vegetation class each and combined (pooled years). Figure a) shows the yearly rainfall against the mean and along the x axis is presented the percent deviation from the maximum mean temperature for each year. LSM=Loamy Sands Mallee, WSM= Woorinen Sands Mallee.
Table 4. Current population estimates of Mallee Emu-wren groups for selected mallee reserves within north-western Victoria. Current estimates are based on DSE EVC mapping and fire mapping provided by the La Trobe/Deakin Mallee Fire Team.

<table>
<thead>
<tr>
<th>Reserve</th>
<th>EVC</th>
<th>Area (km²)</th>
<th>&gt;29</th>
<th>16-29</th>
<th>Total (16+)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Hattah - Kukyne National Park</strong></td>
<td>Loamy Sands Mallee</td>
<td>103</td>
<td>184 (43-778)</td>
<td>382 (102-1,437)</td>
<td>566 (145-2,215)</td>
</tr>
<tr>
<td></td>
<td>Woorinen Sands Mallee</td>
<td>102</td>
<td>364 (157-844)</td>
<td>124 (35-438)</td>
<td>488 (192-1,282)</td>
</tr>
<tr>
<td><strong>SUB-TOTAL</strong></td>
<td></td>
<td><strong>205</strong></td>
<td><strong>548 (200-1622)</strong></td>
<td><strong>506 (137-1,875)</strong></td>
<td><strong>1,054 (337-3,497)</strong></td>
</tr>
<tr>
<td><strong>Murray-Sunset Park Complex</strong></td>
<td>Loamy Sands Mallee</td>
<td>765</td>
<td>1,036 (245-4,379)</td>
<td>5,214 (1,386-19,607)</td>
<td>6,250 (1,631-23,986)</td>
</tr>
<tr>
<td></td>
<td>Woorinen Sands Mallee</td>
<td>981</td>
<td>2,375 (1,024-5,508)</td>
<td>3,824 (1,083-13,501)</td>
<td>6,199 (2,107-19,009)</td>
</tr>
<tr>
<td><strong>SUB-TOTAL</strong></td>
<td></td>
<td><strong>1,756</strong></td>
<td><strong>3,411 (1,269-9,887)</strong></td>
<td><strong>9,038 (2,470-33,109)</strong></td>
<td><strong>12,449 (3,738-42,995)</strong></td>
</tr>
<tr>
<td><strong>Annuello Fauna and Flora Park</strong></td>
<td>Loamy Sands Mallee</td>
<td>109</td>
<td>193 (46-814)</td>
<td>584 (155-2,196)</td>
<td>777 (201-3,010)</td>
</tr>
<tr>
<td></td>
<td>Woorinen Sands Mallee</td>
<td>100</td>
<td>315 (136-730)</td>
<td>216 (61-762)</td>
<td>531 (197-1492)</td>
</tr>
<tr>
<td><strong>SUB-TOTAL</strong></td>
<td></td>
<td><strong>209</strong></td>
<td><strong>507 (181-1544)</strong></td>
<td><strong>800 (216-2959)</strong></td>
<td><strong>1,307 (397-4503)</strong></td>
</tr>
<tr>
<td><strong>GRAND TOTAL</strong></td>
<td></td>
<td><strong>2,175</strong></td>
<td><strong>4,466 (1,650-)</strong></td>
<td><strong>10,344 (2,823-)</strong></td>
<td><strong>14,810 (4,472-50,995)</strong></td>
</tr>
</tbody>
</table>

**Number of Mallee Emu-wren Adults for each Fire Age-class**
7 Discussion

Records of the Mallee Emu-wren

Most records of the Mallee Emu-wren occurred within aggregations or where individuals were recorded in previous years, substantiating the belief that Mallee Emu-wrens are relatively sedentary in nature. Records for all avian species surveyed (data not shown) revealed apparent 'hotspots' which support a diversity of mallee bird species including the Mallee Emu-wren. Several species of conservation concern were recorded in relatively high densities at the northern transects of the South Bore Track. These included a population of the Red-lored Whistler, several Gilbert's Whistler individuals and the Striated Grasswren. A site at the western end of Pheeny's Track that had not been previously surveyed, was found to contain Mallee Emu-wrens and other threatened avian species (Striated Grasswren, Red-lored Whistler and Gilbert's Whistler). It is not clear from the environmental data what particular attributes of these sites make them favourable to a diversity of species, though one can speculate that local productivity must be relatively high. These sites occur within the Woorinen bioregion and are characterised by relatively large areas of continuous Woorinen Sands Mallee greater than 16 years since last burned and associated with the 25 m contour.

All Mallee Emu-wrens were recorded in vegetation which included Triodia, with or without a shrubby understorey. These records are consistent with studies of fine-scale habitat use that show the Mallee Emu-wren is typically associated with a dense understorey including Triodia (Higgins et al. 2001; Mercer unpublished 1998; Smith unpublished 2004).

Density of the Mallee Emu-wren by habitat type

The results show that fire is the overwhelming factor influencing the density and distribution of the Mallee Emu-wren in the Murray-Sunset and Hattah-Kulkyne National Parks, and is consistent with the findings by Brown et al. (2009). Mallee Emu-wrens prefer 16-29 year fire age-class although they also occur in >29 year fire-age classes. Mallee Emu-wrens do not differentiate between Loamy Sands Mallee and Woorinen Sands Mallee in the 16-29 year fire age-class. However in the >29 year fire age-class, Mallee Emu-wrens prefer Woorinen Sands Mallee to Loamy Sands Mallee. Loamy Sands Mallee tends to occur on the tops of dunes, whilst Woorinen Sands Mallee occurs on the dune slacks. This suggest that the underlying soil structure (e.g. depth of sand) and/or environmental attributes influence the structure or primary productivity of the Ecological Vegetation Classes important to Mallee Emu-wrens in age classes greater than 29 years.

The Mallee Emu-wren does not occur in vegetation less than 16 years of age since fire. These results are consistent with Triodia being at its greatest volume between 15-30 years post-fire (Bradstock and Gill, 1993). It is inferred that fire age-classes less than 16 years since last burnt within mallee-Triodia does not contain vegetation structure of appropriate density to afford suitable nesting and foraging sites, or protection from predators.
Extent of Suitable Habitat

Since 2006, the Murray-Sunset and Hattah-Kulkyne National Parks have experienced only one moderately-sized fire and consequently the extent of the distribution of the Mallee Emu-wren has not altered greatly. The 2007 fire to the south of the Hattah town-ship burned habitat that is thought to support Mallee Emu-wrens as they have been recorded in this area. Despite this loss of habitat, extensive areas of suitably aged key vegetation types for the Mallee Emu-wren remain within the Murray-Sunset and Hattah-Kulkyne National Parks (Figure 4).

With time, the proportion of the most suitable fire age-class is decreasing due to ageing of the vegetation, although currently this shift is minor. In the absence of fire, in future decades the overall fire age-class structure will become less favourable to the Mallee Emu-wren, particularly in the Loamy Sands Mallee vegetation type, although it is not known at what age these vegetation types are no longer able to support viable Mallee Emu-wren populations.

Population Size

DISTANCE analysis weakly suggests that the Mallee Emu-wren population may have fluctuated since first monitored in 2001 - with a possible decline from 2001-2003, followed by an increase during the period from 2003 until 2009. However, no conclusive assessment can be made on population trends as the confidence intervals are very broad (discussed further below). Despite this, the total estimated population size of the Mallee Emu-wren for 2009 is comparable with earlier results by Brown et al. (2009)(14,810 this study cf. 16,822). The discrepancy in figures (higher density for 2009 but lower total numbers cf. 2006) can be attributed to 2006 population estimates extrapolating across Woorinen Mallee (albeit at very low densities) which is most likely incorrect. There was no shift in the extent of habitat less than16 years since last burnt to older than 16 years.

The fairy-wrens and emu-wrens (Maluridae) of the arid and semi-arid zones experience unpredictable environmental conditions and are known to exploit favourable conditions (when they occur) by having variable and long breeding seasons (Rowley and Russell 1997). In addition, below-average rainfall is known to prevent breeding attempts and it significantly reduces breeding success in Maluridae (Rowley and Russell 1997). Population fluctuations of the Mallee Emu-wren are also most likely influenced by rainfall. Since 1996, average maximum temperatures have been above the long-term average with generally below-average rainfall (Bureau of Meteorology, 2010). Given that 2006 had temperatures well above average for the region (+4%) and below rainfall average (-57%) it is likely that in 2007 the population size was greatly reduced. This concurs with the author’s observations during 2007 of fewer Mallee Emu-wrens, Striated Grasswrens and honey-eaters, although no systematic monitoring of populations was undertaken. However, 2007 had the first above-average yearly rainfall (+40%) for over 10 years, although temperatures were well above average (+5%). The breeding biology of the Mallee Emu-wren suggests that the species is able to respond to favourable climatic conditions by successfully raising a clutch of three chicks and possibly by raising multiple clutches within a season (Higgins et al, 2001; Schodde 1982; Rowley and Russell 1997). It is probable that at the end of 2007 and into 2008, the Mallee Emu-wren had a relatively good breeding year and that this is reflected in the 2009 estimate of density.
The number of individual Mallee Emu-wrens detected at Hattah-Kulkyne National Park suggests that there has been a local decline in the population there (1 bird detected in 2009 compared with 7 in 2006 for the same transect), although the total population size extrapolated from the extent of suitable habitat does not reflect this. A period of two hours spent at a study site known well to the author, searching for the presence of Mallee Emu-wrens, detected no additional Mallee Emu-wren records. This site is estimated to be over 100 years of age since last burnt (Simon Watson and Rick Taylor, personal communication) and contains a mix of Triodia of different age classes, so senescence of Triodia is not likely to be a factor. The condition of the Triodia, on which the Mallee Emu-wren depends for nesting, foraging and protection, was observed to be in much poorer condition than previous years, with considerable collapse of plants and little recent growth. This suggests that local climatic conditions have been sub-optimal in recent years at Hattah-Kulkyne National Park.

Despite the lack of statistical significance in the results, it is reasonable to suggest that the Mallee Emu-wren, as well as several other mallee bird species, has undergone fluctuations in numbers since 2005; and that this is likely to have been driven by short-term local climate events. This is further supported by the observation during the 2009 survey that very few honeyeaters were present at any of the survey sites, coinciding with the lack of flowering in Eucalyptus species (and long-term lack of rainfall).

Timing of the Survey

Mallee Emu-wrens commence the establishment of territories for breeding in mid to late July and commence nesting activities around this time and during August (personal observations, S Brown). During September, the majority of the population is nesting and contact calls tend to be fewer. In late September and early October the first of the season’s chicks are observed foraging with adults. To avoid the quiet nesting period, the survey was scheduled in early October. However, in 2009 the mallee region had well below average rainfall during the winter, but had an unseasonably heavy rainfall event in September. The composition of family groups observed suggest that breeding was unseasonably delayed in 2009. Family groups observed in the survey indicate that some pairs were nesting in August (as they had fledged chicks with them when observed in October), whilst a proportion of pairs had commenced breeding triggered by the late September rainfall event (as evidenced by bent tails from sitting on the nest), or had yet to breed (no evidence of breeding activity). These observations further substantiate the notion that short-term climatic conditions influence breeding activity and success in the Mallee Emu-wren.

Survey Method

The inability to detect statistically significant trends in the numbers of Mallee Emu-wrens has masked the true status of population trends. This can be attributed to two main factors. First, the timing of surveys is frequently inflexible and as such, surveys are sometimes conducted on sub-optimal days when wind conditions are not ideal. Mallee Emu-wrens have a soft high-pitched call that is inaudible to many people. Under ideal conditions (no wind and rain), contact calls can be heard from about 60-80 m by those with good hearing. However, wind greatly reduces the detectability as the rustling of leaves masks the calls. During spring, when most surveys are conducted,
gentle winds are frequent and consequently surveys may span periods of sub-optimal conditions that vary between survey years as well as days.

Second, random sampling error is likely to be considerable. Distribution of Mallee Emu-wren records and habitat evaluation shows that Mallee Emu-wren populations are locally patchy with much suitable habitat unoccupied. A local population of the Mallee Emu-wren at the Nowingi Track, Hattah-Kulkyne National Park, was estimated in 2006 to be about 0.25-0.35 birds ha\(^{-1}\) with breeding pairs occupying 5 ha territories (S Brown, unpublished data). These figures represent relatively low densities and large territories. Given the large territories, it is probable that Mallee Emu-wrens can be missed at a site on any given visit due to random sampling or alternatively, a couple of family groups may be detected. The small sample size and the overall rarity of the species have resulted in the broad confidence limits.

A modified approach to the transect effort needs to be developed to improve confidence limits. Although this technique is suitable for detecting Mallee Emu-wren presence at broad scales, the results suggest that for this species a more reliable detection of population trends would be obtained from targeted surveys that increase the effort within a localised area. This could be achieved by either replication of transects in areas that are known to support Mallee Emu-wrens or by having a series of parallel 100 m surveys. Either method would require a significant input of human resources. Despite this limitation, the large-scale surveys are no less important as they indicate relative population densities over expansive areas and, importantly, should detect when core areas have reached carrying capacity and individuals expand into previously unoccupied habitat or have become locally extinct.

*Implications for Management*

The distribution of occurrence data from all records of the Mallee Emu-wren (Figure 4) shows that Mallee Emu-wrens are locally patchy but widespread across the Murray-Sunset and Hattah-Kulkyne National Parks. Some areas appear to consistently support Mallee Emu-wrens suggesting they are possibly core, source populations. It is recommended that these areas should be highlighted as important areas for biodiversity protection, particularly the hotspots where other threatened species also occur. Areas of note are the South Bore Track (north of Pheenys Track), Murray-Sunset National Park (for several threatened avian species) and the Nowingi Track area in Hattah-Kulkyne National Park (Mallee Emu-wrens and Striated Grasswrens).

Fire age-class is the overwhelming factor influencing the distribution of the Mallee Emu-wren (this study; Brown et al. (2009). Mallee Emu-wrens do not occupy habitat less than 16 years since last burned and efforts by managers should aim to limit the proportion of this fire age-class in areas that Mallee Emu-wrens occur. However, the conundrum for managers is that fire is essential to renew optimally aged habitat for this species and this may conflict with extant populations of Mallee Emu-wrens as well as the requirements of other mallee species. Given that widespread wildfires are unpredictable but probable events, the overall status of key habitat and distribution of Mallee Emu-wrens (and other threatened species) within mallee ecosystem should be continually monitored. Given the dynamic nature of fire-prone mallee ecosystems, management needs to be adaptive. Species that have poor individual dispersal abilities, such as the Mallee Emu-wren, may need to be translocated where barriers (e.g., agricultural land or large patches of unsuitable habitat) prohibit dispersal and re-
colonisation. If, over a period of decades, no natural fire events have occurred and fine-scale attributes are declining in quality (i.e. senescing Triodia) over extensive areas that once supported Mallee Emu-wrens, ecological burning may need to be considered to enhance the proportion of 16-29 year fire age-class. A major issue is that our knowledge of the environmental attributes that influence the patterns of aging and senescence with Triodia is little understood. This aspect requires further research.

Maluridae species of the arid and semi-arid zones that experience unpredictable environmental conditions are known to exploit favourable conditions by having variable breeding seasons and prolonged breeding seasons (Rowley and Russell 1997). This study gives some weak support to the belief that population size (inferring breeding success) is correlated with rainfall and hence that population numbers may fluctuate significantly between years. The Mallee Emu-wren probably has a relatively short life span (4-6 years) and during consecutive years of poor breeding success the adult population may fail to replace themselves. If prolonged drought conditions persist, such as those experienced in this last decade, an overall decline in the density (and overall population size) of the Mallee Emu-wren would be expected and populations may even become locally extinct.

**Summary**

Although no clear population trend of Mallee Emu-wren could be conclusively deduced from this study (due to broad confidence intervals in the analysis) it is evident that two main factors influence the population size: i) the extent and distribution of key vegetation types of appropriate fire age-class and, ii) short-term climatic conditions.

At the landscape scale, Mallee Emu-wren distribution (and hence total population size) is influenced by fire age-classes within key vegetation types. This study found that key habitat of appropriate fire age-classes remains extensive in the Murray-Sunset/Hattah-Kulkyne National Park complex. Therefore habitat extent and distribution is likely to continue to support the current population of Mallee Emu-wren.

Short-term climatic conditions also influence population size. Mallee Emu-wren numbers are most likely to be adversely affected by low (or unseasonal) rainfall and higher than average temperatures. Long-term adverse climatic conditions from climate warming are thus likely to adversely affect the overall population size of the Mallee Emu-wren and continuing adverse conditions could result in sub-populations becoming locally extinct.

**Future Management and Research Recommendations**

- Appropriate management of wildfire in the Murray-Sunset and Hattah-Kulkyne National Parks is required to prevent a catastrophic widespread wildfire destroying key habitat and therefore reducing the distribution and total population size of this endangered species.

- Core populations such as those at the South-bore Track cluster and the Nowingi Track site should be given priority in protection from wildfires and careful consideration is given before any planned burns are undertaken in these areas. It is also likely that other core populations of the Mallee Emu-wren and other threatened avian species are present. Planned burns should be surveyed by experienced observers before burning. Sites that may potentially
support a diversity of threatened birds (not exhaustive) are highlighted in Appendix 2 and should be targeted in future surveys.

- Frequent monitoring by GIS analysis of the spatial configuration and extent of suitable vegetation types and fire age-classes, coupled with on-ground monitoring, will assist in the detection of long-term population declines or threats to population persistence. GIS analysis could also be used to model long-term population trends as vegetation ages. Areas which become aged and no longer suitable for the Mallee Emu-wren could be considered for ecological burning.

- Translocation and population augmentation may need to be considered where populations are found to be in serious decline or locally extinct and unlikely to re-colonise without assistance. The two potential sites for translocation are Annuello Fauna and Flora Reserve and Ngarkat National Park, South Australia. A translocation protocol is required before this undertaken.

- To improve the statistical certainty of population trends, it is recommended that an improved protocol would employ intensive replicated surveys of parallel 100 m transects at known Mallee Emu-wren sites.

- There is a good understanding of the current extent and fire-age class requirements of Mallee Emu-wrens in the Murray-Sunset and Hattah-Kulkyne National Parks. The broad-scale environmental attributes that influence Mallee Emu-wren distribution within these parks are likely to be applicable to Annuello Fauna and Flora Park. However, there is a paucity of information of the distribution and habitat requirements within the Wyperfeld National Park and Big Desert Wilderness Reserve. Given that vegetation types and climate conditions differ in these parks of the Lowan Mallee bioregion, it is recommended that a GIS desk-top study be undertaken to identify potential areas to survey for Mallee Emu-wrens (and other threatened species). An area to target includes suitable fire age-class Triodia-heath on the south-west boarder near South Australia, where a single bird was sighted in 2008.

### 8 Acknowledgements

Fieldworkers Birgitta Hansen, Rick Taylor and Simon Watson assisted with the 2009 surveys. I am also grateful to the La Trobe/Deakin Mallee Fire Team for access to digital data documenting fire age-classes within the Murray Sunset and Hattah Kulkyne National Parks. Survey data for 2001 to 2006 was previously reported (Brown et al. 2009) and supported by Deakin and La Trobe University and staff and the Department of Sustainability and Environment, Victoria. This study was carried out under permit No. 10005100, the Department of Sustainability and Environment and funded by the Mallee Management Catchment Authority and Parks Victoria.
9 References


Appendix II

Department of Sustainability and Environment. (2004) *Victorian Geospatial Data. EVC Bioregional Conservation Status at 1:100,000* (includes 1:25,000 data if available) (*EVC_BCS100/*).


Appendix I.

Records of the Mallee Emu-wren from Murray-Sunset and Hattah-Kulkyne National Parks, September 2009

<table>
<thead>
<tr>
<th>Location</th>
<th>Place</th>
<th>Transect ID</th>
<th>Time</th>
<th>Date</th>
<th>Group Composition</th>
<th>Distance (m)</th>
<th>Easting# GDA94</th>
<th>Northing# GDA94</th>
<th>Vegetation Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Murray-Sunset NP</td>
<td>Sth Bore Trk Nth</td>
<td>SBN0522</td>
<td>7:40</td>
<td>4/10/2009</td>
<td>unknown</td>
<td>20</td>
<td></td>
<td></td>
<td>30-40% T. tridentata</td>
</tr>
<tr>
<td>Murray-Sunset NP</td>
<td>Sth Bore Trk Nth</td>
<td>SBN021</td>
<td>6:55</td>
<td>4/10/2009</td>
<td>3 Adults and possible 1 Juv</td>
<td>20</td>
<td></td>
<td></td>
<td>50% T. tridentata, shrubs</td>
</tr>
<tr>
<td>Murray-Sunset NP</td>
<td>Sth Bore Trk Nth</td>
<td>SBN021</td>
<td>7:04</td>
<td>4/10/2009</td>
<td>2 Adults</td>
<td>0</td>
<td></td>
<td></td>
<td>50% T. tridentata, shrubs</td>
</tr>
<tr>
<td>Murray-Sunset NP</td>
<td>Sth Bore Trk Nth</td>
<td>SBN022</td>
<td>7:10</td>
<td>4/10/2009</td>
<td>4 adults (?)</td>
<td>10</td>
<td></td>
<td></td>
<td>T. tridentata, shrubs</td>
</tr>
<tr>
<td>Murray-Sunset NP</td>
<td>Sth Bore Trk Nth</td>
<td>SBN04PB</td>
<td>7:50</td>
<td>4/10/2009</td>
<td>unknown</td>
<td>PB</td>
<td></td>
<td></td>
<td>60% T. tridentata, shrubs</td>
</tr>
<tr>
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<td>Sth Bore Trk Sth</td>
<td>SB8041</td>
<td>8:29</td>
<td>5/10/2009</td>
<td>2 adults</td>
<td>25</td>
<td></td>
<td></td>
<td>60% T. tridentata, shrubs</td>
</tr>
<tr>
<td>Murray-Sunset NP</td>
<td>Sth Bore Trk Sth</td>
<td>SB8048</td>
<td>9:15</td>
<td>5/10/2009</td>
<td>2 adults</td>
<td>50</td>
<td></td>
<td></td>
<td>60% T. tridentata, shrubs</td>
</tr>
<tr>
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<td>Sth Bore Trk Sth</td>
<td>SB8048</td>
<td>9:15</td>
<td>5/10/2009</td>
<td>2 adults</td>
<td>20</td>
<td></td>
<td></td>
<td>60% T. tridentata, shrubs</td>
</tr>
<tr>
<td>Murray-Sunset NP</td>
<td>Sth Bore Trk Sth</td>
<td>SB8048</td>
<td>9:15</td>
<td>5/10/2009</td>
<td>2 adults</td>
<td>0</td>
<td></td>
<td></td>
<td>60% T. tridentata, shrubs</td>
</tr>
<tr>
<td>Murray-Sunset NP</td>
<td>Sth Bore Trk Sth</td>
<td>SB8048</td>
<td>9:15</td>
<td>5/10/2009</td>
<td>2 adults</td>
<td>40</td>
<td></td>
<td></td>
<td>60% T. tridentata, shrubs</td>
</tr>
<tr>
<td>Murray-Sunset NP</td>
<td>Pheeneys Trk West</td>
<td>PW0114</td>
<td>*</td>
<td>6/10/2009</td>
<td>1M, 1F BENT TAIL</td>
<td>38</td>
<td></td>
<td></td>
<td>30-40% T. tridentata</td>
</tr>
<tr>
<td>Murray-Sunset NP</td>
<td>Pheeneys Trk West</td>
<td>PW0114</td>
<td>*</td>
<td>6/10/2009</td>
<td>unknown</td>
<td>44</td>
<td></td>
<td></td>
<td>40% T. tridentata, shrubs</td>
</tr>
<tr>
<td>Murray-Sunset NP</td>
<td>Pheeneys Trk West</td>
<td>PW04PB</td>
<td>8:24</td>
<td>6/10/2009</td>
<td>unknown</td>
<td>25</td>
<td></td>
<td></td>
<td>40% T. tridentata, shrubs</td>
</tr>
<tr>
<td>Murray-Sunset NP</td>
<td>Pheeneys Trk West</td>
<td>PW044</td>
<td>8:32</td>
<td>6/10/2009</td>
<td>1M, 1F</td>
<td>21</td>
<td></td>
<td></td>
<td>30-40% T. tridentata</td>
</tr>
<tr>
<td>Murray-Sunset NP</td>
<td>Pheeneys Trk West</td>
<td>PW047</td>
<td>9:40</td>
<td>6/10/2009</td>
<td>1M, 1F</td>
<td>10</td>
<td></td>
<td></td>
<td>30-40% T. tridentata</td>
</tr>
<tr>
<td>Murray-Sunset NP</td>
<td>Pheeneys Trk West</td>
<td>PW04PB</td>
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PB = responded to playback
* = no time recorded
LSM = Leanyne Sand Mallee
WSM = Woorinen Sands Mallee
# Available from Victorian Wildlife Atlas, Department of Sustainability and Environment, Government of Victoria.
Appendix 2.

Extent of fire age-classes for Woorinen Sands Mallee and Loamy Sands Mallee and Mallee Emu-wren records collected during September 2009 and all other years. Black ovals show approximate site of transects. Red ovals show sites that may contain large swathes of Woorinen Sands Mallee of 16-30 year fire age-class.
**Morphological measurements**

Morphological measurements of adult male and female Mallee Emu-wrens, plus one male fledgling.

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Table AIII-b  Morphological measurements for adult male and one fledgling (not included in summary statistics).

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| Mean  | 5.54  | 25.67  | 8.74  | 41.19 | 15.45  | 87.14 |
| ±SE   | 0.07  | 0.07  | 0.06  | 0.14  | 0.14   | 1.66  |
| M<3mth | 6.00  | 25.60  | 8.80  | 42.00 | 15.00  | 90.50 |
APPENDIX IV

Phylogenetic relationship of the Mallee Emu-wren and the Rufous-crowned Emu-wren

*Suggested further research to evaluate the phylogenetic origin of the Mallee Emu-wren*

The control region of mtDNA is the preferred gene for population genetic studies due to its high rate of mutation, making it suitable for the detection of fine-scale genetic structure within species (Brown et al 1993, Taberlet 1996) and reconstruction of phylogenetic relationships between closely allied taxa (Harrison 1989). However the control region is difficult to amplify with PCR in passerines, hence the slower evolving ND2 gene was used in this study. The low genetic diversity in the ND2 gene found within the Mallee Emu-wren was thus not unexpected. The paraphyletic relationship of the Mallee Emu-wren with the Rufous-crowned Emu-wren, and possible explanation of its origin, could be explored by further research. This was beyond the time-frame and scope of this thesis.

Three scenarios have been proposed for the origin of the Emu-wrens; i) a single transcontinental population separated simultaneously into three regional groups, each evolving into the three Emu-wren species, ii) coastal and inland populations becoming separated from each other first, followed by the splitting of the inland group into the Rufous-crowned Emu-wren and Mallee Emu-wren, and iii) the Rufous-crowned Emu-wren and Mallee Emu-wren splitting independently from ancestral stocks of the Southern Emu-wren (Schodde 1982b).

Phylogenetic analyses of cytochrome *b* and ND2 show the Mallee Emu-wren and the Rufous-crowned Emu-wren are sister species, originating from an inland ancestral group that diverged from the Southern Emu-wren ancestral group between 6 and 9.3 Mya (Donnellan et al. 2009), during a period of major diversification and radiation of arid-zone biota (mid to late-Miocene and Pleocene, 20 to 2.5 Mya) (Byrne et al. 2008). This finding is consistent with the second scenario (Ford 1970, 1974).
Although, the phylogenetic analyses of the three haplotypes (this study, Driskell and Christidis 2004, and Donnellan et al. 2009) do not support separate clades for the Rufous-crowned Emu-wren and Mallee Emu-wren (Chapter 5), this finding does not necessarily refute the hypothesis that the Mallee Emu-wren evolved from the Rufous-crowned Emu-wren. Discordance between morphology and genetic phylogenies in recently diverged species is widespread in Australian bird taxa (Joseph and Omland 2009). Reliance on a single mt DNA locus to evaluate phylogenetic relationships has limitations because a single locus is not representative of the entire genome and many processes can influence its evolution (e.g. sex biased dispersal, selective sweeps and mitochondrial introgression between closely related taxa) (Ballard and Whitlock 2004).

The timing of phylogenetic divergence of the Mallee Emu-wren cannot be accurately determined from the data presented in this thesis, other than to suggest that the polyphyletic pattern is consistent with a Pleistocene time frame (<0.8 Mya). During the Pleistocene, cyclic environmental fluctuations are thought to have shaped fine-scale genetic structure of many arid-zone taxa via multiple refugia events at microgeographical scales (Schodde 1982b, Byrne et al. 2008, Byrne 2008). Repeated climatic oscillations separating the mesic south and the aid north of south-eastern Australia could have lead to the divergence of Emu-wrens, given that similar north-south genetic breaks are found in sub-species of the Splendid Fairy-wren (Kearns et al. 2000) and other widespread arid zone birds (Joseph and Omland 2009). The pattern of genetic diversity within the ND2 gene implies the Mallee Emu-wren may have originated from a founder population during a phase of habitat expansion that then became isolated as the interior increased in aridification. Alternatively, or in conjunction, extant Mallee Emu-wrens may represent a relict mtDNA lineage of a species that was once more geographically widespread and contained more mtDNA linearages. Investigation of more suitable phylogenetic markers, inclusion of more Rufous-crowned Emu-wren samples and evaluation of morphological data and the paeleogeographic record may resolve the timing and origin of the Mallee Emu-wren. The haplotype described by Donnellan et al. (2009) appears to be exclusive to Comet Bore, in Ngarkat Conservation Park, South Australia. Given that sample sizes are small, sequencing of further samples would resolve if this is actual or due to sampling bias.
Appendix IV

References


