Population processes in an early successional heathland: a case study of the eastern chestnut mouse (*Pseudomys gracilicaudatus*)

by

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March 2016
Grarock K., Introduction, spread, impact and control of the common myna
Candidate's Declaration

This thesis contains no material that has been accepted for the award of any other degree or diploma in any university. The research, analysis and writing in the thesis are substantially (>90%) my own work. To the best of my knowledge, it contains no material previously published or written by another person, except where due reference is made in the text.

Felicia Pereoglou

Date: 14 March 2016
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Abstract

The eastern chestnut mouse (*Pseudomys gracilicaudatus*) has been described as a fire specialist inhabitant of early successional heathland. There is a global concern that changes to natural disturbance regimes will place early successional habitat specialists like the eastern chestnut mouse at an increased risk of extinction by altering landscape patterns of habitat suitability. Despite this concern, the fundamental population processes that occur in early successional heathlands are currently unknown for many species. This thesis comprises four research articles that investigate the underlying mechanisms used by a species to persist in this spatially and temporally variable habitat.

To determine which features of burned heath were selected as refuge sites, 58 individuals of the eastern chestnut mouse were radio-tracked. Animals preferentially selected multiple aboveground shelter sites characterised by tall, dense vegetation with structural features present. The eastern chestnut mouse was ephemeral and non-gregarious in its refuge use. Refugia were highly flammable. These findings imply land management should ensure retention of vegetation structure on the ground layer and dense habitat patches in burned areas to assist with population viability.

A long-term monitoring data set was analysed to evaluate the effects of landscape structure, fire history, and site-level habitat quality on site occupancy in an early successional heathland. Eastern chestnut mouse site occupancy was strongly related to patch area and landscape heterogeneity. There was no direct effect of recent or historical fire, but site occupancy was associated with dead shrubs in the understory and rock cover on ground layer. Small mammal species associations did not conform to that predicted by contemporary ecological theory. The findings suggest landscape configuration and continuity be used to guide survey work and fire regimes to promote eastern chestnut mouse population growth should retain critical habitat features rather than be based on temporal rates of successional stages.

To examine population genetic structure, dispersal patterns and the effects of landscape variation on dispersal of an early successional specialist, microsatellite markers were used to genotype tissue obtained from 287 individuals. Differentiation between sites fitted an isolation-by-distance pattern. There was spatial autocorrelation of multilocus genotypes to a distance of 2–3 km with no evidence for sex-biased dispersal. Recently burned vegetation had greater conductance for gene flow than unburnt habitat, but variation in habitat quality between vegetation types and occupied patches had no effect on gene flow. These findings indicate a ‘generalist’ dispersal strategy is advantageous for post-fire specialists to access early successional vegetation.

To quantify survival, recruitment and immigration rates in populations of the eastern chestnut mouse, demographic modelling and genetic assignment tests were applied to two years of mark–recapture data. Survival and recruitment rates varied across sites. Survival was
influenced by fire history and elements of habitat structure affected by fire. Immigration contributed very little to recruitment compared to local reproduction, suggesting populations are demographically discrete at this post-fire stage. Demographic and genetic data were consistent; sites with high recruitment also had higher genetic diversity and lower temporal genetic structure, consistent with reduced genetic drift.

This thesis provides an investigation of the strategies used by the eastern chestnut mouse to persist in an early successional heathland and adds significant new knowledge on the critical resources, predictors of occurrence, population genetics, and demographic rates of the species. The major implication of this research is that a predicted increase in fire occurrence will potentially influence the viability of populations of the eastern chestnut mouse by promoting gene flow but concomitantly decreasing critical habitat features that support site occupancy, increase survival rates, and provide nesting refugia. Furthermore, landscape continuity has a secondary influence population processes and this must be considered in conjunction with the disturbance regime to inform management actions.
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Chapter 1

Introduction
Chapter 1: Introduction

1.1 Introduction

1.1.1 Early successional ecosystems

Disturbance plays a fundamental role in the formation and maintenance of ecological communities (Miller et al., 2011, Connell and Slatyer, 1977). Succession refers to the observed changes in an ecological community following a disturbance event (Connell and Slatyer, 1977). Early successional ecosystems are the starting point for post-disturbance community regeneration (Swanson et al., 2011).

In Australia, wildfire is one of the dominant natural forces in creating early successional ecosystems. Wildfire disturbances can be described by their intensity, season of occurrence, extent and patchiness, frequency, and type (Whelan, 1995). Combinations of these factors generate a disturbance regime (Gill, 1975), which then determines the extent and composition of the early successional ecosystem. Many endemic species are dependent on post-fire conditions for survival (Whelan, 1995, Keith et al., 2002, Swanson et al., 2011).

Early successional communities are ephemeral ecosystems confined to the variable length of time between a disturbance, and re-establishment of the later successional stages of community composition (Swanson et al., 2011). Temporal variation in the duration of the early successional stage is influenced by (i) disturbance type (Rossi et al., 2007, Delmoral and Bliss, 1993, Sousa, 1979), (ii) disturbance regime (Bradstock et al., 2012), (iii) habitat type (rainforest, forest, shrubland, heathland, grassland, etc.) (Keith et al., 2002, Gill and Catling, 2002), and (iv) geographic region (Velle and Vandvik, 2014).

Research on the processes occurring in early successional ecosystems links disturbance ecology with habitat fragmentation theory and conservation. Early successional ecosystems occur as habitat patches of varying size, shape and connectedness within the wider landscape, incorporating the importance of landscape continuity. Early successional ecosystems are not communities in ‘recovery’ but ones with significant biological value. Because early successional ecosystems, and the species that occur within them, are limited by duration of seral stage, their distribution, and viability of populations occurring within them, can be threatened by disturbance suppression or changes in the prevailing disturbance regime.

This thesis explores themes relating to population processes that occur in an early successional heathland in south-eastern Australia. The eastern chestnut mouse (Pseudomys gracilicaudatus, Gould) is used as a case study to investigate critical resource requirements, site occupancy, landscape genetics, and population dynamics of an early successional species and habitat specialist. This research is timely given a predicted increase in the frequency and severity of disturbance events with global climate change (Flannigan et al., 2009, Steffen et al.,
Chapter 1: Introduction

2009, Williams et al., 2001) will require a comprehensive understanding of the mechanisms underlying population recovery of early successional habitat specialists following disturbance.

1.1.2 Eastern chestnut mouse

1.1.2.1 Origin, taxonomy and conservation status

All Australian rodents belong to the family Muridae (Lee et al., 1981, Strahan, 2008). Native mice of the *Pseudomys* genus are conilurine rodents, or Australian Old Endemic rodents. This group originated in Australia during the Miocene (Lee et al., 1981) and its closest relatives occur in New Guinea (Breed and Ford, 2007). The *Pseudomys* are the largest group of Australian rodents (Watts and Aslin, 1981) encompassing a heterogeneous assemblage of 24 species (Breed and Ford, 2007). Many are considered the best examples of fire specialist fauna in Australia (Catling and Newsome, 1981).

Native rodents are a group that are poorly conserved in Australia with 55% of species considered either threatened or extinct (Breed and Ford, 2007). Many *Pseudomys* species are of conservation concern. In New South Wales alone, all but one of the 11 species of *Pseudomys* that occur in the state are listed on threatened species schedules (Dickman et al., 2000). The eastern chestnut mouse (*Pseudomys gracilicaudatus*) is one such species, considered Vulnerable to extinction through loss of habitat and long-term fire exclusion and currently listed on Schedule 2 Threatened Species Conservation Act 1995 (NSW).

1.1.2.2 Distribution

The eastern chestnut mouse has a disjunct distribution along the east coast of Queensland and New South Wales, Australia. Existing populations of the species are isolated by substantial distances, often encompassing apparently suitable habitat from which the species is absent (Fox, 2008). As such, the species is now considered rare or extinct in many parts of its range (Breed and Ford, 2007). First recorded in New South Wales in 1971 (Mahoney and Posamentier, 1975), the eastern chestnut mouse was thought to be extinct in southern Australia until 2002 when it was discovered in the Jervis Bay region (Meek and Triggs, 1997). This area now supports the only contemporary population of eastern chestnut mouse south of Gosford, New South Wales and is arguably the most isolated in eastern Australia. The northern limit of the eastern chestnut mouse distribution is Cooktown, Queensland.

1.1.2.3 Response to fire

The eastern chestnut mouse was first described as a ‘fire specialist’ by Fox (1982) in a study of small mammal community recovery following wildfire at a single site in northern New South Wales. The time taken for each species to reach a peak in population abundance was plotted along a continuum, which was then used to determine whether the species was an early-,
mid- or late-successional community specialist. The eastern chestnut mouse population reached maximum densities within the first few years post-fire before a decline in abundance and replacement by a population of the swamp rat (*Rattus lutreolus*) (Fox, 1982).

Subsequent studies of the eastern chestnut mouse focused on understanding whether changes in species’ abundance over time were a result of the competitive response of the sympatric species (Catling, 1986, Morris et al., 2000, Higgs and Fox, 1993), or a response to increasing vegetation cover and changes in habitat structure post-fire (Monamy and Fox, 2000, Fox et al., 2003). To date, the ‘fire-mouse story’ indicates disturbance events sustain populations of the eastern chestnut mouse by removing vegetation cover and reducing habitat structure, subsequently easing competitive pressure by lowering the population abundance of competitor species. No studies of the eastern chestnut mouse have compared the species’ population size and demographic rates, before and/or after fire. Nor is there any data on habitat use, or local- and landscape-scale movements before and after fire. Whether the eastern chestnut mouse is an early successional/fire specialist because (i) it exclusively colonises burned heath, or (ii) it survives a fire event *in situ* and then increases population density post-fire, currently remains unknown.

### 1.1.2.4 Habitat

The eastern chestnut mouse is considered an early seral stage specialist of regenerating heathland (Fox, 1982). Detailed information on eastern chestnut mouse habitat preferences is lacking through limited research in this area. However, of the few studies that have been done, the species has been associated with dense but patchy vegetation in the upper shrub layer, and woody debris on the ground layer (Haering and Fox, 1995). Both vegetation structural attributes and understorey floristic richness also appear to be important (Fox and Fox, 1981). The density of vegetation cover, or rate of vegetation recovery after fire, is considered to have the greatest influence on eastern chestnut mouse abundance (Monamy and Fox, 2000, Monamy and Fox, 2010).

### 1.1.2.5 Appearance

The *Pseudomys* are mainly mouse-sized with common characteristics such as a well haired, bicoloured tail (darker on the upper surface), and females with only two pairs of teats, which distinguishes them from the true rats (*Rattus*) (Watts and Aslin, 1981). Adults of the eastern chestnut mouse show significant sexual dimorphism (Fox and Kemper, 1982); measuring up to 145 mm in length for males and 138 mm for females, and attaining average weights of 90 g for males and 75 g for females (Fox, 2008). The species is named after its characteristic grizzled chestnut fur above and has a pale, greyish belly (Fox, 2008) (Fig. 1.1). The eastern chestnut mouse can be distinguished from the similar appearance of the swamp rat
(Rattus lutreolus) by a pale ring around the eye and ventrally light coloured feet with long, grey-white hairs on the dorsal surface that extend beyond the claws (Fox, 2008).

![Image](image-url)

**Figure 1.1:** The eastern chestnut mouse (*Pseudomys gracilicaudatus*).

### 1.1.2.6 Diet

The eastern chestnut mouse is a generalist herbivore whose diet consists predominantly of seeds and stems, but also includes fungi, insects, leaves, roots and pollen (Luo et al., 1994). The eastern chestnut mouse demonstrates an opportunistic foraging strategy and is less specialised in food selection than any other species within the *Pseudomys* genus (Luo et al., 1994). This foraging strategy is considered beneficial for an early successional habitat specialist because the ability to take advantage of all available food resources is a basic requirement for survival in recently burned areas (Luo et al., 1994). A decrease in dietary diversity in the later successional stages of vegetation regeneration following fire has been linked to a decline in the species’ density over time. This, in turn, has been attributed to changes in the availability of food resources and increasing interspecific competition (Luo and Fox, 1994).

### 1.1.2.7 Breeding, growth and longevity

The eastern chestnut mouse breeding season extends from September to March, but in good years can commence in August (Fox, 2008). Female oestrous cycle is 7 – 8 days with a gestation of approximately 27 days (Fox and Kemper, 1982). Females are capable of producing litters of 1 – 5 offspring (usually three) (Fox, 2008). The species is precocial at birth and shows
rapid early development – the lower incisors have already erupted at birth, young are fully furred by six days, have opened their eyes by 11 days, and are weaned by the fourth week (Fox and Kemper, 1982). Females exhibit a post-partum oestrous and multiple litters may be produced during a single breeding season (Fox and Kemper, 1982). Although no individuals have been observed to breed in the season of their birth, females have been observed to breed in two successive years and males can live through a second summer (Fox, 2008).

A short gestation, precocial young, rapid postnatal development and early weaning accelerate the reproductive rate which is appropriate for a fire-specialist species that reaches maximum abundance in the early successional stage of vegetation regeneration following fire (Fox and Kemper, 1982).

1.2 Context and structure

The following section provides a brief overview of the chapters in the thesis. The body of work is presented as a compilation of separate papers; either already published as journal articles, or submitted journals for publication. As such, it follows The Australian National University’s annotated Thesis by Compilation Guideline of 10 May 2013, available on the following webpage:


1.2.1 Chapter 2 – Refuge site selection in recently burned heath - Pereoglou, et al. (2011) Wildlife Research, 38(4)

Temporal reduction in shelter is an indirect primary impact of fire. Removal of refugia has implications for shelter site selection and fidelity – factors that have been largely overlooked in studies of Australian rodent fauna.

In Chapter 2, diurnal refuge sites were identified through radiotelemetry and their habitat attributes were compared with those of a matched set of control sites. Habitat features and fidelity parameters were used to classify refuge site use.

Animals were found to preferentially select multiple aboveground shelter sites characterised by tall, dense vegetation with structural features present. These refugia were highly flammable and do not provide protection from fire. Mice were ephemeral and non-gregarious in their refuge use. There was some evidence for inheritance of refuge sites from a parent, as well as inter-season shelter site fidelity.

Knowledge of species’ nest requirements and daytime refuge habitat and use is fundamental for conservation efforts in fire-prone landscapes.
1.2.2 Chapter 3 – Early successional heathland site occupancy - Pereoglou, et al. (2016) *Landscape Ecology*, 31(2)

Changes to natural disturbance regimes can place early successional habitat specialists at an increased risk of extinction by altering landscape patterns of habitat suitability.

In Chapter 3, a series of hypotheses were developed to evaluate the effects of fire history, landscape structure, and site-level habitat quality on site occupancy by the eastern chestnut mouse.

Patch area and landscape heterogeneity were strongly related to site occupancy. Site occupancy was associated with dead shrubs in the understorey and rock cover on the ground layer, but was not directly influenced by recent or historical fire. There was no evidence for predictable species associations in the early successional ecosystem.

Fire regimes in areas supporting populations of the eastern chestnut mouse should be sensitive to the retention of critical habitat features rather than be based on temporal rates of successional stages. For management to adequately account for post-disturbance patterns in early successional ecosystems, a species-by-species, multi-scaled approach to research, replicated throughout a species’ range is necessary.

1.2.3 Chapter 4 – Landscape genetics in disturbance-prone environments - Pereoglou, et al. (2013) *Molecular Ecology*, 22(5)

Species that specialise in disturbed habitats may have considerably different dispersal strategies than those adapted to more stable environments. However, little is known of the dispersal patterns and population structure of such species.

In Chapter 4, microsatellite markers were used to assess the effect of landscape variation and recent disturbance history on eastern chestnut mouse dispersal. Significant differentiation between sites that fitted an isolation-by-distance pattern was demonstrated, and spatial autocorrelation of multilocus genotypes occurred up to a distance of 2–3 km. There was no consistent genetic evidence for sex-biased dispersal.

The influence of different habitat and fire-specific landscape resistance scenarios on genetic distance between individuals were tested. A significant effect of fire was found indicating recently burned vegetation had greater conductance for gene flow than unburnt habitat, but variation in habitat quality between vegetation types and occupied patches had no effect on gene flow.

Post-fire specialists must evolve an effective dispersal ability to move over distances that would ensure access to early successional stage vegetation. Natural disturbance and natural heterogeneity may therefore not influence population genetic structure as negatively as expected.
1.2.4 Chapter 5 – Estimating survival and recruitment - Pereoglou, et al. Ecology and Evolution Submitted

Understanding how demographic parameters of post-fire specialists vary with fire history can provide insights into the population viability and distribution of such species, including their response to landscape management and novel fire regimes.

In Chapter 5, demographic and genetic analyses were used to quantify survival, recruitment and immigration rates in populations of the eastern chestnut mouse.

Survival and recruitment rates varied across sites. Survival models that included fire history and elements of habitat structure affected by fire had the most support. Recruitment was attributed to immature animals entering the adult breeding population prior to the breeding season. Recruitment through immigration was negligible compared to the survival and reproduction of local residents. High levels of recruitment corresponded to increased genetic diversity within a site and lower temporal genetic structure, consistent with reduced genetic drift.

In light of landscape genetics analyses showing that fire promotes population connectivity, this study suggests a two-phase model of spatial population dynamics, where post-fire colonization is followed by locally driven population dynamics, in which survival rates are influenced by fire-history effects on habitat quality. Thus, post-fire specialists can be dependent on landscape-level connectivity and site-level habitat quality, both of which are influenced by fire history.

1.2.5 Chapter 6 – Conclusion

Chapter 6 discusses the major findings of this thesis: (i) the indirect importance of fire in creating and maintaining habitat features that effect the selection of diurnal refugia, success of site occupancy, and demographic rates of habitat specialists of early successional heathland; and (ii) the life history strategies of species that occur in spatially and temporally variable environments as demonstrated by the eastern chestnut mouse i.e. fire-mediated gene flow, ‘generalist’ dispersal, recruitment through local reproduction, etc.

1.3 Thesis summary

This thesis comprises four research articles that combine to provide a detailed investigation of the population processes occurring in an early successional heathland. This research adds significant new knowledge on the refuge requirements, predictors of site occurrence, landscape genetics, and population dynamics, of the eastern chestnut mouse in a spatially and temporally variable environment. These findings are timely due to the growing concern about managing fire-prone landscapes and attempts to conserve species that specialise
in ephemeral ecosystems originating from disturbance events.

### 1.4 Publication summary, candidate contribution and co-author acknowledgement

The material presented in this thesis is an accurate representation of research conducted during my candidature for the degree of Doctor of Philosophy between February 2008 and March 2016. This material is presented as contributions to the published scientific literature. These contributions are listed below in order of their appearance in this thesis:


The research, analysis and writing in the above publications was substantially (>90%) my own work. I am also the corresponding author for each publication.

Felicia Pereoglou

Date: 14 March 2016

Co-author acknowledgement:

David B. Lindenmayer

Date: 14 March 2016
Chapter 1: Introduction

1.5 References


Chapter 1: Introduction


Chapter 2

Refuge site selection

Published as:

Refuge site selection by the eastern chestnut mouse in recently burned heath

Manuscript: Appendix 1
2.1 Abstract

Temporal reduction in shelter is an indirect primary impact of fire. Removal of animal refugia has implications for shelter site selection and fidelity – factors that have been largely overlooked in studies of Australian rodent fauna. This information is critical for guiding species conservation and appropriate land management including prescribed burning practices. We sought to determine which features of burned heath were selected as shelter sites by the eastern chestnut mouse, whether there was sex and/or seasonal variation in shelter site selection and whether we could identify primary refugia. We completed a radiotelemetry study to identify diurnal refuge sites and compare habitat attributes with those of a matched set of control sites. We then used habitat features and fidelity parameters to classify refuge site use. We found the eastern chestnut mouse selected shelters with the presence of specific structures and had taller, denser vegetation than randomly selected control sites. There were no differences in habitat selection between the sexes. Shelter sites in the non-breeding season had greater vegetation density compared to those used in the breeding season. In the breeding season, the eastern chestnut mouse showed no evidence of increased fidelity to particular refuges. Vegetation density in winter was the best predictor of a primary refuge compared to whether or not an animal returned to a shelter site or the amount of time spent in a shelter site. Mice were ephemeral and non-gregarious in their refuge use. There was some evidence for inheritance of refuge sites from a parent, as well as inter-season shelter site fidelity. The eastern chestnut mouse selected refugia that had habitat attributes offering maximum protection. Seasonality in refuge site selection is likely to reflect the reproductive and environmental trade-offs in critical resources during different seasons. The maintenance of multiple, rarely occupied shelters by the eastern chestnut mouse is consistent with data for other mammals. Fire management should ensure retention of vegetation structure on the ground layer, dense habitat patches in burnt areas, and be carefully planned during the winter season to maintain shelter and refuge sites to assist population persistence.

2.2 Introduction

The response of small mammal populations to fire has been studied extensively in Australia (Newsome et al. 1975; Cockburn et al. 1981; Fox 1982; Newsome and Catling 1983; Catling 1986; Thompson et al. 1989; Catling 1991; Masters 1993; Letnic 2003; Letnic et al. 2004; Lindenmayer et al. 2008). A pattern of post-fire irruption followed by decline has been observed for some Australian native rodents (Whelan et al. 2002). The eastern chestnut mouse (Pseudomys gracilicaudatus) is one example. Existing evidence suggests the species is a pyric specialist with peak population density in recently burned heathland and a subsequent decline in abundance with time since fire (Fox 1982; Higgs and Fox 1993; Thompson and Fox 1993; Monamy and Fox 2000; Fox et al. 2003; Monamy and Fox 2010).
The eastern chestnut mouse occurs at low densities when present, is rare or extinct in many parts of its range (Breed and Ford 2007) and is classified as vulnerable under the Threatened Species Conservation Act 1992 (NSW). Inappropriate fire regimes including fire suppression in areas supporting populations of the eastern chestnut mouse may affect the species’ persistence and viability. However, the mechanisms underlying the species’ fire response are unknown.

Terrestrial small mammals can be affected by fire through direct mortality, and indirectly through changes in resource availability (Whelan et al. 2002). Studies of the eastern chestnut mouse’s dietary requirements indicate the species is a generalist herbivore with an opportunistic foraging strategy able to utilise a diverse food resource (Luo and Fox 1994; Luo et al. 1994). A diverse diet is a basic requirement for rapid colonisation of recently burnt areas and is an essential attribute for a fire opportunist to take advantage of all available food resources (Luo et al. 1994). Given this, it is unlikely that depletion of the food resource alone would be a determinant of the species’ fire response.

The role of animal refugia in facilitating population recovery and persistence after a fire is poorly understood for Australian rodent fauna. A reduction in available shelter sites is one of the primary impacts of fire on populations (Newsome and Catling 1983; Friend 1993) and may have multiple consequences including distributional, demographic and behavioural change (Sutherland and Dickman 1999). The presence, size and location of refugia are landscape attributes that may influence the processes of mortality, colonisation, post-fire survival, establishment, reproduction and population increase (Whelan et al. 2002). Daytime refugia and shelter sites are critical for surviving disturbance events (Braithwaite 1990), environmental extremes, predation and for providing security while weaning young (Frank and Layne 1992). Identification of habitat components that might represent refuges and the question of how important they are for maintenance of post-fire populations requires additional study (Keith et al. 2002).

The rate of reappearance after fire is dependent on a species’ mobility, dispersal capacity, dietary specialisation and habitat preferences (Keith et al. 2002), including the level of protection provided by refugia during and after a fire. An assumption of survival within burnt areas would lead us to predict rapid reappearance and population growth (Keith et al. 2002). Recruitment from residual animals after disturbance has been shown to be important (Lindenmayer et al. 2005; Banks et al. 2011). This suggests refugia may play a critical role in a species’ ability to survive fire and the subsequent population response. The identification, distribution, and protection of animal shelter sites and refuges should be an essential component of conservation strategies in fire-prone landscapes.

In this paper, we document the results of a radiotelemetry study of daytime refuge habitat requirements and nest fidelity of the eastern chestnut mouse. We sought to answer the following questions:
(i) Does the eastern chestnut mouse preferentially select shelter sites based on specific habitat attributes? We expected that mouse-selected shelter sites would be characterised by denser, taller vegetation than control sites.

(ii) Are there sex differences or seasonal variation in shelter site selection and fidelity? We hypothesised the female mice would select shelter sites that offer optimal cover and protection during summer and would show greater shelter site fidelity than males. We expected these differences to be driven by different requirements of the sexes during the breeding season – care of offspring in females versus proximity to mates for males. We predict there would be no difference between male and female mice in shelter site selection and fidelity during winter.

(iii) Is there a primary–secondary model of refuge use? We hypothesised that animals would show increased fidelity to shelters characterised by particular attributes including the presence of a mouse-made nesting structure (Wolfe 1970; Klein and Layne 1978; Hartung and Dewsbury 1979). These primary refuges would be used more frequently and would have habitat attributes that distinguish them from secondary shelters.

(iv) Does the eastern chestnut mouse share shelter sites? We expected that individuals would not share shelter sites, instead likely to be solitary in their nesting habits. The closely related western chestnut mouse (P. nanus) also has a dispersed, solitary social organisation (Breed and Ford 2007) and other Pseudomys species have been shown to engage in agonistic nest defence (Happold 1976).

Identification of small mammal shelter requirements and an understanding of refuge site fidelity and nesting behaviour could be used by land managers when designing appropriate burning regimes or promoting post-fire population recovery. For threatened species, knowledge of nest requirements and daytime refuge habitat and use is fundamental for conservation efforts.

2.3 Materials and methods

2.3.1 Study sites

We selected six sites for study in Booderee and Jervis Bay national parks in south-eastern Australia (Fig. 2.1). These adjoining reserves are located approximately 200 km south of Sydney on the south coast of New South Wales. We based site selection on survey data of Townley (2007), Lindenmayer et al. (2008) and a pilot study indicating the presence of the eastern chestnut mouse at sufficiently high densities to enable attachment of radio-transmitters to at least two individuals per site. We classified study sites as heath (defined by Taws (1997) as vegetation dominated by shrubs with small narrow leaves), generally less than 2 m tall and varyingly dominated by Banksia ericifolia and Sprengelita incarnata, with Allocasuarina distyla, Isopogon anemonifolius and Hakea teretifolia also being common. Each of our six field sites had been burnt by wildfire within the last six years.
2.3.2 Trapping and radio-collaring

We completed trapping and radio-collaring during the 2008–2009 summer breeding season (November–March) and the winter 2009 non-breeding season (June–August). We captured animals using grids of type A Elliot traps open for four consecutive nights using a bait of rolled oats, peanut butter and fennel seed. During winter, we insulated traps with non-absorbent cotton wool and covered them with a plastic sleeve. Our grid arrangement comprised lines at 20 m intervals with traps 10 m apart. We provide a summary of field site details, trapping and radio-collaring data (Table 2.1).

We assessed the weight, sex, age cohort and breeding condition of captured animals. We marked mice for permanent identification using Trovan ID100 implantable transponders (Microchips Australia Pty Ltd, Keysborough, Victoria, Australia). We selected mice for radio-collar attachment if they were (i) an adult, (ii) weighed >70 g to ensure collar weight was less than 5% of an individual’s body weight, and (iii) not visibly pregnant. We fitted individuals with a single-stage transmitter on a replaceable cable tie weighing 2.5-3.5 g (Sirtrack Limited, Havelock North, Hawkes Bay, New Zealand) in the field before release at the point of capture. We tracked animals to their diurnal shelter site daily for a period of one month using a Yagi hand-held antenna and a Communications Specialist R1000 receiver (Sirtrack Limited, Havelock North, Hawkes Bay, New Zealand). Transmission was highly directional at close
range allowing us to pinpoint animals to within 1 m². We numbered and permanently marked shelter sites, and recorded location (GPS coordinates).

### Table 2.1: Trapping and radio-collaring site summary

<table>
<thead>
<tr>
<th>Location</th>
<th>Site</th>
<th>Area (ha)</th>
<th>Trap nights</th>
<th>No. of captures</th>
<th>No. of collars fitted</th>
<th>Trap nights</th>
<th>No. of captures</th>
<th>No. of collars fitted</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>summer</td>
<td></td>
<td></td>
<td>winter</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BNP 7-44B</td>
<td>2.40</td>
<td>960</td>
<td>18</td>
<td>4</td>
<td>1</td>
<td>3</td>
<td>480</td>
<td>10</td>
</tr>
<tr>
<td>BNP 7-I</td>
<td>2.05</td>
<td>820</td>
<td>17</td>
<td>6</td>
<td>4</td>
<td>2</td>
<td>400</td>
<td>8</td>
</tr>
<tr>
<td>BNP 7-2</td>
<td>2.00</td>
<td>400</td>
<td>19</td>
<td>4</td>
<td>3</td>
<td>1</td>
<td>400</td>
<td>13</td>
</tr>
<tr>
<td>BNP 7-46</td>
<td>3.25</td>
<td>1280</td>
<td>36</td>
<td>7</td>
<td>2</td>
<td>5</td>
<td>480</td>
<td>7</td>
</tr>
<tr>
<td>BNP 7-H</td>
<td>2.20†</td>
<td>850</td>
<td>20</td>
<td>5</td>
<td>2</td>
<td>3</td>
<td>400</td>
<td>5</td>
</tr>
<tr>
<td>JNP 7-ST1</td>
<td>2.50</td>
<td>500</td>
<td>7</td>
<td>3</td>
<td>1</td>
<td>2</td>
<td>500</td>
<td>11</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>14.40</td>
<td>4840</td>
<td>117</td>
<td>29</td>
<td>13</td>
<td>2660</td>
<td>54</td>
</tr>
</tbody>
</table>

**2.3.3 Assessment of shelter sites**

We assessed shelter sites for vegetation density, height and structure. We measured vegetation density with a light meter (in lux) at 20 cm intervals of a 1 m profile (in duplicate) through the centre of the shelter site. We used an umbrella to shade the light meter from direct sunlight to enable assessment to occur in diffuse light conditions on any given day or time of day. We also recorded the maximum height of vegetation and the structure(s) providing the greatest cover. We searched shelter sites for the presence of a mouse-made nest structure. For each shelter site, we also assessed a control site using the identical procedure. We located control sites at a random compass bearing and a random distance between 2 and 20 m from a known shelter site.

**2.3.4 Data analysis**

We used paired t-tests to determine whether shelter sites differed from controls in vegetation density (estimated as mean lux at 0, 20, 40, 60, 80 and 100 cm), vegetation height and total structure(s) present. We used two-sample binomial tests (Collett 2002) to determine whether mice preferentially selected the presence of structures of different types. To identify effects of sex and/or season in the selection of shelter sites, we used linear mixed models (McCulloch et al. 2008) with the response variables being vegetation height and log-transformed standardised light intensity (as a surrogate for vegetation density, calculated as the proportion of light reaching the ground layer relative to what was available at 1 m). We fitted animal identifier and site as random terms to evaluate individual animal and site variation. We excluded control sites from this analysis.

Using control sites only, we investigated vegetation structure for its effect on standardised light intensity (where standardised light intensity approaching zero would approximate greater ‘cover’). We fitted all possible regression models and ranked them using the Schwarz information criterion (SIC) (Schwarz 1978). The candidate variables were the representative structural categories: *Xanthorrhoea*, buttongrass, dead stems, shrub and no cover.
We considered a primary refuge to be one with a nest structure present. Mouse-made nest structures consisted of finely processed dried grass or sedge woven into either (i) a pad approximately 10 cm in diameter, or (ii) a sphere approximately 10 cm in diameter and height with an inconspicuous opening approximately 2 cm wide. We fitted generalised linear models (GLMs) (McCullagh and Nelder 1989) assuming a Bernoulli response with a logit link function for the probability of occurrence of a nest. The candidate predictors were sex, season, habitat attributes (vegetation density=log-transformed standardised light intensity, vegetation height and structure) and fidelity parameters (re-use, count of fixes standardised by number of radiotracking days). We ranked all possible models using SIC.

2.4 Results

2.4.1 Trapping and radio-tracking

We attached radio-collars to 58 of the 140 individuals of eastern chestnut mouse that we captured. We summarised data on the number of mice captured and radio-collared at each site in each season (Table 2.1). On average, we tracked each animal 22 ± 1.53 times (mean ± s.e.) to diurnal shelter sites. The overall success rate of radio-tracking individuals for >20 consecutive fixes was 67 % with the remaining animals tracked less intensively due to predation, radio-collar loss or signal failure.

2.4.2 Shelter site selection

We identified 453 unique shelter sites from 1300 tracking fixes. On average, each animal had 8 ± 0.5 shelter sites, spent 2.5 ± 0.1 days (total consecutive and non-consecutive fixes) in a shelter site and re-visited shelter sites 0.8 ± 0.1 times (defined as the number of times a mouse returned to a previously identified shelter site). Above ground nest structures were present in 15% of shelter sites. We did not locate any below ground burrow systems.

We found shelter sites had lower lux values (=more dense vegetation) up to 60 cm above the ground (Fig. 2.2) and taller vegetation with more structure compared to control sites (Table 2.2). The type of structure present also differed between shelter and control sites with Xanthorrhoea, buttongrass and dead stems preferentially selected by the eastern chestnut mouse (Table 2.3). These structures were significant predictors of decreasing standardised light intensity when we analysed control site data separately (Table 2.4).

Irrespective of individual animal and site variation, male and female mice did not differ in the standardised light intensity of sites they selected for sheltering but showed a tendency to choose sites with lower standardised light intensity during winter (F1,88=9.6, p=0.003, Fig. 2.3). The height of shelter sites did not differ significantly between sexes or across seasons.
Chapter 2: Refuge site selection

Figure 2.2: Light intensity measured in lux at 20 cm intervals of a 1m profile through eastern chestnut mouse shelter sites (solid line) and paired control sites (broken line). Loss of light is a surrogate for vegetation density. Bars indicate mean ± s.e. Values were significantly different at the 0 – 0.6 m height categories.

Table 2.2: Means (± s.e.), t-statistics and significance levels for differences in height and total number of structures present between paired shelter and control sites

<table>
<thead>
<tr>
<th>Variate</th>
<th>Shelter</th>
<th>Control</th>
<th>T</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height (m)</td>
<td>0.869 ± 0.012</td>
<td>0.785 ± 0.013</td>
<td>4.99</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Total structures</td>
<td>1.589 ± 0.028</td>
<td>1.243 ± 0.023</td>
<td>10.43</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Table 2.3: Proportion of successes, test statistic and significance level for differences in the types of structures present in shelter and control sites

<table>
<thead>
<tr>
<th>Structure type</th>
<th>Shelter</th>
<th>Control</th>
<th>s.e. difference</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Xanthorrhoea</td>
<td>0.496</td>
<td>0.211</td>
<td>0.029</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Buttongrass</td>
<td>0.068</td>
<td>0.008</td>
<td>0.123</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Dead stems</td>
<td>0.380</td>
<td>0.257</td>
<td>0.030</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Shrub</td>
<td>0.384</td>
<td>0.696</td>
<td>0.031</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>No cover</td>
<td>0.255</td>
<td>0.458</td>
<td>0.030</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Table 2.4: Multiple regression statistics for a test of the effect of type of structure on standardised light intensity. Analysis excluded shelter sites due to mouse-selection bias

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>s.e.</th>
<th>t-statistic</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-1.25</td>
<td>0.025</td>
<td>-49.98</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Xanthorrhoea</td>
<td>-0.39</td>
<td>0.047</td>
<td>-8.28</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Buttongrass</td>
<td>-1.08</td>
<td>0.205</td>
<td>-5.24</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Dead stems</td>
<td>-0.13</td>
<td>0.044</td>
<td>-2.91</td>
<td>0.004</td>
</tr>
</tbody>
</table>
2.4.3 Refuge use and fidelity

We were able to predict a primary refuge (i.e. those scored present for a nest structure) based on log-transformed standardised light intensity and season (Table 2.5). We found primary refugia were characterised by vegetation that was denser than secondary shelters (i.e. mouse-selected shelter sites that did not have a nest structure present). This relationship was significant in the non-breeding season indicating mice preferentially chose to construct a nest in a shelter site if it comprised very dense vegetation (Table 2.5). During the breeding season, mice did not appear to be as selective and any given shelter site was equally likely to have a nest structure.

The eastern chestnut mouse was generally a solitary nester. We observed 1165 instances of solitary refuge use. We observed only very occasionally shelter site sharing and confirmed one record of cohabitation. The most common types of sharing we recorded were (i) where two different mice used the same shelter site during different seasons (mice ‘inherited’ the shelter site from a previous occupant – 14 observations); or (ii) where two different mice used the same shelter site at different times during the same season of radio-tracking (sequential shelter site use – 14 observations; six in summer and nine in winter). We observed a male-female pair of radio-collared mice in the same shelter site on one occasion for 14 contiguous daily fixes during winter. This was the only record of cohabitation. We were unable to determine the genetic relationship (if any) between these two mice. We also recorded seven observations of long term shelter site fidelity where the same individual was radio-tracked in multiple seasons and used
the same shelter sites in both periods. This is potentially more common than recorded here due to the small number of mice we re-collared and radio-tracked during both seasons.

### Table 2.5: Parameters for predicting presence of a primary refuge. Season refers to the difference between summer breeding and winter non-breeding seasons

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>s.e.</th>
<th>Statistic</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-3.69</td>
<td>0.90</td>
<td>-4.09</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Log10 sLI</td>
<td>-0.63</td>
<td>0.39</td>
<td>-1.61</td>
<td>0.108</td>
</tr>
<tr>
<td>STD count of fixes</td>
<td>0.74</td>
<td>1.25</td>
<td>0.59</td>
<td>0.553</td>
</tr>
<tr>
<td>Season</td>
<td>-3.22</td>
<td>1.42</td>
<td>-2.27</td>
<td>0.023</td>
</tr>
<tr>
<td>Log10 sLI * season</td>
<td>-1.55</td>
<td>0.59</td>
<td>-2.60</td>
<td>0.009</td>
</tr>
<tr>
<td>STD count of fixes * season</td>
<td>3.58</td>
<td>1.86</td>
<td>1.93</td>
<td>0.054</td>
</tr>
</tbody>
</table>

### 2.5 Discussion

#### 2.5.1 Refuge site selection

Selection of appropriate refuge sites represents a substantial investment of time and energy by an animal. Animals spend periods of inactivity in these locations and shelter and raise their young in them. Therefore, the construction of nests and selection of refuge sites should afford the best protection from predation for both adults and offspring to maximise fitness (Stokes 1995). The eastern chestnut mouse preferentially selected refuge sites with particular habitat attributes. We found shelter sites were selected that had taller, denser vegetation compared to the surrounding habitat. Sites with multiple structures, such as _Xanthorrhoea_, _Gymnoschoenus_ (buttongrass) and the collapsed dead shrubs were also often selected. We suggest these features have a combined effect in providing safety from trampling and predation, insulation against unfavourable climatic conditions, access to foraging areas and protection from aggressive interactions with competitors. For the eastern chestnut mouse, the selection of dense, protected areas for shelter may reflect competitor avoidance. Previous studies indicate competitive exclusion by the swamp rat (_Rattus lutreolus_) on eastern chestnut mouse access to food resources (Luo and Fox 1995; Luo *et al.* 1994) and preferred habitat (Higgs and Fox 1993; Morris *et al.* 2000). In our study, the swamp rat was absent from four of the six study sites. Refugia selected by the eastern chestnut mouse in the two sites where swamp rats were present, were not consistently different from those selected in the sites where the swamp rat was absent. From the results of our study, it is impossible to determine the extent of competition for shelter. However, dense cover has been shown to be important for the swamp rat (Catling 1986; Haering and Fox 1995; Monamy and Fox 2000; Fox and Monamy 2007). The height of vegetation and areas of dense cover have been shown to be an important factor in the choice of refuge location for other terrestrial rodent species (Frank and Layne 1992; Stokes 1995; Gray *et al.* 1998; Wagner *et al.* 2000). The silky mouse’s (_P. apodemoides_) preference for low, dense
vegetation and the availability of desert banksia (*B. ornata*) was considered a major influence on the distribution and location of refugia purposes (Cockburn 1981a).

### 2.5.2 Refuge site use and fidelity

Daytime refuges can include both long-term shelter sites and temporary resting places (Wolff and Hurlbutt 1982). Given the multiple functions of a refuge site, we expected to see a primary–secondary model of refuge use. Refuges offering the best protection are likely to be used most frequently and for long periods of time. The acquisition of refugia has a spatial element. To take advantage of dispersed food resources, animals might have many, less frequently used refuge sites (Ward 1978). We found evidence for hierarchical refuge selection. We considered the presence of a nesting structure to be indicative of a primary refuge. The number of days spent in a shelter and whether a shelter site was re-visited during the course of the study were not significant predictors of a primary refuge. However, we did find a seasonal effect with the density of the vegetation in winter being the best predictor of whether a shelter site would be selected for building a nesting structure. Even though females produced litters during the breeding season, they were no more likely to build nesting structures than males. Any shelter site in the breeding season had an equal likelihood of being a primary refuge. We suggest this may be a result of (i) reproductive constraints including competition for mates, (ii) predator avoidance during the summer months, (iii) competition for foraging resources among females weaning litters, and an (iv) an insufficient survey of breeding females because we did not attach radio-collars to visibly pregnant animals. Retaining primary refuge sites over winter is essential for animals to regulate against thermal extremes and ensure access to foraging resources while competing with other adult animals, sub-adults and juvenile offspring from the previous breeding season. Seasonality in shelter site use has been recorded for other rodent species (Madison *et al.* 1984; Wolton and Trowbridge 1985; Bubela and Happold 1993) and was attributed to environmental factors (i.e. shift in shelter site location dependent on ambient temperature (Madison *et al.* 1984)) and functionality (i.e. different refuges for weaning litters (Morzillo *et al.* 2003)) compared to refugia solely for sheltering.

Many mammals defend multiple, rarely occupied refuge sites (Happold 1976; Cockburn 1981a; Wolff and Hurlbutt 1982; Lindenmayer *et al.* 1996; Hall and Morrison 1997; Moro and Morris 2000; Woods and Ford 2000; Morzillo *et al.* 2003; Sanecki *et al.* 2006; Hinkelman and Loeb 2007; Ebensperger *et al.* 2008). Refuge fidelity and site attachment has links to social organisation and animal behaviour. The eastern chestnut mouse was transient in their refuge use. Our observations indicate the eastern chestnut mouse was most commonly a solitary nester. Solitary sheltering might reflect sparse food resource availability or a territorial social organisation (West and Dublin 1984; Ostfeld 1985). There was some evidence for sharing of refuge sites and long-term fidelity to particular sites. Long-term site fidelity is potentially more common than was possible to record in this study due to the small number of animals we were
ref-collared during both seasons. The most commonly recorded instances of shelter site sharing were temporal segregation or inheritance of a shelter site from a previous occupant. There was only one record of a pair-bond and this was observed during winter. The benefits of refuge site fidelity and defence include: (i) highlighting ownership of, and defence of a shelter site against conspecifics; (ii) reduced parasite burden; (iii) avoiding predators learning patterns of emergence behaviour; and (iv) periodic change in foraging area utilised (Lindenmayer et al. 1996). Familiarity with an area and a known location of proven shelter is probably crucial to survival when exploring unknown territory (Gray et al. 1998). Shelter site replacement (occupation by alternate animals) is not necessarily a random event (Haim and Rozenfeld 1995).

We propose that shelter sites used by different individuals of the eastern chestnut mouse in different seasons may result from parent-offspring or sibling relationship between animals. Bonds resulting from genealogical relationships (parent-offspring and sibling bonds) are not uncommon for pseudomyine rodents (Happold 1976). The silky mouse has been recorded from communal burrows in groups comprising a breeding pair with one or more litters of varying developmental stages (Cockburn 1981b). The Hastings River mouse (P. oralis) has high shelter site fidelity (Townley 2000) and there is some evidence to suggest offspring inherit the maternal range (S. Townley pers. comm.). Further research is needed to confirm if this is the case in the eastern chestnut mouse and it would be of interest to determine whether the relationship between animals is a significant determinant of spatial patterns in sheltering.

2.5.3 Prescribed burning practices

Fire management in areas supporting populations of the eastern chestnut mouse should ensure the retention of tall, dense vegetation and structural features in burnt landscapes. We speculate that as time since fire increases, eastern chestnut mouse shelter sites have the potential to become a limiting resource. Vegetation regeneration in heathland would result in a sparse ground layer and in the complete absence of fire we could expect fewer structural components to be available. That is: (i) the current collapsed shrub layer would decompose; (ii) although a long-lived, slow-growing species, the thatched, dead leaves of unburned Xanthorrhoea would no longer provide cover at ground level as plants grew taller (Gill and Ingwersen 1976); and (iii) woody species would dominate or eliminate the herbaceous plants increasing in biomass and height (Ingwersen 1977; Specht 1981; Keith et al. 2002). Conversely, immediately after a fire, it is also reasonable to expect shelter sites and refugia to be limiting, particularly following a high intensity burn. In contrast to other Pseudomys species (ash-grey mouse P. albocinereus (Happold 1976), silky mouse (Cockburn 1981a), smoky mouse P. fumeus (Woods and Ford 2000), New Holland mouse P. novaehollandiae (Kemper 1981), and heath rat P. shortridgei (Taylor and Horner 1972; Happold 1976)) and Fox (1995), we did not find the eastern chestnut mouse to use a below ground burrow complex. Burrows provide a more fire resilient shelter (Happold 1976; Kemper 1981; Friend 1993; Sutherland and Dickman 1999; Whelan et al.
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With the complete removal of above ground vegetation, the ability of refugial populations to survive in unburnt patches would be a critical factor affecting population persistence (Friend 1993; Whelan 1995). In a manipulative experiment designed to promote small mammal responses to a simulated fire, there was no effect of a reduction in cover on the eastern chestnut mouse (Fox et al. 2003). However, the spatial scale and structural effect of wildfire is likely to be different from that of experimental clipping, which, for instance contained intact patches of vegetation within treatment plots (i.e. buttongrass). Further studies are necessary to determine whether the changes in vegetation regrowth after fire affect habitat preferences of shelter sites and refugia.

Assuming the occurrence of fire in heathland is important for retention of habitat features selected by the eastern chestnut mouse for refugia, appropriate timing of prescribed burning practices may be important. Within mouse-selected refuge sites, those with denser vegetative cover were used for over-wintering. These shelters were significantly more likely to have a nest structure present. The eastern chestnut mouse builds an above ground surface nest comprised of dried sedge or grassy material woven into a pad or spherical structure. These are highly flammable refuges. Protection from fire by such a shelter would be limited and the likelihood of direct mortality by fire would be very high. The eastern chestnut mouse nest structure resembles that of the eastern bristle bird (Dasyornis brachypterus); a co-occurring heathland species which has also been found absent immediately after wildfire from sites that were previously occupied (Lindenmayer et al. 2009). The only other Pseudomys species known exclusively to build an above ground grass nest is the western chestnut mouse (P. nanus) which is also now extinct from the southern part of the species’ historical range and is rare or extinct throughout current distribution (Strahan 1995; Breed and Ford 2007). Management practices that allow burning during winter months would remove valuable primary refuge sites and may result in the post-fire residual eastern chestnut mouse population expending greater energy to re-establish over-wintering nesting structures at a cost of reduced foraging capacity.

2.5.4 Conclusion

The eastern chestnut mouse preferentially selects relatively taller, denser vegetation (up to 1 m) with structural features present at the ground layer for refuge. Refugia are highly flammable and do not provide protection from fire. These shelter site requirements have implications for land management and prescribed burning practices. There is some evidence for a primary-secondary model of refuge use. Primary refuge sites had a nesting structure present and were the more dense shelter sites selected by the eastern chestnut mouse. Any shelter had an equal likelihood of being a primary or secondary refuge during the summer breeding season but dense vegetation was the best predictor of a primary refuge for over-wintering animals. There are likely to be several reasons for this seasonal aspect of shelter site use including reproductive constraints and intra-specific competition for reproductive resources in the summer breeding
season and environmental constraints including regulation against thermal extremes in the absence of huddling behaviour in winter. The maintenance of multiple, rarely occupied shelters is consistent with data for other mammals and is likely to be the result of territorial defence, access to dispersed resources and predator avoidance. The eastern chestnut mouse is mostly solitary in its sheltering habits but there is some evidence for short-term sharing, temporal segregation in the use of the same sites, or familial inheritance in the longer time frame.

2.6 Acknowledgements

We most gratefully acknowledge the Wreck Bay Aboriginal Community and the Wandandian People of the Dharawal and Dhurga language groups on whose lands this study was conducted. For valuable field assistance, advice and discussions, we thank Wendy Hartman, Alfred Wellington, Tony Carter, Geoff Kay, Steve Phillips, Marama Hopkins, Nick Dexter, Karen Viggers, Sally Townley, Les Mitchell and Martin Westgate. This research was funded by the Norman Wettenhall Foundation and the MA Ingram Trust and conducted under The Australian National University Animal Experimentation Ethics Committee protocol C.RE.49.08, NSW National Parks and Wildlife Service Scientific Licence S12690 and Booderee National Park Permit BDR08/00009.

2.7 References


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Chapter 2: Refuge site selection


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Chapter 2: Refuge site selection


Chapter 2: Refuge site selection


Chapter 3

Site occupancy

Published as:

Landscape, fire and habitat: which features of recently burned heathland influence site occupancy of an early successional specialist?

Manuscript: Appendix 2
3.1 Abstract

Multiple ecological drivers generate spatial patterns in species’ distributions. Changes to natural disturbance regimes can place early successional habitat specialists at an increased risk of extinction by altering landscape patterns of habitat suitability. We developed a series of hypotheses to evaluate the effects of landscape structure, fire history, and site-level habitat quality on site occupancy by an early successional specialist, the eastern chestnut mouse (Pseudomys gracilicaudatus). We obtained eight years of monitoring data from 26 sites in recently burned heathland in southeast Australia. We used generalised linear models to determine which explanatory variables were related to occupancy. We also explored predictability in patterns of small mammal species co-occurrence.

Landscape structure (patch area, landscape heterogeneity) was strongly related to site occupancy. Site occupancy was associated with dead shrubs in the understory and rock cover on ground layer, but was not directly influenced by recent or historical fire. Contrary to contemporary ecological theory, we found no predictable species associations in our early successional community. We recommend surveys take account of landscape configuration and proximity to suitable habitat for optimal results. Fire regimes expected to promote eastern chestnut mouse population growth should encourage the retention of critical habitat features rather than be based on temporal rates of successional stages. For management to adequately account for post-disturbance patterns in early successional communities, a species-by-species, multi-scaled approach to research is necessary.

3.2 Introduction

Early successional communities are the starting point for recovery after major disturbance. These communities are comprised of residual individuals, colonising opportunists and habitat specialist species (Connell and Slatyer 1977; Swanson et al. 2011). Understanding the ecological processes operating in early successional communities is important, given these ephemeral habitats are confined to the variable length of time between a disturbance, and re-establishment of the later successional stages of community composition (Swanson et al. 2011). Estimating the duration of the early successional community is difficult as it is related to the type of ecosystem and is likely to fluctuate within ecosystems of the same type (Bradstock et al. 2012); for example, years for heathlands (Keith et al. 2002) compared to decades or even centuries in some forests (McCarthy et al. 1999). This time frame is likely to vary geographically (Velle and Vandvik 2014), and be dependent on the type and frequency of disturbance events (e.g. Sousa 1979; Delmoral and Bliss 1993; Rossi et al. 2007; Gill and Allan 2008).
Chapter 3: Site occupancy

Heathland communities often occur in the early successional stage of regeneration after disturbance. In Australia, heathlands are one of the most fire-prone and flammable ecosystems (Williams 1995; Keith et al. 2002). Following disturbance, these heathlands can accumulate sufficient plant biomass for fire ignition every two years (Williams 1995) and reach a mature to senescent phase after 25 to 50 years (Specht 1981). The compositional dynamics of heathland are primarily driven by the fire regime. High fire frequency (i.e. every two years) can reduce a heathland to a sedgeland by eliminating woody shrubs and allowing herbaceous species to dominate (Williams 1995). Long intervals between fires (i.e. greater than 20 years) will produce closed scrubs with diminished understory floristic richness (Williams 1995; Keith et al. 2002). Heathlands generally occur as patches of various sizes within a heterogeneous landscape (Williams 1995).

Fire occurs over multiple spatial and temporal scales, with variable impacts on biodiversity and key ecosystem processes that are strongly site- and species-specific (Pickett and White 1985; Turner et al. 1998; Whelan et al. 2002). For small mammals, patterns of population responses to fire have been studied over multiple decades (Newsome et al. 1975; Masters 1993; Letnic et al. 2013). Small mammals are associated with a range of fire frequencies; from high (e.g. heath rat (*Pseudomys shortridgei*), Cockburn et al. 1981; eastern chestnut mouse (*P. gracilicaudatus*), Fox 1982) to low (e.g. desert mouse (*P. desertor*), Letnic and Dickman 2005; brown antechinus (*Antechinus stuartii*), brown antechinus (*Antechinus stuartii*), Fox 1982; letnic and dickman 2005; bush rat (*Rattus fuscipes*), swamp rat (*R. lutreolus*), Lindenmayer et al. 2008a; silky mouse (*P. apodemoides*), Lindenmayer et al. 2008a). Changes to fire regimes can reduce habitat suitability for some species (e.g. Fox 1982; Baker et al. 2010).

Contingent upon a species’ location along the continuum, increased fire frequency may improve population viability. For early successional species, fire suppression can lead to population extinction through habitat degradation and impaired demographic processes (Hutto 2008; Templeton et al. 2011). For example, with the re-introduction of fire, Templeton et al. (2011) showed isolated patches could transition into a stable metapopulation with concomitant changes in the amount and patterns of animal movements across the landscape. Furthermore, fire-specialist fauna have been shown to occur with increasing likelihood as spatial proximity to fire, or fire severity increases (Hutto 2008), and have positive population growth rates in habitat created by fire (Rota et al. 2014). For early successional heathland specialists, the local physical conditions that are associated with their presence are likely to be in a continual state of change. The ability to reverse population declines for these species is complicated by the unpredictable, spatially and temporally variable nature of their habitats. However, whether fire plays a positive role in species occurrence and assists in maintaining habitat suitability in early successional communities is poorly understood.

Research across multiple spatial scales is necessary for identifying the processes underlying species’ responses in patchy and temporally-dynamic communities (Levin 1992;
Thornton et al. 2011). Most theoretical and empirical research in disturbance ecology has focussed on site-level disturbance history (e.g. time since fire). However, multiple ecological drivers together generate spatial patterns in species’ distributions (Turner 2005). For instance, research in landscape ecology has a strong focus on landscape pattern variables such as patch size and landscape heterogeneity, as well as site-level habitat quality (Burel and Baudry 2003). Here, we tested the effects of landscape patterns on spatial processes by integrating fire history (sensu landscape legacy (Turner 2005) or ecological memory (Peterson 2002)), with classic landscape ecology themes of patch size and landscape heterogeneity, as well as community ecology themes of interspecific interactions. We investigated landscape patterns of habitat suitability across multiple spatial scales using a species described as an early successional specialist, the eastern chestnut mouse (*Pseudomys gracilicaudatus*, Gould 1845). Specifically, we assessed a series of hypotheses relating to the perceived importance of fire history, landscape, community and site-level habitat features influencing site occupancy in an early successional heathland (Fig. 3.1).

**Figure 3.1:** Conceptual diagram showing the predicted effects of explanatory variables on eastern chestnut mouse site occupancy; black arrows indicate a positive effect, white arrows indicate a negative effect, grey arrows indicate no effect.

*Hypothesis 1 (fire history):* We predicted occupancy was positively related to the distribution of the most recent fire, positively related to a high incidence of fires, and negatively related to the years since last fire (Fig. 3.1). Recent fire creates suitable habitat for early successional specialists (Monamy and Fox 2000). Therefore, with either a recent fire or an
increased incidence of fire at a site, post-fire recruitment by residual survivors should offset the potential for local extinction.

Hypothesis 2 (site-level habitat quality): We predicted occupancy was positively related to understory floristic richness, the number of dead shrubs in the understory, and live vegetative cover on the ground layer (Fig. 3.1). The distribution of species after disturbance is dependent on the availability of suitable local habitats, and has been linked to shelter (Fox et al. 2003; Robinson et al. 2013), food (Luo and Fox 1996; Vieira and Briani 2013), and breeding resource requirements (Banks et al. 2005b; Watson et al. 2012). The floristic richness of early successional heathland provides a varied diet for an opportunistic generalist herbivore like the eastern chestnut mouse (Luo et al. 1994). Dense vegetation on the ground layer and a collapsed dead shrub layer are significant components of the species’ diurnal shelter requirements (Pereoglou et al. 2011).

Hypothesis 3 (interspecific interactions): We predicted eastern chestnut mouse site occupancy was negatively related to swamp rat (Rattus lutreolus) occurrence, but was not influenced by the occurrence of the bush rat (R. fuscipes) or brown antechinus (Antechinus stuartii) (Fig. 3.1). After a disturbance, species are added to the community assemblage when their specific habitat requirements are met (habitat accommodation model; Fox 1982). Species replacement is a result of subsequent competitive interactions that occur with time since fire or vegetation succession (Fox et al. 2003). The swamp rat is the only one of the co-occurring species that is similar to the eastern chestnut mouse in its resource requirements and has also been shown to be competitively superior (Higgs and Fox 1993).

Hypothesis 4 (landscape context): We predicted site occupancy was positively related to heathland patch area and negatively influenced by landscape heterogeneity (Fig. 3.1). The probability of species occurrence in a habitat patch varies as a function of patch size (MacArthur and Wilson 1967) with a species’ area sensitivity being greater when the intervening matrix is inhospitable (Prugh et al. 2008). The eastern chestnut mouse is considered a heathland habitat specialist (Fox 1982) but there has been no study of how habitat availability and heterogeneity influences the species’ local distribution across a landscape.

3.3 Materials and Methods

3.3.1 Study species

The eastern chestnut mouse is an endemic Australian murid rodent. It has a disjunct distribution along the east coast of Australia (inset Fig. 3.2) and is absent throughout much of its range. The species inhabits heathland in southern Australia and has been recorded in woodland in the northern parts of its range (Fox 2008). Usually reported at low density, populations peak in abundance post-fire before declining as vegetation regenerates (Fox 1982). Threats to the
viability of populations of the species are thought to include fire suppression, loss of heath habitat, and predation (Fox 2008). A summarised description of the eastern chestnut mouse and the co-occurring small mammal species with which it is expected to have competitive interactions is provided (Table 3.1; a full version of species’ descriptions available in Appendix 4).

### 3.3.2 Study area and survey design

Booderee National Park is a ~6 500 ha reserve located in the Jervis Bay region, approximately 200 km south of Sydney, Australia (Fig. 3.2). Booderee National Park is characterised by natural heterogeneity in vegetation with six broad vegetation types (forest, rainforest, woodland, heathland, shrubland and sedgeland) identified in previous vegetation surveys (Taws 1997) (Fig. 3.2).

Monitoring heathland sites (n = 26) began in 2003 as part of a long-term study on the effects of fire on vertebrate biota (see Lindenmayer et al. 2008a). Site monitoring was conducted annually during the summer months for the period 2003 – 2011. Sites comprised a single 100 m transect with: (i) a black plastic drift fence connecting 380 mm deep x 300 mm diameter pitfall traps at 0 and 20 m, 40 and 60 m, and 80 and 100 m; (ii) large wire cage traps (30 x 30 x 60 cm) placed at 0 m and 100 m with four small wire cage traps (20 x 20 x 50 cm) at 20 m intervals between; and (iii) ten aluminium box traps (Elliott Scientific Equipment, Australia) placed every 10 m along the transect line from 0 – 90 m (Fig. 3.3). We baited wire cage traps and aluminium box traps with rolled oats and peanut butter. Effort varied between sites and survey years, but on average, we opened traps for three consecutive nights each survey year. We checked all traps daily during the trapping period and recorded species, sex, age class, trap number and trap type. Animals were marked to identify recaptures within a single survey year trapping period before release at the point of capture.

Vegetation was sampled during the survey years of 2004/05, 2006/07, 2007/08, and 2009/10 in two 20 x 20 m plots located at the 20 – 40 m and 60 – 80 m sections of each transect (Fig. 3.3). We counted the number of dead shrubs (where a shrub was defined as single woody plant either multi-stemmed at the base or, if single stemmed, less than 2m tall; dead shrubs, Table 3.2), the number of understory plant species present (floristic richness, Table 3.2), and visually estimated the understory (< 2 m) percent live cover of all plant species combined (cover, Table 3.2). Values were averaged across the two vegetation plots. Percent rock cover, bare ground and regenerating shrubs in the ground layer were visually estimated in four 1 x 1 m sub-plots nested within the larger vegetation plot, values were averaged (Table 3.2).

Fire history data was extracted from GIS layers available for Booderee National Park using ArcGIS version 9.2 (ESRI 2009). At each site, for each survey year, we calculated the
### Table 3.1: Summarized description of the eastern chestnut mouse and co-occurring small mammal species. Full description provided in Appendix S1 in Appendix 4

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat</th>
<th>Average adult weight (grams)</th>
<th>Breed: all year (A) or season (S)</th>
<th>Litter size</th>
<th>Breed season of birth</th>
<th>Lifespan (years)</th>
<th>Diet</th>
<th>Habit</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eastern chestnut mouse</td>
<td>Woodland</td>
<td>90 (male)</td>
<td>S</td>
<td>1 – 5 (3)</td>
<td>No</td>
<td>&lt; 2</td>
<td>Herbivorous</td>
<td>Nocturnal, terrestrial</td>
<td>Fox 1982; Fox and Kemper 1982; Luo et al. 1994; Fox 2008</td>
</tr>
<tr>
<td>(Pseudomys gracilicaudatus)</td>
<td>Heathland</td>
<td>75 (female)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>terrestrial</td>
<td></td>
</tr>
<tr>
<td>Bush rat</td>
<td>Widespread</td>
<td>&gt; 200</td>
<td>A, S</td>
<td>1 – 7 (5)</td>
<td>Yes</td>
<td>1 – 2</td>
<td>Omnivorous</td>
<td>Nocturnal, terrestrial</td>
<td>Warneke 1971; Watts and Aslin 1981; Robinson 1987; Breed and Ford 2007; Lunney 2008a</td>
</tr>
<tr>
<td>(Rattus fuscipes)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>mostly territorial</td>
<td></td>
</tr>
<tr>
<td>Swamp rat</td>
<td>Heathland</td>
<td>200</td>
<td>A, S</td>
<td>3 – 5</td>
<td>Yes</td>
<td>1 – 2</td>
<td>Herbivorous</td>
<td>Partially diurnal, terrestrial, territorial</td>
<td>Watts and Aslin 1981; Braithwaite 1982; Lunney 2008b</td>
</tr>
<tr>
<td>(R. lutreolus)</td>
<td>Sedgeland</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brown antechinus</td>
<td>Forest</td>
<td>35 (male)</td>
<td>S</td>
<td>8 – 10</td>
<td>No</td>
<td>1 (male)</td>
<td>Insectivorous</td>
<td>Terrestrial or arboreal, communal nesting</td>
<td>Fox and Archer 1984; Cockburn and Lazenby-Cohen 1992; Crowther 2002; Crowther and Braithwaite 2008; Dickman 2008</td>
</tr>
<tr>
<td>(Antechinus stuartii)</td>
<td>Heathland</td>
<td>20 (female)</td>
<td></td>
<td></td>
<td></td>
<td>1 – 2 (female)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 3.2: Map of Booderee national park indicating study sites and vegetation types. Inset shows the distribution of the eastern chestnut mouse and the study area location.

Figure 3.3: Layout of a site transect and the location of vegetation plots. Diagram is not to scale.
number of years elapsed since the last fire (years since fire, Table 3.2), and counted the number of fires affecting the site since fire mapping began in the mid-1950s (previous fires, Table 3.2). Sites were scored with a 0 or 1 to indicate whether they were burned in the most recent major fire in December 2003 (burned 2003, Table 3.2). Eighty percent of heathland sites were burned in the 2003 fire.

Landscape structure was measured from GIS layers of the vegetation mapping of Taws (1997) available for Booderee National Park, using ArcGIS version 9.2 (ESRI 2009). As a measure of landscape heterogeneity, we determined the number of vegetation types within a polygon of 500 m radius around each site (landscape heterogeneity, Table 3.2). A 500 m radius was chosen because the closest sites were 1 km apart. We calculated the area of the mapped polygon of heathland within which a site was located (patch area, Table 3.2). Landscape heterogeneity and patch area were fixed for the study period.

### 3.3.3 Statistical analysis

We used Spearman’s rank correlation (Conover 1999) to identify redundant variables.

We explored the individual significance of the explanatory variables (Table 3.2, Fig. 3.1) using a series of univariate hierarchical generalised linear models (HGLMs; Lee et al. 2006) with an over-dispersed Poisson distribution and logarithm-link function. Our model response variable, site occupancy, was the total number of eastern chestnut mouse captures across trap nights at each site. We fitted each explanatory variable individually in separate models that included site as a random term to account for variation among sites, and survey year as a fixed effect (except where site occupancy was predicted by years since the last fire, survey year was fitted as a random term). We calculated effort as the total number of traps open at each site multiplied by the total number of nights that traps were open within a survey year and we included the log of effort as an offset variable to account for unequal survey effort between sites and survey years (Table S1 in Appendix 4).

To check for possible interrelationships between the effects of the explanatory variables, we also fitted generalized linear models (GLMs; McCullagh and Nelder 1989) for all possible subsets of the set of potential explanatory variables (Table 3.1, Fig. 3.1). We evaluated the fits using Schwarz information criterion (SIC; Schwarz 1978) and Akaike’s information criterion (AIC; Burnham and Anderson 2002). Complex fixed effects models are computationally much easier to fit using GLMs. Terms that did not contribute anything useful in the HGLMs might be retained, but it was very unlikely we would omit a term that was important. We also looked for an indirect effect of fire via other explanatory variables by testing whether the apparent effect of fire was removed when another explanatory variable was included in our models, and in turn fitting a model to test whether that variable was significantly affected by fire. Based on the explanatory variables identified in the GLM of all subsets and the univariate HGLMs, we then fitted a multivariate HGLM using the predictors from the ‘best’ model.
Finally, we fitted the captures of other small mammals (bush rat, swamp rat and brown antechinus) as dependent variables in a series of separate models to determine whether the eastern chestnut mouse responded differently compared to sympatric species in relation to fire history, landscape structure and site-level habitat quality.

Table 3.2: Description of explanatory variables used to predict eastern chestnut mouse site occupancy

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Mean</th>
<th>S.E.</th>
<th>Min</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>Survey year</td>
<td>2003 – 2010/11 (n = 9)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site</td>
<td>Unique site identifier (n = 26)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Effort</td>
<td>Total number of traps open x total number of nights traps were open</td>
<td>63.30</td>
<td>2.09</td>
<td>0</td>
<td>138</td>
</tr>
<tr>
<td>Species associations</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eastern chestnut mouse</td>
<td>Eastern chestnut mouse captures (new animals + recaptures)</td>
<td>0.63</td>
<td>0.11</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>Bush rat</td>
<td>Bush rat captures (new animals + recaptures)</td>
<td>2.78</td>
<td>0.28</td>
<td>0</td>
<td>24</td>
</tr>
<tr>
<td>Swamp rat</td>
<td>Swamp rat captures (new animals + recaptures)</td>
<td>0.45</td>
<td>0.10</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>Brown antechinus</td>
<td>Brown antechinus captures (new animals + recaptures)</td>
<td>1.89</td>
<td>0.16</td>
<td>0</td>
<td>11</td>
</tr>
<tr>
<td>Fire history</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Burned 2003</td>
<td>Site burned (1) or not (0) in the December 2003 fire</td>
<td>4.54</td>
<td>0.12</td>
<td>1</td>
<td>9</td>
</tr>
<tr>
<td>Number of previous fires</td>
<td>Count of previous fires recorded at each site</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Years since fire</td>
<td>Number of years elapsed since the last fire at each site</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site-level habitat quality</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dead shrub</td>
<td>Count of dead shrubs&lt;sup&gt;a&lt;/sup&gt;</td>
<td>28.10</td>
<td>3.25</td>
<td>0</td>
<td>270</td>
</tr>
<tr>
<td>Floristic richness</td>
<td>Number of understory species&lt;sup&gt;a&lt;/sup&gt;</td>
<td>13.09</td>
<td>0.46</td>
<td>4.5</td>
<td>26.50</td>
</tr>
<tr>
<td>Percent cover</td>
<td>Percent live cover of all understory species combined&lt;sup&gt;a&lt;/sup&gt;</td>
<td>85.44</td>
<td>1.79</td>
<td>15</td>
<td>100</td>
</tr>
<tr>
<td>Percent rock</td>
<td>Percent rock cover in ground layer&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.24</td>
<td>0.39</td>
<td>0</td>
<td>24.38</td>
</tr>
<tr>
<td>Percent bare</td>
<td>Percent cover of bare ground in ground layer&lt;sup&gt;b&lt;/sup&gt;</td>
<td>17.41</td>
<td>2.12</td>
<td>0</td>
<td>81.88</td>
</tr>
<tr>
<td>Percent regenerating vegetation</td>
<td>Percent cover of regenerating vegetation in ground layer&lt;sup&gt;b&lt;/sup&gt;</td>
<td>16.71</td>
<td>2.63</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>Landscape structure</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Patch area</td>
<td>Number of hectares of contiguous patch of vegetation of type i</td>
<td>88.59</td>
<td>8.74</td>
<td>0.93</td>
<td>362.20</td>
</tr>
<tr>
<td>Landscape heterogeneity</td>
<td>Number of vegetation types in 500 m radius of site</td>
<td>4.00</td>
<td>0.07</td>
<td>2</td>
<td>6</td>
</tr>
</tbody>
</table>

<sup>a</sup>Average of data measured in two 20 x 20 m plots
<sup>b</sup>Average of data measured in four 1 x 1 m subplots

3.4 Results

We completed a total of 14812 trap nights and made 1346 captures (including 366 recaptures) of the eastern chestnut mouse and co-occurring terrestrial small mammal species.

3.4.1 Correlation between explanatory variables

We found a low level of correlation between explanatory variables (Table 3.3). Variable pairs with the highest levels of correlation included patch area and landscape heterogeneity, previous fires and landscape heterogeneity, years since last fire and burned 2003, and bush rat and effort. The landscape structure variables represented different effects and were not so highly correlated that inclusion together substantially reduced the reliability of the further modelling. The extent of the 2003 fire meant insufficient fire ages were available to model a time since fire
effect on occupancy so we removed years since fire from further analysis and retained the binary variable.

3.4.2 Fire history

Although the eastern chestnut mouse was only observed on burned sites, the direct effect of burning in 2003 was not significant. This partly reflects the small number of heathland sites that were not burned in the most recent fire. Whether a site was burned in 2003 had a positive effect on eastern chestnut mouse site occupancy when the percent rock cover on the ground layer was included in the model (Table 3.4). However, all of the sites that were not burned in 2003 had no rock, so the effects are confounded to some extent and it is mainly a percent rock cover effect. Hence, H₁ was rejected, as we were unable to detect a direct effect of either previous fires or burning in the 2003 fire on eastern chestnut mouse site occupancy (Table S2 in Appendix 4, Fig. 3.4).

3.4.3 Site-level habitat quality

The number of dead shrubs in the understory had a weak positive effect on eastern chestnut mouse site occupancy (Fig. 3.4). An exponential increase in the number of dead shrubs in the understory was associated with a small increase in eastern chestnut mouse captures per 100 trap nights (Fig. 3.5a). As an indirect effect of fire, we found the number of dead shrubs significantly increased with burning in 2003. Percent rock cover on the ground layer positively influenced eastern chestnut mouse site occupancy in burned sites (Table 3.4). Understory floristic richness and percent cover did not affect eastern chestnut mouse site occupancy, nor did the percent bare ground or regenerating shrubs in the ground layer. We accepted H₂, habitat features of the understory and ground layer influence eastern chestnut mouse site occupancy (Table S2 in Appendix 4, Fig. 3.4).

3.4.4 Species associations

We found a negative effect of bush rat abundance on eastern chestnut mouse site occupancy (Fig. 3.4). There was no significant influence of swamp rat or brown antechinus abundance on eastern chestnut mouse site occupancy. When we included the occurrence of the bush rat, swamp rat and brown antechinus as fixed terms in a model together, no species had a significant influence on eastern chestnut mouse site occupancy (Table S2 in Appendix 4). Hence, H₃ was rejected, as co-occurring small mammal species did not influence eastern chestnut mouse site occupancy as predicted (Table S2 in Appendix 4, Fig. 3.4).
Table 3.3: Correlation matrix showing Spearman's rank correlation coefficients for explanatory variables. Correlated variables ± >0.5 are bold.

<table>
<thead>
<tr>
<th>Variable</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eastern chestnut mouse</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Bush rat</td>
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<td>-0.18</td>
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<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
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<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Brown antechinus</td>
<td>-0.02</td>
<td>0.03</td>
<td>0.19</td>
<td>0.25</td>
<td>1</td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Burned 2003</td>
<td>-0.02</td>
<td>0.17</td>
<td>-0.50</td>
<td>-0.29</td>
<td>-0.40</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of previous fires</td>
<td>-0.08</td>
<td>0.02</td>
<td>-0.12</td>
<td>-0.02</td>
<td>0.08</td>
<td>0.18</td>
<td>1</td>
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<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Years since fire</td>
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<td>0.48</td>
<td>0.01</td>
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<td>-0.16</td>
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<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Dead shrub</td>
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<td>-0.06</td>
<td>0.04</td>
<td>-0.13</td>
<td>-0.10</td>
<td>0.21</td>
<td>0.05</td>
<td>-0.14</td>
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<tr>
<td>Floristic richness</td>
<td>0.15</td>
<td>0.17</td>
<td>-0.18</td>
<td>0.01</td>
<td>-0.18</td>
<td>0.15</td>
<td>0.05</td>
<td>0.11</td>
<td>-0.09</td>
<td>1</td>
<td></td>
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<td></td>
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<tr>
<td>Percent cover</td>
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<td>-0.08</td>
<td>0.17</td>
<td>0.09</td>
<td>0.08</td>
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<td>-0.07</td>
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<td></td>
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<tr>
<td>Percent bare</td>
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<td>0.02</td>
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<td>0.06</td>
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<td>-0.16</td>
<td>-0.09</td>
<td>-0.08</td>
<td>0.11</td>
<td>0.08</td>
<td>-0.12</td>
<td>0.05</td>
<td>-0.03</td>
<td>-0.34</td>
<td>0.16</td>
<td>1</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Percent regenerating vegetation</td>
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<td>0.06</td>
<td>-0.15</td>
<td>-0.04</td>
<td>-0.02</td>
<td>0.10</td>
<td>0.19</td>
<td>-0.29</td>
<td>0.23</td>
<td>0.03</td>
<td>0.08</td>
<td>-0.12</td>
<td>0.21</td>
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<td>Patch area</td>
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<td>0.22</td>
<td>0.45</td>
<td>0.13</td>
<td>0.32</td>
<td>0.04</td>
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<td>0.40</td>
<td>0.49</td>
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</tr>
<tr>
<td>Landscape heterogeneity</td>
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<td>0.03</td>
<td>-0.19</td>
<td>-0.03</td>
<td>0.10</td>
<td>-0.52</td>
<td>-0.02</td>
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<td>-0.22</td>
<td>0.08</td>
<td>-0.13</td>
<td>-0.32</td>
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Table 3.4: Ten best generalized linear models from fitting all possible subsets of explanatory variables. ΔSIC and ΔAIC are the differences in SIC and AIC for the given models from the value for the optimal model.

<table>
<thead>
<tr>
<th>ΔSIC</th>
<th>ΔAIC</th>
<th>Model terms</th>
</tr>
</thead>
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<tr>
<td>0</td>
<td>1.22</td>
<td>Survey year + percent rock + burned 2003</td>
</tr>
<tr>
<td>1.37</td>
<td>0</td>
<td>Dead shrub + survey year + percent rock + burned 2003</td>
</tr>
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<td>2.44</td>
<td>1.07</td>
<td>Survey year + percent regenerating vegetation + percent rock + burned 2003</td>
</tr>
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<td>3.17</td>
<td>1.80</td>
<td>Survey year + percent rock + percent bare + burned 2003</td>
</tr>
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<td>3.84</td>
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<td>Survey year + percent cover + percent rock + burned 2003</td>
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<td>4.09</td>
<td>2.72</td>
<td>Survey year + floristic richness + percent rock + burned 2003</td>
</tr>
<tr>
<td>4.16</td>
<td>2.79</td>
<td>Survey year + percent rock + brown antechinus + burned 2003</td>
</tr>
<tr>
<td>4.40</td>
<td>3.03</td>
<td>Survey year + percent rock + patch area + burned 2003</td>
</tr>
<tr>
<td>4.41</td>
<td>3.04</td>
<td>Survey year + percent rock + bush rat + burned 2003</td>
</tr>
<tr>
<td>4.45</td>
<td>3.08</td>
<td>Survey year + percent rock + burned 2003 + landscape heterogeneity</td>
</tr>
</tbody>
</table>

Figure 3.4: Conceptual diagram showing the modelled effects of explanatory variables on eastern chestnut mouse site occupancy; black arrows indicate a positive effect, white arrows indicate a negative effect, broken line represents indirect effect.

We found direct effects of fire history and landscape structure for the sympatric small mammal species. Burning in the 2003 fire had a strong negative effect on both swamp rat and brown antechinus site occupancy estimates (Table S2 in Appendix 4). A weak negative effect of patch area on brown antechinus and swamp rat site occupancy indicates a potential sensitivity to landscape heterogeneity (Table S2 in Appendix 4).
3.4.5 Landscape structure

Landscape heterogeneity had a strong negative effect on eastern chestnut mouse site occupancy (Fig. 3.4), with the number of captures per 100 trap nights decreasing significantly as habitat diversity increased (Fig. 3.5b). To a lesser extent, eastern chestnut mouse site occupancy was affected by patch area (Fig. 3.5c). Hence, we accepted $H_4$, landscape structure affected eastern chestnut mouse site occupancy (Table S2 in Appendix 4, Fig 3.4).

Figure 3.5: Number of eastern chestnut mouse captures predicted from hierarchical generalised linear models over a range of values of significant explanatory variables; (a) number of dead shrubs, (b) patch area, and (c) landscape heterogeneity.
3.4.6 ‘Best’ model for predicting eastern chestnut mouse site occupancy

When significant explanatory variables determined from the univariate HGLMs and all subsets regression were included in a single model, burned 2003 and percent rock cover were the only variables whose coefficients were not significantly different from zero (Table 3.5).

Table 3.5: Multivariate HGLM of significant explanatory variables. Model included eastern chestnut mouse site occupancy as response variable, site as a random effect, survey year as a fixed effect, and the log of effort as an offset variable.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Estimate</th>
<th>S.E.</th>
<th>t</th>
<th>P</th>
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</thead>
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<tr>
<td>Bush rat</td>
<td>-0.116</td>
<td>0.051</td>
<td>-2.26</td>
<td>0.024</td>
</tr>
<tr>
<td>Burned 2003</td>
<td>1.035</td>
<td>0.653</td>
<td>1.59</td>
<td>0.113</td>
</tr>
<tr>
<td>Percent rock</td>
<td>0.022</td>
<td>0.031</td>
<td>0.72</td>
<td>0.471</td>
</tr>
<tr>
<td>Dead shrub</td>
<td>0.010</td>
<td>0.005</td>
<td>2.15</td>
<td>0.032</td>
</tr>
<tr>
<td>Patch area</td>
<td>0.004</td>
<td>0.001</td>
<td>2.86</td>
<td>0.004</td>
</tr>
<tr>
<td>Landscape heterogeneity</td>
<td>-0.354</td>
<td>0.179</td>
<td>-1.98</td>
<td>0.048</td>
</tr>
</tbody>
</table>

3.5 Discussion

3.5.1 Importance of landscape structure versus site-level habitat selection

Our study tested the importance of key themes of ecological theory from disturbance ecology (site-level disturbance history), landscape ecology (site-level habitat quality and landscape patterns) and community ecology (interspecific interactions) on the distribution of an early successional species in a fire-prone environment. A key finding from our study was that site occupancy was strongly influenced by landscape (i.e. broad-scale landscape structure, hypothesis 4), and to a lesser extent, elements within the landscape (i.e. resource availability at a site-level, hypothesis 2) (Fig. 3.4). Large heathland habitat patches, a less heterogeneous intervening habitat matrix, and the presence of dead shrubs indicated a greater likelihood of sites being occupied by the eastern chestnut mouse. This reflects the species’ known shelter resource requirements and presumed habitat specialisation.

The basic principle of landscape ecology is that the spatial organization of the environment controls ecological processes (Burel and Baudry 2003). Species respond to patch-level variables because they are important predictors of distribution and abundance (Prugh et al. 2008; Thornton et al. 2011). Habitat specialists that inhabit patchy terrestrial landscapes could be expected to occur predominantly in large habitat patches of the preferred vegetation type and this was the case in our study. Large habitat patches can support higher rates of occupancy compared to smaller ones for species in disturbed landscapes (Thomas et al. 1992; Banks et al.
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2005a). For early successional species, large habitat patches may facilitate post-fire population recovery as a result of both population expansion from within the fire boundary (Banks et al. 2011) and colonisation of individuals from outside the fire boundary (Watson et al. 2012).

Properties of the matrix surrounding habitat patches are also important (Prugh et al. 2008). The surrounding landscape influences patch dynamics and the networks of exchange that exist between habitat patches, facilitating the processes of recolonization (Pickett and White 1985; Burel and Baudry 2003). Therefore, species in isolated patches should have a lower probability of persistence (Turner 1989). In our study, patches were less likely to be occupied as landscape heterogeneity increased. Movement through peripheral habitat can result in direct mortality through predation, or indirectly influence survival through increased competition for sub-optimal resources (Higgs and Fox 1993; Chesson 2000). As other vegetation communities replace heathland, or late seral stage heath replaces early successional communities, species that track suitable environmental conditions may become locally extinct (Templeton et al. 2011). For example, to avoid eastern chestnut mouse extinction, early successional heathland would need to become available close to an extant local population or alternatively, fire itself would need to improve conditions suitable for dispersal (e.g. Templeton et al. 2011; Banks et al. 2013). Analysis of eastern chestnut mouse genetic data supports the latter proposal that recently burned vegetation has greater conductance for gene flow than unburnt habitat (Pereoglou et al. 2013). The interaction between dispersal processes and landscape pattern influences the temporal dynamics of populations (Turner 1989). The capacity of individuals of a population to leave one patch to colonize another similar patch is an essential process of landscape dynamics after disturbance (Burel and Baudry 2003). Conservation must emphasise management of existing habitats and creation of new habitats within colonising distance (Thomas 1994).

Species distribution and abundance patterns are influenced by fine-scale features of the environment with which they interact most directly (Thornton et al. 2011). Within-patch habitat attributes such as dead shrubs were important predictors of site occupancy and were positively associated with the most recent major wildfire (Fig. 3.4). This demonstrates that site occupancy of early successional specialists can be facilitated indirectly through the role of fire in creating or maintaining critical habitat features and is indicative of the eastern chestnut mouse preference for sheltering in the collapsed dead shrub layer in recently burned heath (Pereoglou et al. 2011). Habitat features expected to provide shelter have been correlated with animal density for other Pseudomys species – e.g. Xanthorrhoea skirt for the heath rat P. shortridgei (Di Stefano et al. 2011), presence of Banksia ornata shrubs for the silky mouse P. apodemoides (Cockburn 1981), and rock cover for the Hastings river mouse P. oralis (Townley 2000). Rock cover was also identified in our modelling as an influence on eastern chestnut mouse occupancy. However, unlike the Hastings river mouse, rock crevasses have not previously been identified as a shelter resource or a preferred microhabitat, so the reasons for this result remain unclear. The variable
rock cover may be confounded with fire history because sites that were not burnt in the 2003 fire had no rock cover.

The level of floristic and structural complexity in regenerating communities has been linked to small mammal species assemblages, and underpins assumptions on species occurrence in successional ecosystems (Catling 1991; Masters 1993; Monamy and Fox 2010). In our study, floristic richness as well as the amount and type of cover were not significant predictors of eastern chestnut mouse site occupancy (Fig. 3.4). Our result is consistent with other investigations, which have uncovered strong species- and site-specific variation in habitat preferences (see also Cockburn 1978; Di Stefano et al. 2011).

3.5.2 Fire history as a predictor of site occupancy for an early successional specialist

Natural disturbances leave legacies that persist for decades to centuries and integrating this history with current understanding of landscape patterns and processes remains an important goal of landscape ecology (Turner 2005). A key finding of this study was that eastern chestnut mouse site occupancy was not directly affected by fire history (hypothesis 1) (Fig. 3.4). Potential explanations for an absence of direct fire history effects are two-fold. First, by comparison with the common co-occurring small mammal species which showed negative responses to fire, the ability to endure disturbance seems to be a necessary trait amongst habitat specialists (Hutto 2008). In another study, where researchers experimentally simulated the effects of fire, populations of the eastern chestnut mouse were also unaffected (Fox et al. 2003). Individuals of the eastern chestnut mouse that survive after fire could be considered ‘biological legacies’ (sensu Franklin et al. 2000). In another investigation in our study region, eastern bristlebirds (*Dasyornis brachypterus*) that persisted in burned sites also were considered to be survivors of a pre-fire fauna (Lindenmayer et al. 2009).

Secondly, the effects of fire history were either captured by, or confounded with other variables. Eighty percent of heathland sites were burned in the 2003 fire, and it is possible that fire history and vegetation type were confounding one another in our analyses. Research that replicates equal numbers of burned and unburned heathland sites may show a different result. We have shown fire to indirectly affect eastern chestnut mouse site occupancy by creating critical habitat features used for diurnal refugia. Therefore, the effects of fire may have been captured entirely by the variable dead shrub. Finally, we may simply not have measured enough fire attributes to model in our analyses. For example, fire regimes are possibly more important than fire history in predicting species occurrence and we were unable to distinguish the relative effects of fire frequency, season and severity (Whelan 1995; Keith et al. 2002).
3.5.3 Species interactions and the habitat accommodation model

The habitat accommodation model (Fox 1982) has been shown to be a poor predictor of ecological patterns in relation to fire in other systems (Letnic et al. 2004; Driscoll and Henderson 2008; Di Stefano et al. 2011). The absence of predictable sympatric small mammal species effects on eastern chestnut mouse site occupancy (Fig. 3.4) suggested competitive exclusion was not the strongest biological mechanism structuring the small mammal community as predicted in a mammalian secondary succession (Fox 1982). There was some indication that site occupancy of the eastern chestnut mouse increased in the absence of the bush rat but this effect disappeared when all co-occurring species were modelled together. In other studies, the departure from theoretical predictions has been attributed to various processes including the absence of competitors (Catling 1986; Di Stefano et al. 2011), rapid recovery of vegetation (Lindenmayer et al. 2008b; Lindenmayer et al. 2009) and correlation with alternative explanatory variables (Letnic et al. 2004; Driscoll and Henderson 2008). However, in situ survival of individuals during a fire event probably has a greater influence on population persistence after fire (Lindenmayer et al. 2005; Banks et al. 2011) compared to relative thresholds of habitat suitability. Therefore, it seems unrealistic to expect theoretical models to accurately forecast species assemblages, as they are likely to vary with the complexities of disturbance regimes, spatial patterns of landscape continuity, site-level habitat features, and the interactions among these factors.

3.5.4 Conclusion

Our study evaluates the effects of disturbance, spatial patterns of landscape structure and site-level habitat features on species occupancy in an early successional community. We found a positive effect of heathland patch area and a negative effect of landscape heterogeneity on site occupancy by the eastern chestnut mouse. Eastern chestnut mouse site occupancy also was associated with habitat features, such as a collapsed dead shrub layer, that may be created by burning. We found recent fire and the effect of multiple fires per se did not have a strong influence on eastern chestnut mouse site occupancy. We recommend surveys targeting the species take account of landscape configuration for optimal results. Furthermore, fire regimes expected to promote eastern chestnut mouse population growth should encourage the retention of critical habitat features rather than be based entirely on temporal rates of successional stages. We confirmed the general importance of the multi-level approach to landscape ecology studies, as our study species responded to landscape, patch, and within-patch variables (Thornton et al. 2011). Our work suggests that a multi-scaled approach to investigations of site occupancy should be taken to ensure species- and site-specific resource requirements are identified and that the impacts of changes to disturbance regimes on these resources can be effectively evaluated.
3.6 Acknowledgement

We most gratefully acknowledge the Wreck Bay Aboriginal Community and the Wandandian People of the Dharawal and Dhurga language groups on whose lands this study was conducted. Mason Crane, Damien Michael, Rebecca Montague-Drake, and Sachiko Okada provided fieldwork assistance. This project is part of a major study in Booderee National Park funded by the Australian Research Council, the Department of Environment and Water Resources and the Department of Defence.

3.7 References


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Chapter 3: Site occupancy


Chapter 4

Landscape genetics

Published as:

Landscape genetics of an early successional specialist in a disturbance-prone environment

Manuscript: Appendix 3
4.1 Abstract

Species that specialise in disturbed habitats may have considerably different dispersal strategies than those adapted to more stable environments. However, little is known of the dispersal patterns and population structure of such species. This information is important for conservation because many post-fire specialists are at risk from anthropogenic changes to natural disturbance regimes. We used microsatellite markers to assess the effect of landscape variation and recent disturbance history on dispersal by a small mammal species that occupies the early seral stage of vegetation regeneration in burnt environments. We predicted that a post-fire specialist would be able to disperse over multiple habitat types (generalist) and not exhibit sex-biased dispersal; as such strategies should enable effective colonisation of spatially and temporally variable habitat. We found significant differentiation between sites that fitted an isolation-by-distance pattern, and spatial autocorrelation of multilocus genotypes to a distance of 2–3 km. There was no consistent genetic evidence for sex-biased dispersal. We tested the influence of different habitat and fire-specific landscape resistance scenarios on genetic distance between individuals and found a significant effect of fire. Our genetic data supported recently burned vegetation having greater conductance for gene flow than unburnt habitat, but variation in habitat quality between vegetation types and occupied patches had no effect on gene flow. Post-fire specialists must evolve an effective dispersal ability to move over distances that would ensure access to early successional stage vegetation. Natural disturbance and natural heterogeneity may therefore not influence population genetic structure as negatively as expected.

4.2 Introduction

Dispersal behaviour and landscape configuration are primary determinants of population genetic structure (Bowler & Benton 2005; Baguette & Van Dyck 2007). The landscape matrix can facilitate or impede movement of organisms between populations (Taylor et al. 1993; Lindenmayer & Fischer 2006; Fahrig 2007) with dispersal behaviour influencing spatial patterns in abundance (Fahrig & Paloheimo 1988) and habitat selection (Morris 1992). Recently, landscape genetics research has contributed to our understanding of population connectivity in relation to landscape elements (Manel et al. 2003; Storfer et al. 2010). However, threatened species with habitat preferences for disturbed environments are not well represented in the population genetics literature. The ecological requirements of these specialist species suggest that their patterns of dispersal and demography differ considerably from species that utilise more stable environments and that this is likely to be revealed in patterns of genetic diversity and structure.

In conjunction with landscape data, spatial genetic information can identify habitat variables that maintain connectivity among populations or serve as barriers to animal
movements (Scribner et al. 2005). Current research on landscape connectivity has focussed on the influence of ‘habitat breaks’ (i.e. anthropogenic landscape fragmentation) (Gauffre et al. 2008; Macqueen et al. 2008; Spear & Storfer 2008; Pavlacky et al. 2009), natural barriers (e.g. rivers, mountains and topography) (Spear et al. 2005; Murphy et al. 2010), or a combination of both (Cushman et al. 2006; Perez-Espona et al. 2008; Short Bull et al. 2011). There is limited information on the effect of natural disturbance such as wildfire, naturally heterogeneous landscapes, or natural variation in habitat suitability on patterns of genetic diversity, population structure and gene flow.

Fire is a major form of natural disturbance (Turner et al. 1998). Different fire regimes produce distinct landscape patterns and species arrays (Bond & Keeley 2005). Population recovery and persistence in post-fire environments is influenced by fire regimes, and their effects on landscape features including patch isolation and connectivity (Clarke 2008). With altered fire regimes and increased fire occurrence being a likely impact of climate change (Williams et al. 2001; Flannigan et al. 2009; Steffen et al. 2009), our understanding of how fire events influence biota is a critical contemporary environmental issue. Fire playing a positive role in maintaining habitat suitability is an effect that is plausible for post-fire specialist fauna and those that colonise early successional ecosystems, but one that is not well studied.

In this paper, we examined the population genetic structure of the eastern chestnut mouse (Pseudomys gracilicaudatus Gould 1845), a threatened small mammal endemic to the east coast of Australia and dependent on regular fire. We addressed a series of hypotheses relating to the dispersal strategy of a post-disturbance specialist mammal, including:

1. Fire/burned areas will promote gene flow. Several studies have shown that fire affects genetic structure through environmental changes that cause demographic variation such as population expansion (including colonisation) or decline, and variation in connectivity (Templeton et al. 2001; Schrey et al. 2010, 2011; Templeton et al. 2011). For species that specialise in early seral stage, post-disturbance habitats, we expect a reduction in genetic structure in recently burned areas. This is because fire increases the area of suitable habitat, so small and relatively isolated pre-fire populations will expand and individuals will disperse to colonise newly-suitable habitat. Population expansion, increased connectivity between existing populations and colonisation of new areas (particularly with a large number of colonists) are expected to weaken genetic structure (Wade & McCauley 1988; Templeton et al. 2001; Excoffier et al. 2009). Our prediction may be incorrect if the number of individuals colonising newly suitable habitat after fire is very small and ongoing migration in subsequent generations is rare (Wade & McCauley 1988). However, our hypothesis was that the former prediction would hold.

2. Natural habitat heterogeneity will not restrict gene flow. Habitat suitability has been considered as a correlate of ‘conductance’ to dispersal across a landscape, on the assumption that environmental types that rank poorly by occupancy or abundance criteria will also be poor
for dispersal (Spear et al. 2010, e.g. Wang et al. 2008). The eastern chestnut mouse has a naturally patchy distribution within our study area due to very specific requirements for vegetation type and fire history (Pereoglou et al. 2011). Habitat suitability is thus spatially patchy and temporally dynamic. We predicted that an effective dispersal strategy to access and colonise suitable habitat under such dynamic environmental conditions would be one in which dispersal is possible across all landscape types and is not restricted by perceived habitat preferences.

(3) Dispersal will not be strongly sex-biased. Male-biased dispersal is common among mammals (Greenwood 1980) and occurs in other small mammal species that occur in our study area, including the brown antechinus (Antechinus stuartii) and the bush rat (Rattus fuscipes) (Cockburn et al. 1985; Peakall et al. 2003). However, we predicted a lack of strong sex-bias in dispersal for an early seral specialist. Modelling suggests that strong sex-biased dispersal is not favoured under high demographic stochasticity (Gros et al. 2008). After fire, dispersal by eastern chestnut mice is likely to be associated with colonisation of newly suitable habitat, and greater colonisation ability by males compared to females would be disadvantageous in that it would increase the likelihood of settling in unoccupied habitat with no potential mates.

4.3 Methods

4.3.1 Study species

Pseudomyine rodents provide some of the best examples of fire specialist fauna (Catling & Newsome 1981) due to their rapid establishment and early breeding after fire, rapid population increase, and ability to maintain viable breeding populations from first colonisation (Fox 1982). The eastern chestnut mouse is an early seral specialist that colonises heathland habitat, peaking in abundance post-fire before declining over time as vegetation regenerates (Fox 1982; Monamy & Fox 2000; Fox et al. 2003). It has a disjunct distribution along the east coast of Australia and occurs at low density throughout much of its range. The species was considered extinct in southern Australia until 2002 when it was discovered in the Jervis Bay region (Meek & Triggs 1997). This area now supports the only contemporary population of the eastern chestnut mouse south of Gosford, New South Wales (33°23’S 151°18’E) and is arguably the most isolated population of the species in eastern Australia.

The eastern chestnut mouse is an annual summer breeder capable of producing multiple litters of one to five (usually three) offspring (Fox 2008). The species lives for less than two years in wild populations (Watts & Kemper 1989). Early development is rapid which contrasts with a slow growth rate to reach maturity (Fox & Kemper 1982). Adults show significant sexual dimorphism (Fox & Kemper 1982) and attain average weights of 90 g for males and 75 g for females (Fox 2008). Little is known about social organisation and behaviour in this species. Radio-tracking data suggests that adult eastern chestnut mice are solitary, territorial and
maintain female home ranges of 0.5–1 ha and up to 4 ha for males (Pereoglou et al. unpublished data).

4.3.2 Study area and sampling

We collected tissue from 26 sites surveyed between 2008 and 2010 in Booderee National Park, located approximately 200 km south of Sydney, Australia (Fig. 4.1). We genotyped 287 individual animals and sample sizes ranged from 1 to 58 mice per site (Fig. 4.1). We used two approaches to survey the study area. Initial site selection was randomly stratified by vegetation type and consisted of a single 100 m transect. Each transect comprised: (i) a black plastic drift fence connecting 380 mm deep x 300 mm diameter pitfall traps at 0–20 m, 40–60 m, and 80–100 m; (ii) large wire cage traps (30 x 30 x 60 cm) placed at 0 m and 100 m with four small wire cage traps (20 x 20 x 50 cm) at 20 m intervals between; and (iii) ten aluminium box traps (Elliot Scientific Equipment, Australia) placed every 10 m along the transect line from 0–90 m. Data on the number of transects in each vegetation type, the number with eastern chestnut mouse captured, and the corresponding occupancy estimates are given in Table S1 (in Appendix 5). We then chose five transects and selected an additional four sites for intensive grid trapping to sample sufficiently high densities of the eastern chestnut mouse to allow for population genetic analyses. We classified all grid sites as dry heath (Taws 1997) and each had been burned by wildfire in December 2003. Our grid arrangement comprised lines at 20 m intervals with traps 10 m apart covering an area ranging from 1–3 ha (1.9 ± 0.19 ha). Transect sites were surveyed annually during the eastern chestnut mouse breeding season (November – February) and grid sites were surveyed twice each year, during the breeding season and also during the non-breeding season (June – August). We opened traps for three or four consecutive nights (31 548 trap nights in total) and baited with rolled oats, peanut butter and fennel seed. We assessed captured animals for weight, sex, age cohort, breeding condition, and collected a 2 mm ear biopsy stored in 100% ethanol.

4.3.3 DNA extraction, PCR amplification and genotyping

We extracted DNA from ear tissue using the method of (Bruford et al. 1988) and re-suspended the DNA pellet in 100µl of TE buffer (10 mM Tris and 0.1 mM EDTA). We genotyped samples at 10 microsatellite loci (Moro & Spencer 2003) (Table S2). Microsatellite PCRs with a total volume of 30 µL contained 10X buffer (Qiagen), 200 µM dNTPs, 1.8 mM MgCl2, 0.5 µL BSA, 4 pmoles reverse primer, 1.5 pmoles forward tailed primer, 2.5 pmoles fluorescent end-labelled M13 primer sequence (Schuelke 2000), 0.2 units Taq polymerase (Qiagen), and 1.5 µL template DNA. We ran all reactions on a thermal cycler (Applied Biosystems, Inc.) with initial denaturation of 94–95o C for 3 min, then cycled using PCR conditions described in Table S2, followed by a final extension step of 72o C for 10 min. We ran the PCR products on an ABI 3130 (Applied Biosystems Inc.) automated sequencer with the LIZ
500 size standard. We ran negative controls in PCRs and in each sequencer run to check for contamination. We used GeneMapper Version 3.7 (Applied Biosystems Inc.) to score each locus for each sample.

![Study area and distribution of survey sites. Solid symbol indicates site with eastern chestnut mouse presence and the number of genotyped individuals is provided above symbol. Hollow symbol indicate sites with no eastern chestnut mouse captures.](image)

**Figure 4.1:** Study area and distribution of survey sites. Solid symbol indicates site with eastern chestnut mouse presence and the number of genotyped individuals is provided above symbol. Hollow symbol indicate sites with no eastern chestnut mouse captures.

### 4.3.4 Genetic data analysis

We used the genotype matching function of MSTOOLS (Park 2001) to identify identical genotypes. Duplicate genotypes were re-labelled if the corresponding capture records were consistent with multiple captures and samples from the same individual (e.g. due to temporary marking or tag loss). We ran analyses separately for each survey year. Survey years included a twelve-month period from the beginning of the eastern chestnut mouse breeding season in September to August of the following year (September–August 2008-09 and September–August 2009-10).

#### 4.3.4.1 Population genetic summary statistics

We excluded locations from the population-level analyses if sites had less than 10 individuals genotyped. We calculated standard population genetic summary statistics for all loci and sites including the number of alleles, observed and expected heterozygosities, and $F_{IS}$ using
GENALEX version 6.3 (Peakall & Smouse 2006). We tested for departures from Hardy-Weinberg equilibrium using FSTAT (Goudet 2001).

4.3.4.2 Population subdivision and isolation by distance (IBD)

We used AMOVA to estimate population subdivision and calculated pairwise values of $F_{ST}$ for all sites where sample sizes were greater than 10 individuals. We used Mantel tests to test for isolation by distance on pairwise $F_{ST}$ between sites ($F_{ST}/1 - F_{ST}$ vs log geographic distance). Unless otherwise stated, all permutational tests were performed 999 times and analyses were completed using GENALEX.

To further investigate the spatial pattern of genetic structure, we calculated the spatial autocorrelation ($r$) of pairwise multilocus genetic distances over a set of geographic distance classes (Smouse & Peakall 1999). We calculated pairwise multilocus genetic distances (GD) according to the methods of Smouse & Peakall (1999) and tested the null hypothesis of no spatial genetic pattern ($r = 0$) against the alternative that spatial autocorrelation was positive at some distances and negative at others ($r \neq 0$). For each survey year (2008-09 $n = 172$, 2009-10 $n = 141$), we ran two different analyses. In the first analysis we selected 500 m distance classes up to 5 km. The second was a finer-scaled analysis, where we investigated spatial autocorrelation at 50 m intervals up to 250 m (i.e. fine scale structure within sampling sites). The choice of distance classes primarily relates to our sampling scheme, where the first (coarse-scaled) distance classes were larger than our sampling sites so we were testing differences between spatial autocorrelation among individuals within sites (0-500m) and at increasing distances between sites. The finer-scaled analysis focussed on testing for spatial clustering of similar genotypes within the scale of our sampling grids. We used 999 permutations with a bootstrap re-sampling procedure run 1000 times to estimate the 95% confidence interval.

We used the programs STRUCTURE version 2.3 (Pritchard et al. 2000) and GENELAND version 3.2.4 (Guillot et al. 2005) to complement our other analyses of population structure with the specific aim of testing whether our samples could be clustered into spatially discrete sub-populations (parameters in Appendix S1 in Appendix 5).

We used the program GESTE v2 (Foll & Gaggiotti 2006) to estimate effects of landscape variables on population-specific $F_{ST}$. For this analysis, we restricted dataset to nine sites with the greatest sample sizes, from which a mean of 28 individuals was sampled (s.d. = 16). All of these sites were within areas burnt in 2003, so we were unable to test for effects of fire history. However, we tested for effects of vegetation heterogeneity with variables representing the proportion of heath (the most-preferred vegetation type) within 200m and 500m buffers, as well as sample size (as a proxy for local population density), and X and Y coordinates to test for broad spatial gradients in the strength of genetic structure (e.g. an east-west peninsula effect). For this analysis, we pooled individuals from both years within the same sites. Many individuals
were sampled in both years and previous analyses showed no major differences in the patterns detected in either year.

4.3.4.3 Sex-biased dispersal

To test the hypothesis that genetic structure and corresponding philopatry is not sex-biased we used two approaches. First, we used the heterogeneity test of Smouse et al. (2008) to compare the spatial autocorrelation $r$-values of males and females with the multi-populations procedure in GENALEX. We assessed spatial autocorrelation at two scales: 500 m distance classes up to 5 km and 50 m distance classes up to 250 m. If there was a sex-bias, for the philopatric sex we expected declining correlations of $r$-values with increasing distance if the null hypothesis of $r = 0$ was not correct. If both sexes showed a similar pattern of decline, we expected the $r$-values in the first distance would be largest for the philopatric sex (Smouse et al. 2008). We focussed on the first distance class because if one sex remains relatively philopatric (such that relatives are spatially clustered), any differences in spatial autocorrelation between the sexes are expected to be most apparent in this class (Banks & Peakall 2012). We used 999 permutations with a bootstrap re-sampling procedure run 1000 times to estimate the 95% confidence interval. Sample size differed by survey year: 2008-09 male $n = 79$, female $n = 90$, and 2009-10 male $n = 65$, female $n = 76$. Secondly, we used a set of one-sided biased dispersal tests in FSTAT (Goudet et al. 2002). We permuted these tests 10000 times to compare the estimated metrics including mean corrected assignment index, variance of corrected assignment index, $F_{ST}$, $F_{IS}$ and $HS$ between male and female animals. Sample size differed by survey year: 2008-09 $n = 160$ animals in 12 sites and 2009-10 $n = 132$ animals in 10 sites. Sites without adequate sample sizes of both sexes were excluded from analysis in FSTAT.

4.3.4.4 Landscape resistance

We used partial Mantel tests in a causal modelling framework to analyse the influence of habitat on gene flow and to determine the extent to which possible landscape resistance models explained the spatial pattern of genetic distances between individuals. We created a matrix of genetic distances based on the same genetic distance measure used for the spatial autocorrelation analysis described above (Smouse & Peakall 1999). We produced landscape resistance surfaces representing different hypotheses about the difficulty in traversing different habitat types using CIRCUITSCAPE version 3.5 (McRae & Shah 2009). CIRCUITSCAPE uses circuit theory (McRae & Beier 2007; McRae et al. 2008) to predict connectivity in heterogeneous landscapes and allows for multiple pathways of gene flow rather than a single corridor with user-defined dimensions. We used the pairwise source/ground modelling mode to calculate connectivity between genotype point locations with habitat data specifying per cell conductance values, an eight neighbours cell connection, and calculations based on average conductance.
We assigned conductance values to raster cells in ARCGIS version 9.2 (ESRI 2009) representing hypotheses about the influence of distance, fire and vegetation type on genetic connectivity (Fig. 4.2; Table 4.1). (1) Distance: Our first hypothesis and simplest model was a test of isolation by distance across a uniform-resistance terrestrial landscape (Wright 1943). We did not use the classic Euclidean distance measure as it was inappropriate to represent straight line distances given the study area was a peninsula and the coastline and ocean create a substantial barrier for a terrestrial small mammal. Therefore, in our null model we assumed movement could occur in any direction, all raster cell values were equal in conductance, and the only limit to gene flow was that imposed by the coastline and ocean. (2) Fire: Our second hypothesis was that fire promotes genetic connectivity for fauna that specialise in early successional ecosystems. We expected to find a positive effect of fire (i.e. a relative negative effect of unburnt areas) because it resets the vegetation succession creating suitable habitat for post-fire specialist species (Monamy & Fox 2000). Residual survivors become responsible for post-perturbation population recovery (Turner et al. 1998; Banks et al. 2011) potentially following burned vegetation to recolonise and reproduce. Because causal modelling provides only significance tests and does not yield estimates of resistance from which we could assess the effect of fire, we took the approach of testing a series of models covering what we considered to be the range of plausible conductance values of fire (Table 4.1). (3) Vegetation type: Our third hypothesis was that for species with spatially and temporally variable habitat requirements, movement across unsuitable vegetation types would need to occur to access newly created habitat patches post-fire. In our study, the eastern chestnut mouse was highly habitat specific in occurrence across a landscape characterised by a heterogeneous mosaic of vegetation types. Therefore, we took two approaches to test the influence of vegetation type on genetic connectivity: firstly we classified vegetation types as habitat versus non-habitat based on whether they were occupied or not and parameterised the models according to the range of plausible conductivity values (with the conductance value of habitat ranging from equal to non-habitat up to 1000 times greater than non-habitat); and secondly we considered conductivity was proportional to habitat quality as assessed by the percentage of sites of each vegetation type that were occupied (Table 4.1).

We proposed nine alternative landscape models (Table 4.1) that we tested against the ‘null landscape’ isolation by distance hypothesis. We used Mantel and partial Mantel correlations as the tests statistics for causal modelling, including (1) simple Mantel tests between genetic distance and landscape resistances; (2) partial Mantel tests between genetic distance and landscape resistances, partialling out the effects of the null model; and (3) for those landscape resistance scenarios for which (2) was significant, partial Mantel tests between genetic distance and the null model, partialling out the effects of the landscape resistance models. We conducted Mantel and partial Mantel tests using the ECODIST package (Goslee & Urban 2007) in R version 2.7 (R Development Core Team 2008) with 10000 randomisations. To infer an effect of
a landscape resistance scenario on dispersal, we expected (1) and (2) to be significant, and we expected (3) to be non-significant if that scenario ‘correctly’ explained population connectivity in our study population (Cushman et al. 2006). As an alternative statistical test of the effect of landscape resistance after accounting for the ‘null’ model, we used multiple regression on distance matrices (Lichstein 2007).

**Table 4.1:** Raster cell values used to create resistance landscapes. Water was assigned a value of zero

<table>
<thead>
<tr>
<th>Model</th>
<th>Hypothesis</th>
<th>Cell conductance values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Null</td>
<td>All habitat types exert the same level of permeability to gene flow</td>
<td>All cells = 1</td>
</tr>
<tr>
<td>Firemodel1</td>
<td>Areas burnt in the 2003/4 fire are twice as permeable to gene flow as unburned habitat</td>
<td>Burnt areas = 2, All other cells = 1</td>
</tr>
<tr>
<td>Firemodel2a</td>
<td>Areas burnt in the 2003/4 fire are 10 times as permeable to gene flow as unburned habitat</td>
<td>Burnt areas = 10, All other cells = 1</td>
</tr>
<tr>
<td>Firemodel2b</td>
<td>Areas burnt in the 2003/4 fire are 100 times as permeable to gene flow as unburned habitat</td>
<td>Burnt areas = 100, All other cells = 1</td>
</tr>
<tr>
<td>Firemodel2c</td>
<td>Areas burnt in the 2003/4 fire are 1000 times as permeable to gene flow as unburned habitat</td>
<td>Burnt areas = 1000, All other cells = 1</td>
</tr>
<tr>
<td>Vegmodel3</td>
<td>Vegetation types where mice have been captured are twice as likely to facilitate gene flow</td>
<td>Cells in heathland, woodland, and sedgeland = 2, Cells in other vegetation types = 1</td>
</tr>
<tr>
<td>Vegmodel4a</td>
<td>Vegetation types where mice have been captured are 10 times as likely to facilitate gene flow</td>
<td>Cells in heathland, woodland, and sedgeland = 10, Cells in other vegetation types = 1</td>
</tr>
<tr>
<td>Vegmodel4b</td>
<td>Vegetation types where mice have been captured are 100 times as likely to facilitate gene flow</td>
<td>Cells in heathland, woodland, and sedgeland = 100, Cells in other vegetation types = 1</td>
</tr>
<tr>
<td>Vegmodel4c</td>
<td>Vegetation types where mice have been captured are 1000 times as likely to facilitate gene flow</td>
<td>Cells in heathland, woodland, and sedgeland = 1000, Cells in other vegetation types = 1</td>
</tr>
<tr>
<td>Vegmodel6</td>
<td>Permeability to gene flow is associated with habitat quality</td>
<td>Cells in heathland, woodland, and sedgeland = percentage of surveyed sites of that vegetation type that were occupied (1-100), Cells in other vegetation types = 1</td>
</tr>
</tbody>
</table>

† Indicates cell values were estimated from unpublished annual monitoring data (refer to Table S1 in Appendix 5)
Figure 4.2: Habitat quality relating to movement across a null landscape (A), burned areas (B), selected vegetation types (C), and occupied habitat (D). Gray-scale based on cell conductance values listed in Table 1. Darker colour indicates a lower resistance value assigned.
4.4 Results

4.4.1 Population genetic summary statistics

Genotype proportions deviated from H-W expectations in 2008-09 at locus 7D12 in site 7-P, and in 2009-10 at locus 9A8 in site 7-I, locus 10G6 in site 7-46, and locus 1A7 in site 7-95. Locus 6D4 showed consistent significant departures from HWE (in sites 7-44B, 7-2 and 7-H in 2008-09 and at 7-44B, 7-46 and 7-M in 2009-10) and was removed from subsequent analyses. With the exception of locus 6D4, the departures from H-W expectations in our dataset were not beyond the false error rate for multiple testing (i.e. seven out of 130 tests were likely to be significant), nor were they consistent across sites or years. Overall, we identified between three and six alleles per locus. Genetic diversity across sites ranged from 0.499–0.652 in 2008-09 and 0.415–0.632 in 2009-10, with observed heterozygosity averaged across sites greater than expected in both survey years (Table 4.2).

4.4.2 Population subdivision and spatial genetic structure

We found significant genetic differentiation among sites across the study area (2008-09 $F_{ST}$=0.161, $p=0.001$; 2009-10 $F_{ST}$ =0.195, $p=0.001$) (Table S3 in Appendix 5) and an effect of isolation by distance. Euclidean distance (log-scale geographic distance) was a significant predictor of $F_{ST}$ between sites (2008-09 Mantel $r=0.703$, $p=0.007$; 2009-10 Mantel $r=0.377$, $p=0.044$) ($r=0.377$, $p=0.044$) (Fig. 4.3).

At a broad scale, we detected positive and significant spatial autocorrelation in distance classes up to 2 km (Fig. 4.4A, B). At distances exceeding 3–3.5 km, pairwise multilocus genotypes were less similar than those assigned to distance classes at random. At a fine scale, the within-site distribution of genotypes was significant and positively autocorrelated up to 200–250 m (Fig. 4.4C, D).

We did not identify discrete, spatially segregated, genetic populations above the scale of sampling grids using the clustering methods. STRUCTURE did identify the presence of three groups in both years. However, it could not assign individuals to a population with > 90% confidence (Table S5 in Appendix 5). Further, these groups did not correspond to spatially discrete clusters of individuals and we found that samples from a particular site included a mixture of individuals from different STRUCTURE groups (Appendix S2 and Figure S1 in Appendix 5). GENELAND identified seven groups in 2008-09 and eight in 2009-10. Individuals were assigned to clusters that reflected population subdivision based on pairwise $F_{ST}$, suggesting field sites comprised distinct demographic units (Appendix S2 and Table S4 in Appendix 5). However, GENELAND could not assign individuals to a population with > 90% confidence (Table S5 in Appendix 5). Broadly, GENELAND results matched with pairwise $F_{ST}$ between sites, but did not add any higher-level spatial groupings of individuals.
**Table 4.2:** Population genetic parameters for the eastern chestnut mouse. The number of samples (n), the number of alleles (Na), observed heterozygosity (H_0), expected heterozygosity (H_E) and F_IS for each site averaged across loci ± standard error.

<table>
<thead>
<tr>
<th>Site</th>
<th>n</th>
<th>Na</th>
<th>H_0</th>
<th>H_E</th>
<th>F_IS</th>
<th>N</th>
<th>Na</th>
<th>H_0</th>
<th>H_E</th>
<th>F_IS</th>
</tr>
</thead>
<tbody>
<tr>
<td>7-44</td>
<td>8</td>
<td>2.9 ± 0.2</td>
<td>0.597 ± 0.093</td>
<td>0.589 ± 0.028</td>
<td>0.005 ± 0.134</td>
<td>0</td>
<td></td>
<td>0.585 ± 0.048</td>
<td>0.551 ± 0.042</td>
<td>-0.075 ± 0.055</td>
</tr>
<tr>
<td>7-46</td>
<td>38</td>
<td>3.8 ± 0.3</td>
<td>0.610 ± 0.069</td>
<td>0.567 ± 0.058</td>
<td>-0.070 ± 0.037</td>
<td>24</td>
<td>3.2 ± 0.2</td>
<td>0.530 ± 0.069</td>
<td>0.526 ± 0.052</td>
<td>-0.002 ± 0.069</td>
</tr>
<tr>
<td>7-95</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>11</td>
<td>3.0 ± 0.2</td>
<td>0.524 ± 0.068</td>
<td>0.500 ± 0.044</td>
<td>-0.029 ± 0.073</td>
</tr>
<tr>
<td>7-2</td>
<td>23</td>
<td>3.1 ± 0.3</td>
<td>0.528 ± 0.078</td>
<td>0.471 ± 0.065</td>
<td>-0.112 ± 0.037</td>
<td>18</td>
<td>3.1 ± 0.2</td>
<td>0.530 ± 0.069</td>
<td>0.526 ± 0.052</td>
<td>-0.002 ± 0.069</td>
</tr>
<tr>
<td>7-44B</td>
<td>21</td>
<td>3.3 ± 0.2</td>
<td>0.579 ± 0.038</td>
<td>0.556 ± 0.039</td>
<td>-0.048 ± 0.031</td>
<td>17</td>
<td>3.3 ± 0.2</td>
<td>0.572 ± 0.024</td>
<td>0.569 ± 0.028</td>
<td>-0.021 ± 0.055</td>
</tr>
<tr>
<td>7-H</td>
<td>23</td>
<td>2.9 ± 0.3</td>
<td>0.499 ± 0.058</td>
<td>0.462 ± 0.055</td>
<td>-0.093 ± 0.040</td>
<td>21</td>
<td>2.9 ± 0.2</td>
<td>0.415 ± 0.055</td>
<td>0.434 ± 0.055</td>
<td>0.032 ± 0.055</td>
</tr>
<tr>
<td>7-I</td>
<td>19</td>
<td>3.3 ± 0.2</td>
<td>0.567 ± 0.045</td>
<td>0.569 ± 0.020</td>
<td>0.008 ± 0.066</td>
<td>14</td>
<td>3.1 ± 0.2</td>
<td>0.492 ± 0.067</td>
<td>0.473 ± 0.060</td>
<td>-0.018 ± 0.093</td>
</tr>
<tr>
<td>7-M</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>13</td>
<td>2.9 ± 0.2</td>
<td>0.632 ± 0.028</td>
<td>0.519 ± 0.038</td>
<td>-0.246 ± 0.059</td>
</tr>
<tr>
<td>7-P</td>
<td>12</td>
<td>3.0 ± 0.2</td>
<td>0.652 ± 0.067</td>
<td>0.555 ± 0.039</td>
<td>-0.172 ± 0.093</td>
<td>8</td>
<td>2.8 ± 0.2</td>
<td>0.621 ± 0.062</td>
<td>0.520 ± 0.048</td>
<td>-0.203 ± 0.077</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>3.2 ± 0.1</td>
<td>0.576 ± 0.025</td>
<td>0.538 ± 0.018</td>
<td>-0.069 ± 0.027</td>
<td>3.0</td>
<td>0.547 ± 0.020</td>
<td>0.511 ± 0.016</td>
<td>-0.070 ± 0.025</td>
<td></td>
</tr>
</tbody>
</table>
Analyses in GESTE v2 identified a mean population-specific $F_{ST}$ estimate of 0.105 (s.d. of 0.044 across sites) (Figure S2 in Appendix 5). The constant-only model was best supported (posterior probability = 0.727). This suggests that none of the modelled variables representing vegetation heterogeneity or spatial location affected pop-specific $F_{ST}$.

### 4.4.3 Sex-biased dispersal

We found some evidence that spatially proximal females were more genetically similar than males in one of our analyses in on year of sampling, however this pattern was inconsistent. We did not find strong evidence for heterogeneity between correlograms for males and females. In 2008-09, female $r$-values were significantly greater than males in the 0–50 m distance class according to the $T_2$ test ($T_2$=4.182, $p$=0.033) but not in the 0–500 m distance class ($T_2$=0.001, $p$=0.977). However, the bootstrap 95% CIs of the $r$ values, a more conservative test (Banks & Peakall 2012) for males and females overlapped (Table S6 in Appendix 5). In 2009-10, female $r$-values were not significantly greater than males in the 0–50 m distance class ($T_2$=0.087, $p$=0.751) but they were in the 0–500 m distance class ($T_2$=14.258, $p$=0.001). This was the only spatial autocorrelation value test of sex-biased dispersal to be supported by the conservative bootstrap 95% CI overlap test (Table S6 in Appendix 5). There were no consistent biological patterns in the other distance class comparisons in either survey year (Table S6 in Appendix 5).
Figure 4.4: Correlograms indicating spatial autocorrelation of pairwise multilocus genetic distances over 5 km (A) 2008-09, (B) 2009-10; and over 250m (C) 2008-09, (D) 2009-10. Broken lines represent the 95% CI for the null hypothesis of a random distribution of genotypes. Error bars represent the 95% CI around $r$ for a specific distance class.

None of the sex-biased dispersal tests in FSTAT provided evidence for female philopatry and male dispersal and none of the test statistics were significant in either survey year (Table S7 in Appendix 5). The test statistics were conflicting in regards to expectations of male-biased dispersal (e.g. $F_{ST}$, $F_{IS}$ and $H_{S}$; Table S7 in Appendix 5). The lack of apparent sex-biased
4.4.4 Landscape resistance

(1) Simple Mantel tests between genetic distance and landscape resistances. All of the simple Mantel tests were significant (Table 4.3). Both the null model and the alternate resistance landscapes explained variation in genetic distance between individuals. However, when the models were ranked based on Mantel r, only Firemodel1 performed better than the null model.

(2) Partial Mantel tests between genetic distance and landscape resistances, partialling out the effects of the null model. We found significant effects of the fire models 1, 2a, 2b and 2c (conductance across burned habitat was twice, 10, 100 and 1000 times greater than unburned habitat, respectively; Table 4.1) after accounting for variation in genetic distance explained by the null landscape. After we accounted for the null model, the partial correlations of the vegetation models (with increases in relative conductivity of preferred habitat to other vegetation types and with conductance parameterised to reflect the distribution of capture records and habitat preferences) with genetic distance were non-significant (Table 4.3).

(3) Partial Mantel tests between genetic distance and the null model, partialling out the effects of the landscape resistance models. Of the landscape resistance scenarios that explained a significant component of the variation in genetic distance between individuals when the null model was partialled out (the four fire models: Table 4.1), the null model was non-significant after Firemodel1 was accounted for (Table 4.3). This model featured a conductance of recently burned habitat twice that of unburned habitat. The null model explained a significant component of the variation in genetic distance even after the remaining fire models (Firemodel2a-c, featuring relatively higher conductance values of burned habitat: Table 4.1) were fitted (Table 4.3). This suggests that the latter models potentially overestimate the relative conductivity of burnt habitat.

4.5 Discussion

Our study provides support for a ‘generalist’ dispersal strategy, which would be advantageous for a species that prefers ephemeral habitat, conditional on spatial and temporal variability. We found significant genetic differentiation between sites that followed an isolation by distance pattern, and significant spatial autocorrelation between genotypes, indicating dispersal was restricted relative to the overall scale of the study. However, we did not find strong evidence for dispersal to be male-biased and limited to only one sex. Our data suggested no effect of heterogeneity in heterogeneous native vegetation on genetic structure, despite
strong habitat selection for specific vegetation types, and there was evidence for a positive effect of fire in promoting connectivity.

Table 4.3: Results of Mantel and partial Mantel tests of landscape resistance on gene flow. GD = pairwise multilocus genetic distance. Data for both survey years is combined. Significance levels from multiple regression on distance matrices (MRDM) are included for comparison

<table>
<thead>
<tr>
<th>Matrix 1</th>
<th>Matrix 2</th>
<th>Partial</th>
<th>( r_M )</th>
<th>p-value</th>
<th>( p )-value</th>
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</thead>
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<td>&lt;0.001</td>
</tr>
<tr>
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<td>0.006</td>
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<tr>
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<td>0.110</td>
<td>0.012</td>
<td>0.012</td>
</tr>
<tr>
<td>GD</td>
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<td>&lt;0.001</td>
</tr>
<tr>
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<td>&lt;0.001</td>
</tr>
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<td>&lt;0.001</td>
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<tr>
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<td>&lt;0.001</td>
</tr>
<tr>
<td>GD</td>
<td>vegmodel6</td>
<td>null</td>
<td>0.157</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

(2) Partial Mantel tests between genetic distance and landscape resistances, partialling out the effects of the null model

| GD      | firemodel1 | null   | 0.085    | 0.028   | 0.026       |
| GD      | firemodel2a | null  | 0.084    | 0.032   | 0.028       |
| GD      | firemodel2b | null  | 0.084    | 0.033   | 0.034       |
| GD      | firemodel2c | null  | 0.016    | 0.524   | 0.511       |
| GD      | vegmodel3  | null   | 0.038    | 0.180   | 0.174       |
| GD      | vegmodel4a | null   | -0.050   | 0.061   | 0.068       |
| GD      | vegmodel4b | null   | -0.054   | 0.053   | 0.055       |
| GD      | vegmodel4c | null   | -0.042   | 0.112   | 0.109       |
| GD      | vegmodel6  | null   | -0.033   | 0.322   | 0.316       |

(3) Partial Mantel tests between genetic distance and the null model, partialling out the effects of the null landscape resistance models

| GD      | firemodel1 | null   | -0.029   | 0.405   | 0.308       |
| GD      | firemodel2a | null  | 0.125    | <0.001  | <0.001      |
| GD      | firemodel2b | null  | 0.197    | <0.001  | <0.001      |
| GD      | firemodel2c | null  | 0.204    | <0.001  | <0.001      |
| GD      | vegmodel3  | null   | 0.011    | 0.614   | 0.605       |
| GD      | vegmodel4a | null   | 0.098    | <0.001  | <0.001      |
| GD      | vegmodel4b | null   | 0.175    | <0.001  | <0.001      |
| GD      | vegmodel4c | null   | 0.19      | <0.001  | <0.001      |
| GD      | vegmodel6  | null   | 0.154    | <0.001  | <0.001      |

4.5.1 Landscape connectivity and gene flow

For a pyric specialist species with preference for early successional stage vegetation, we predicted fire would promote gene flow and enhance connectivity because following burned vegetation would potentially lead dispersers to unoccupied suitable habitat. While we identified significant genetic differentiation between populations, we found no evidence for discrete structure above the level of sampling sites (i.e. broad spatial population groupings, or clusters), suggesting that a model of isolation by distance is an appropriate interpretation of this system. The population-specific \( F_{ST} \) analysis in GESTE provided no evidence for genetic structure being influenced by the distribution of preferred and non-preferred habitat (vegetation heterogeneity).
Consistent with this finding, landscape genetics analyses of the relationships between pairwise individual genetic distances and a set of landscape resistance scenarios did not support an effect of vegetation-mediated habitat suitability on spatial genotypic patterns. This suggests that occupancy and abundance are not appropriate surrogates for landscape permeability to movement in disturbance adapted species (see Spear et al. 2010). However, these analyses did support an increased relative permeability of burnt landscapes over unburnt landscapes, suggesting that fire promotes connectivity in this species.

The support for increased permeability of burnt relative to unburnt habitat came from simple Mantel tests of inter-individual genetic versus landscape resistance distances, in which Firemodel 1 (Table 4.1), where the conductance of recently-burned habitat was twice that of unburned habitat, had the strongest simple Mantel correlation (Table 4.3). Although our Mantel correlations were not high (maximum r = 0.229), we expected that geographical correlations with individual multilocus distances to be ‘messier’ than population-based distances as the latter do not include intrapopulation (inter-individual) variation. Further, partial Mantel tests and multiple regression on distance matrices (MRDM) identified this model as being significantly associated with genetic distance after accounting for a ‘null’ landscape model. This model that satisfied the classic causal modelling criteria for acceptance (see Cushman et al. 2006) was Firemodel1 (Table 4.1), in which the conductance of recently-burned habitat was twice that of unburned habitat. Landscape resistance scenarios in which recently burned habitat had a conductance 10, 100 or 1000-fold greater than unburned habitat were significant after accounting for the null model, but the null model was also significant after these models were accounted for. This suggests that these latter models overstate the relative conductance value of recently-burned habitat and that Firemodel1 is a reasonably accurate representation of the resistance landscape for the studied population. While this finding was consistent with our prediction for this species, and with other lines of evidence (the observed heterozygosity excess in both years is consistent with increased dispersal and admixture of populations that were likely to have been considerably smaller and more isolated before the 2003 fire), we do interpret the partial Mantel and MRDM analyses with some caution, as recent simulation work has shown that these tests can, under some circumstances, have unacceptable error rates for the significance of spatially-structured explanatory variables (Jaquiéry et al. 2011, Guillot & Rousset 2012). Statistical caveats aside, we discuss the implications of fire for connectivity in post-fire specialists below.

Potentially, fire promotes connectivity for early successional specialist fauna in two ways. First, fire improves habitat suitability for such species and habitat suitability improves landscape conductance to gene flow. Where long-term fire suppression occurred in a previously fire-maintained ecosystem, Templeton et al (2001) observed a significant increase in dispersal and colonisation rate of new patches by collared lizards after re-initiation of burning. The increase in dispersal was attributed not to the fire itself but to the change in structure of the intervening
habitat matrix and opening of the understorey (Templeton et al. 2001). For example, burned areas may not be an impediment to movement as long as some structure, native plant regeneration, or patches of remnant vegetation are present. A post-fire collapsed shrub layer may even provide cover and protection facilitating movement (Spear et al. 2005). Spear and Storfer (2010) found gene flow was maintained across burned areas and suggested movement was facilitated by biological legacies (sensu Franklin et al. 2000) in the form of downed trees and debris. For dispersing individuals of the eastern chestnut mouse, a fire boundary of unburned habitat or late successional stage vegetation might be a greater deterrent to movement than the burnt landscape (i.e. habitat cues can assist directional movement; Bowler & Benton 2005). Under this scenario, the underlying mechanism for persistence of post-fire specialist fauna may be the disperser’s ability to follow fire in an attempt locate suitable habitat.

Second, an alternative explanation is that the resistance landscape for dispersal by the eastern chestnut mouse is not static, and that dispersal is increased dramatically in burnt areas in association with colonisation immediately after the fire, then returns to levels described under a 'null landscape' model. Genetic signals of recent (but not current) dispersal scenarios can persist for a number of generations (Landguth et al. 2012). Under this scenario, fire causes substantial mortality but also results in rapid colonisation of newly created early successional habitat by residual survivors and thus increased gene flow over the immediate short-term post-fire. Once the empty territories have been colonised, there is no longer any reason for higher dispersal across burnt areas. Our data do not distinguish these two explanations.

For species with spatially and temporally variable habitat requirements, we predicted natural habitat heterogeneity would not restrict gene flow because dispersal would still need to occur through landscapes which do not meet specific habitat requirements. A heterogeneous cover of native vegetation types is unlikely to restrict gene flow because dispersal is still possible through landscapes which are considered inappropriate when conditional on perceived habitat preferences. Although the eastern chestnut mouse has specific habitat requirements including early successional stage heathland vegetation, we found genetic connectivity across the study area was not limited by vegetation type and that other native vegetation communities interspersed throughout heathland did not restrict movement. While barriers to dispersal may funnel movement in one direction (Gustafson & Gardner 1996), dispersal through unfavourable habitat has been recorded for many species (Ruscoe et al. 1998; Mossman & Waser 2001; Selonen & Hanski 2004; Gauffre et al. 2008; Macqueen et al. 2008). Selectivity for preferred habitat during dispersal has also been recorded for other species (Lorenz & Barrett 1990; Baur & Baur 1992; Schultz 1998; Lindenmayer & Peackall 2000; Banks et al. 2005), indicating the effect (or not) of habitat heterogeneity on gene flow is likely to be strongly species-specific and/or site-specific. A species’ capacity for movement through heterogeneous landscapes is likely to depend on whether heterogeneity is provided by indigenous vegetation of varying composition (as demonstrated in our study) or by small, remnant patches of native vegetation
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interpersed with anthropogenic modified landscapes (i.e. agricultural land, non-native forest plantations, built environments, etc.).

4.5.2 – Population genetic structure and dispersal behaviour

A generalist dispersal strategy (i.e. one where movement is not restricted to particular vegetation types or landscape attributes) is advantageous for a species which prefers ephemeral habitats that are less predictable and more variable in temporal and spatial dispersion of resources (Lee et al. 1981). For small mammals in relatively stable environments, dispersal is often restricted (Peakall et al. 2003; Kraaijeveld-Smit et al. 2007; Macqueen et al. 2008; Gardner-Santana et al. 2009). Temporal instability of habitat quality may enhance effective dispersal and/or increase dispersal propensity (Gauffre et al. 2008). For example, a dispersal strategy with movement restricted to neighbouring habitat patches would be ineffective for the eastern chestnut mouse to take advantage of recently burned heathland and access early successional stage vegetation. While there is not a clear relationship between dispersal distance and the scale of genetic spatial autocorrelation, the scale of positive autocorrelation that we identified (2–3 km; Fig. 4.4) is similar to the movement patterns of other pseudomyine mice. The smoky mouse *Pseudomys fumeus* and eastern pebble-mound mouse *P. patrius* have both been observed to make minimum movements greater than 600 m and 1 km, respectively in a single night (Ford 2003, 2008). The sandy inland mouse *P. hermannsburgensis* is capable of dispersing very large distances (>16 km) (Dickman et al. 1995) suggesting the eastern chestnut mouse may be physiologically capable of much longer dispersal subject to landscape constraints.

Given that colonisation is limited by the dispersal-limited sex, a generalist dispersal strategy that includes an absence of sex-biased dispersal would be beneficial for a post-fire specialist species to access available high quality but unoccupied habitat. Our results show no obvious evidence for sex-bias in dispersal by the eastern chestnut mouse. This indicates that both sexes disperse or that our dataset was not large enough to discern the philopatric sex. Whether a low, or temporally inconsistent, level of sex-biased dispersal occurs and was not detectable in our genetic data is difficult to determine. However, clear genetic signals of sex-biased dispersal were detected using similar sample sizes for two other species that also occur in this landscape (or are closely-related to species in this landscape), the agile antechinus (*Antechinus agilis*) and the bush rat (*Rattus fuscipes*) (Peakall et al. 2003; Banks et al. 2005; Banks & Peakall 2012). These species are not post-fire specialists. So whatever the absolute level of dispersal by male and female eastern chestnut mice, the evidence suggests that the relative strength of sex-bias in dispersal is weaker in the eastern chestnut mouse than in other small mammals studied in this region. The lack of a signal of sex-biased dispersal (a consistent significant difference in pairwise spatial autocorrelation of male and female animals) suggests an atypical mammalian structure exists (Gardner-Santana et al. 2009). This is because male-
biased dispersal in mammals is considered an effective mechanism for inbreeding avoidance (Greenwood 1980; Bowler & Benton 2005). Eastern chestnut mouse dispersal behaviour may have evolved as a response to acquisition of suitable habitat rather than inbreeding avoidance, and therefore it is an advantageous strategy for both sexes to be capable of dispersal. An interesting area for future research would be to investigate whether patterns of sex-biased dispersal differ between colonisation and migration (between existing populations) dispersal events, a point raised by Wade and McCauley (1988). There is evidence that the tendency of one sex or another towards dispersal may be unpredictable and dependent on habitat quality or landscape pattern (Banks et al. 2005). For example, in the Australian bush rat *Rattus fuscipes*, sex-biased dispersal was absent in populations studied in south-eastern Australian forest (Kraaijeveld-Smit et al. 2007) but distinct female philopatry was found in fragmented rainforest in Queensland (Macqueen et al. 2008). Further research into eastern chestnut mouse dispersal behaviour should be replicated over multiple study areas before we are able to confirm the mechanisms postulated above.

### 4.5.3 – Conclusion

Landscape resistance was a better predictor of genetic structure in the eastern chestnut mouse population than isolation by distance alone. Genetic connectivity was provided by burnt habitat, indicating fire may play a positive role in structuring populations of some species. Dispersal was possible through unsuitable habitat and any effect of landscape heterogeneity is likely to depend on whether heterogeneity is provided by indigenous vegetation or by anthropogenic modified landscapes. We postulate that a generalist dispersal strategy – where movement is not restricted to particular vegetation types, landscape attributes, or sex-biased – is advantageous for a species which prefers ephemeral habitat conditional on spatial and temporal variability.

### 4.6 Acknowledgement

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Permit BDR08/00009. The comments of four anonymous reviewers and subject editor Lisette Waits substantially improved earlier versions of this manuscript.

4.7 References


Chapter 4: Landscape genetics


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Chapter 4: Landscape genetics


Chapter 4: Landscape genetics


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Chapter 5

Population dynamics

Submitted as:

How does fire history influence demographic parameters and genetic patterns in an early successional specialist small mammal?
Ecology and Evolution, Submitted


5.1 Abstract

Understanding how demographic parameters of post-fire specialists vary with fire history can provide insights into the population viability and distribution of such species, including their response to landscape management and novel fire regimes. We used an innovative combination of demographic and genetic analyses to quantify survival, recruitment and immigration rates in populations of an early successional specialist small mammal, the Australian eastern chestnut mouse (*Pseudomys gracilicaudatus*). Our aim was to understand how key demographic parameters vary across the landscape in response to fire history related environmental factors. Estimates of survival and recruitment varied across sites. Survival was influenced by fire history and elements of habitat structure affected by fire. Survival was highest among adults with recruitment driven predominantly by juveniles entering the population prior to the breeding season. Genetic assignment tests revealed immigration contributed little to recruitment compared to reproduction, suggesting populations are demographically discrete at this post-fire stage. This was concordant with findings of significant genetic differentiation between sites. Demographic and genetic data were consistent; sites with high recruitment also had higher genetic diversity and lower temporal genetic structure, consistent with reduced genetic drift. In light of landscape genetics analyses showing that fire promotes population connectivity, this study suggests a two-phase model of spatial population dynamics, where post-fire colonization is followed by locally driven population dynamics, in which survival rates are influenced by fire-history effects on habitat quality. Thus, post-fire specialists can be dependent on landscape-level connectivity and site-level habitat quality, both of which are influenced by fire history.

5.2 Introduction

Why do populations of successional specialists show such strong associations with disturbance history? Many early successional specialist species are sensitive to changes in land management and disturbance regimes. For post-fire specialists, understanding how fire history influences population dynamics through key demographic processes like survival, recruitment and migration is important for understanding the viability and distribution of such species in fire-prone landscapes. Site- and landscape-level processes drive environmental variation and thus are expected influences on these demographic rates. Estimating survival and recruitment is a basic requirement for identifying factors that influence the rate of population change and limit population viability (Sandercock, 2006, Lebreton et al., 1992, Mills, 2013). Immigration and emigration also contribute to the change of population size in open populations (Schaub et al., 2013), with the exchange of individuals among populations affecting their dynamics and persistence (Schaub et al., 2012). The rate of immigration is notoriously difficult to estimate and
consequently relatively little is known about its role in population dynamics (Abadi et al., 2010).

Innovative combinations of demographic and genetic data can overcome this problem, producing estimates of survival and recruitment in addition to evaluating the relative contributions of reproduction and immigration to recruitment. Variation in ecological conditions generated by disturbance can alter demographic and genetic patterns (Banks et al., 2013). For instance, fire influences habitat suitability for many species, and populations of species that specialize in fire-related successional conditions can occur in transient, or ephemeral, patches of habitat that are defined by fire history. Understanding fundamental population processes such as recruitment, immigration and survival, and how these respond to disturbance history will be important for predicting and managing the impacts of changing disturbance regimes on the persistence of successional specialist species. Studies on a number of species have shown that fire history influences dispersal by early successional species, with consequences for genetic structure (Pereoglou et al., 2013, Templeton et al., 2011, Pierson et al., 2013). Genetic variation can be lost by increasing genetic drift as vegetation regeneration progresses and late successional communities develop, impacting the quality, spatial configuration and connectivity of habitat (Templeton et al., 2001). Reduced habitat quality and connectivity for early successional species as a consequence of succession can result in associated population declines of early successional fauna (Betts et al., 2010). The integration of genetic and demographic data will enable us to understand how population processes of such species are impacted by environmental variation, accounting for the effects of survival, breeding success and animal movements in an open population by identifying the origin of recruits (Mills, 2013).

Measuring demographic rates can be difficult as they vary with individual characteristics and fluctuate in response to environmental variability (Lima et al., 2001, Villella et al., 2004, Boyce et al., 2006, Ives, 2009). Individual-level drivers are those regulated by internal processes and include sex and age, which have been associated with survival, movement and recruitment in many species (Aars and Ims, 2002, Holland and Bennett, 2010, Pryde et al., 2005, Troyer et al., 2014, Sibly et al., 1997). External processes are those occurring at the site- and landscape-levels. For species with fire-related successional habitat specialization, site-level drivers of population dynamics relate to fire history or other fixed, geographically driven environmental variables relating to habitat quality. For early successional species, fire can generate resources that are critical for survival and reproductive success (Hutto, 1995, Templeton et al., 2011). Landscape-level drivers of population dynamics include patch size, landscape heterogeneity, and structural connectivity of habitat. Landscape structure influences animal movements (i.e. dispersal, immigration), which subsequently influence colonization, reproduction and genetic structure (Hanski, 2009, Donner et al., 2010). Survivorship has been often been positively associated with patch size (Barbour and Litvaitis, 1993, Bowers et al., 1996, Villafuerte et al., 1997). However, the effect of landscape heterogeneity, or fragmentation, on key demographic
parameters appears to be much more complicated and inconsistent (see also Umapathy and Kumar, 2000, Dooley and Bowers, 1998, Nupp and Swihart, 1996, Soga and Koike, 2013). To understand how population processes respond to environmental variation, we need to evaluate internal drivers on key demographic rates like survival, recruitment and immigration, and investigate site- and landscape-level factors as external drivers of those processes.

In this study, we used a combination of demographic mark-recapture analyses and microsatellite genetic data to address questions about drivers of demographic processes. We used mark-recapture and genetic analyses to test hypotheses about effects of internal ‘state’ variables (such as sex and age), external site-level factors (such as fire history and fire-driven habitat variables) and landscape-level factors (such as patch size and heterogeneity) on survival. We also tested how these factors influence recruitment, separating the contributions of immigration and reproduction to recruitment with analyses of microsatellite genetic data. Integrating demographic and genetic analyses has benefits in both directions, improving our understanding of demographic population processes, but also improving our understanding of the demographic drivers of spatial and temporal variation in genetic diversity and structure. We show that species with genetically structured populations have demographic processes influenced more strongly by site-level factors than landscape-level factors, because populations that are discrete are likely to be strongly influenced by local resources.

5.3 Materials and methods

5.3.1 Study species

The eastern chestnut mouse is an early successional specialist that occurs in heathland regenerating after fire (Fox, 1982). Distributed in disjunct populations along the east coast of Australia, the species is considered extinct in many parts of its range (Breed and Ford, 2007) and is currently listed as Vulnerable on Schedule 2 of the Threatened Species Conservation Act 1995 (NSW) (Available at http://www.austlii.edu.au/au/legis/nsw/consol_act/tsca1995323/). Breeding occurs annually during the summer months when adult females can produce multiple litters of one to five (usually three) offspring (Fox, 2008). Adults show significant sexual dimorphism (Fox and Kemper, 1982) and attain average weights of 90 g for males and 75 g for females (Fox, 2008). Diurnal refuge sites are associated with the presence of specific structures including grass trees (Xanthorrhoea spp.), buttongrass (Gymnoschoenus sp.), collapsed dead stems, and areas of tall, dense vegetation (Pereoglou et al., 2011). Individuals are transient and non-gregarious in their use of refugia (Pereoglou et al. 2011). Little is known about social organization and behavior. Radio-tracking data suggests that adults are solitary and territorial, with females having a home range of 0.5 – 1 ha and up to 4 ha for males (Pereoglou et al. unpublished data).
5.3.2 Study area

Booderee National Park is located approximately 200 km south of Sydney, Australia (Fig. 5.1). Six types of vegetation occur in the Park consisting of forest, woodland, rainforest, heathland, sedgeland, and shrubland (Taws, 1997). We selected seven sites in heathland for a two-year mark-recapture study. In heathland sites, vegetation was generally less than 2 m tall and varyingly dominated by Banksia ericifolia and Sprengelia incarnata, with Allocasuarina distyla, Isopogon anemonifolius and Hakea teretifolia also being common.

![Map of Booderee national park indicating study sites and vegetation types.](image)

**Figure 5.1:** Map of Booderee national park indicating study sites and vegetation types.

5.3.3 Animal capture and marking

We captured animals using grids of aluminium box traps (Elliott Scientific Equipment, Australia) open for a minimum of four consecutive nights during each survey season: November 2008 – March 2009 (S89), June – August 2009 (W9), November 2009 – March 2010 (S910), and June – August 2010 (W10). Grid arrangement comprised lines at 20 m intervals, with traps set 10 m apart, and with sites covering an area of 1 – 2.5 hectares. We baited traps with rolled oats, peanut butter and fennel seed, checked them daily and replaced traps that captured a non-target species. During winter, we insulated traps with non-absorbent cotton wool and a plastic sleeve. We marked captures using Trovan ID100 implantable transponders (Microchips Australia Ltd, Australia), assessed species, sex and age (breeder, B or non-breeder,
NB), and collected a 2 mm ear biopsy that was stored in 100% ethanol. All required ethics guidelines were followed. Our research was conducted under The Australian National University Animal Experimentation Ethics Committee protocol C.RE.49.08 and Booderee National Park Permit BDR08/00009.

5.3.4 Genetic data analysis

We genotyped individuals (n = 223) at nine microsatellite loci. DNA extraction, PCR amplification and genotyping protocols were undertaken as described in Pereoglou et al. (2013). To identify identical genotypes and putative recaptured individuals in different trapping seasons (to account for potential microchip loss), we used the genotype matching function of MSTOOLS (Park, 2001). Duplicate genotypes were re-labelled if the corresponding capture records were consistent with multiple captures and samples from the same individual (e.g. due to temporary marking or tag loss). We pooled genotypes from all survey seasons to calculate standard population genetic summary statistics for all loci and sites including the number of alleles (Na), observed (H0) and expected (He) heterozygosities, and fixation index (F). We tested for departures from Hardy-Weinberg equilibrium using FSTAT (Goudet, 2001). We estimated population subdivision (overall FST), temporal genetic differentiation between years (tFST) at each site, and pairwise FST between sites. To test for isolation by distance on pairwise FST between sites (FST/1-FST versus geographic distance), we used a Mantel test. We estimated population-specific genetic differentiation (pFST) using GESTE 2.0 (Foll and Gaggiotti, 2006). Unless otherwise stated, we performed all permutational tests 999 times and analyses were completed in GENALEX 6.3 (Peakall and Smouse, 2006).

To assess annual immigration at each site, we pooled genotype data from survey seasons in each year. We used the assignment or exclusion of individuals test in GENECLASS 2.0 (Piry et al., 2004) to compute the probability that an individual belonged to its sample population. Individuals were simulated 100 times using the Rannala and Mountain (1997) criteria for computation, the Monte-Carlo re-sampling algorithm described in Paetkau et al. (2004), and assignment probability thresholds of 0.05 and 0.01.

5.3.5 Estimating survival and recruitment

For each individual, we constructed an encounter history consisting of a contiguous series of 1’s and 0’s representing each survey season, where ‘1’ indicates that an animal was recaptured (or otherwise known to be alive and in the sampling area), and ‘0’ indicates the animal was not recaptured (or otherwise seen) (Cooch and White, 2014). We used Program MARK 7.1 (White and Burnham, 1999) to model factors influencing variation in seasonal survival and recruitment. We estimated survival using the standard Cormack-Jolly-Seber (CJS) model based on live animal captures in an open population (Lebreton et al., 1992), and survival and recruitment using Pradel models (Pradel, 1996a). We used terminology as defined by
Cooch and White (2014): ‘apparent survival’ (phi or $\phi$), ‘recapture probability’ ($p$) and ‘recruitment probability’ ($f$). Apparent survival is the probability of remaining in the study population. Recapture probability is the probability that an animal alive in the study population at the time of survey will be captured. Recruitment probability is the number of individuals entering the population between time, and time, + 1 per individual already in the population at time, We categorised data into seven groups based on the site of capture. Because the length of inter-session periods varied, we set time intervals to the number of days, averaged across the seven sites. To test for departure of data from the underlying assumptions of the CJS model, we used the global goodness-of-fit method available in the program U-CARE version 2.0 (Choquet et al., 2009). The general model was an adequate fit for our data (GOF test $df=13$, $x^2=11.591$, $p=0.561$) and no adjustment to subsequent model metrics was necessary because the variance inflation factor ($c$-hat), obtained by dividing the model $x^2$ statistic by the degrees of freedom, was < 1.

We analysed data for sex, age, site and season effects, with a set of covariates describing habitat, landscape features and genetic composition of local populations (= site). We sampled vegetation in two 20 x 20 m plots at each site, and averaged values for the number of dead shrubs present (DEAD SHRUB), the number of understorey species present (FLORISTIC RICHNESS), and the understorey (< 2 m) percent cover of all plant species combined (COVER) across the two vegetation plots. We measured landscape features from digital layers of vegetation mapping by Taws (1997) and spatially-explicit fire mapping conducted by Booderee National Park in ArcGIS 9.2 (ESRI, 2009). For each site, we recorded the number of fires that had occurred within a 100 m radius of each site since fire mapping began in the mid-1950s (FIRES), and the contiguous area of the heathland habitat patch within which each site was located (AREA) were recorded. As a measure of landscape heterogeneity, we counted the number of vegetation types within a 500 m radius of each site (LANDSCAPE). We calculated the genetic composition of local populations (=sites) according to the analytical methods in the preceding section and included genetic diversity (observed heterozygosity, $H_O$), population-specific genetic differentiation ($pFST$), and temporal $FST$ within each site ($tFST$).

We fit data to CJS models that tested the main effects of site and individual-state variables (AGE, SEX) over time (SEASON). We then constructed models with fire (FIRES), habitat (DEAD SHRUB, FLORISTIC RICHNESS, COVER) and landscape-level (AREA, LANDSCAPE) variables to evaluate major influences of survival variation. Models were run with a constant recapture probability. We also modeled survival and recruitment probabilities (Pradel, 1996b) to explore relationships between individual-state, habitat, landscape-level variables, and genetic variability ($H_O$, $pFST$, $tFST$) on recruitment patterns. While fire, habitat and landscape-level variables potentially influence recruitment variation among sites, the genetic site variables respond to the recruitment patterns (e.g. was recruitment rate related to genetic drift), so we expected to learn something different by evaluating these. Following on from the
Chapter 5: Population dynamics

CJS models, we set Pradel models to have both site-dependent survival rates and a constant recapture probability. Model selection was based on Akaike’s information criterion corrected for small sample size bias (AICc, Burnham and Anderson, 2002, Cooch and White, 2014). The difference between AICc for each model ($\Delta_i$, AICc difference) and that for the model with the smallest observed AICc from the set of models considered was calculated along with the Akaike weight for each model ($w_i$). As a guide, $\Delta_i < 2$ should be considered to have substantial support and used for making inferences, models with $\Delta_i$ of 4-7 have considerably less support, and models with $\Delta_i > 10$ essentially have no support (Burnham and Anderson, 2002). Model averaging of parameter estimates and their unconditional standard errors were calculated according to Burnham and Anderson (2002).

5.4 Results

Seasonal encounters (n = 278) represented 181 individuals of the eastern chestnut mouse from the seven populations (Table 5.1). No recaptures were recorded outside of the population of their initial capture.

5.4.1 Population genetics summary statistics

Departures from Hardy-Weinberg expectations were not beyond the false error rate for multiple testing (i.e. seven out of 130 tests were likely to be significant), nor were they consistent across sites or years (e.g. at locus 7D12, sites 7-44 and 7-P in 2008-09, and site 7-46 in 2009-10). We identified between two and five alleles per locus. Expected heterozygosity across sites ranged from 0.463 – 0.644, with observed heterozygosity greater than expected in all sites except 7-44 (Table 5.1).

5.4.2 Population subdivision and spatial genetic structure

We identified significant genetic differentiation among sites across the study area (overall $F_{ST} = 0.170$, p = 0.001) (Table 5.2) and an effect of isolation by distance. Euclidean distance (geographic distance) was significantly correlated with pairwise $F_{ST}$ between sites (Mantel r = 0.766, p = 0.004). Population-specific genetic differentiation ($pF_{ST}$) ranged from 0.047 – 0.207 and temporal (among subsequent years) $F_{ST}$ within each site ($tF_{ST}$) ranged from 0 – 0.168 (Table 5.1).

5.4.3 Assignment tests

Immigration appeared to be a negligible source of recruitment. When data were pooled over all seasons, we excluded only three individuals (out of a total of 223 individuals analysed) from the populations in which they were sampled. When the genetic reference populations for
Table 5.1: Eastern chestnut mouse capture data, population genetics summary statistics, and assignment tests by site. E = seasonal encounters, \( n_{TC} \) = total individual captures, M = male, F = female, \( pF_{ST} \) = population specific genetic differentiation, \( tF_{ST} \) = temporal \( F_{ST} \) within each site, \( n_{TG} \) = total genotyped samples, \( Na \) = average number of alleles, \( H_O \) = observed heterozygosity, \( H_E \) = expected heterozygosity, \( F \) = fixation index, \( n_{A89} \) = number of genotypes assigned to populations in 2008-09, \( n_{A910} \) = number of genotypes assigned to populations in 2009-10, \( A_{0.05} \) = number of individuals that were excluded from their sampled population at \( p = 0.05 \), \( A_{0.01} \) = number of individuals that were excluded from their sampled population at \( p = 0.01 \).

<table>
<thead>
<tr>
<th>Site</th>
<th>Data pooled</th>
<th>E</th>
<th>( n_{TC} )</th>
<th>M</th>
<th>F</th>
<th>A_{0.05}</th>
<th>A_{0.01}</th>
<th>( pF_{ST} )</th>
<th>( tF_{ST} )</th>
<th>( n_{TG} )</th>
<th>Na</th>
<th>s.e.</th>
<th>( H_O )</th>
<th>s.e.</th>
<th>( H_E )</th>
<th>s.e.</th>
<th>F</th>
<th>s.e.</th>
<th>( n_{A89} )</th>
<th>A_{0.05}</th>
<th>A_{0.01}</th>
<th>( n_{A910} )</th>
<th>A_{0.05}</th>
<th>A_{0.01}</th>
</tr>
</thead>
<tbody>
<tr>
<td>7-2</td>
<td>48</td>
<td>29</td>
<td>13</td>
<td>16</td>
<td>0</td>
<td>0</td>
<td>0.100</td>
<td>0.020</td>
<td>38</td>
<td>3.33</td>
<td>0.24</td>
<td>0.53</td>
<td>0.07</td>
<td>0.50</td>
<td>0.06</td>
<td>-0.06</td>
<td>0.03</td>
<td>23</td>
<td>0</td>
<td>0</td>
<td>15</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>7-44</td>
<td>8</td>
<td>6</td>
<td>1</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>0.097</td>
<td>10</td>
<td>2.89</td>
<td>0.20</td>
<td>0.57</td>
<td>0.09</td>
<td>0.59</td>
<td>0.03</td>
<td>0.06</td>
<td>0.12</td>
<td>8</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>7-44B</td>
<td>53</td>
<td>28</td>
<td>13</td>
<td>15</td>
<td>1</td>
<td>0</td>
<td>0.103</td>
<td>0.000</td>
<td>31</td>
<td>3.44</td>
<td>0.24</td>
<td>0.59</td>
<td>0.03</td>
<td>0.58</td>
<td>0.03</td>
<td>-0.03</td>
<td>0.04</td>
<td>21</td>
<td>0</td>
<td>0</td>
<td>10</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>7-46</td>
<td>62</td>
<td>48</td>
<td>22</td>
<td>26</td>
<td>1</td>
<td>0</td>
<td>0.047</td>
<td>0.021</td>
<td>58</td>
<td>3.78</td>
<td>0.28</td>
<td>0.60</td>
<td>0.06</td>
<td>0.57</td>
<td>0.05</td>
<td>-0.06</td>
<td>0.03</td>
<td>38</td>
<td>0</td>
<td>0</td>
<td>20</td>
<td>1</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>7-H</td>
<td>49</td>
<td>36</td>
<td>17</td>
<td>19</td>
<td>0</td>
<td>0</td>
<td>0.207</td>
<td>0.012</td>
<td>41</td>
<td>3.00</td>
<td>0.29</td>
<td>0.46</td>
<td>0.05</td>
<td>0.46</td>
<td>0.05</td>
<td>-0.03</td>
<td>0.03</td>
<td>23</td>
<td>0</td>
<td>0</td>
<td>18</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>7-I</td>
<td>37</td>
<td>22</td>
<td>10</td>
<td>12</td>
<td>1</td>
<td>0</td>
<td>0.106</td>
<td>0.168</td>
<td>28</td>
<td>3.33</td>
<td>0.17</td>
<td>0.54</td>
<td>0.05</td>
<td>0.55</td>
<td>0.03</td>
<td>0.03</td>
<td>0.06</td>
<td>19</td>
<td>0</td>
<td>0</td>
<td>9</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>7-P</td>
<td>21</td>
<td>12</td>
<td>5</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>0.063</td>
<td>0.000</td>
<td>17</td>
<td>3.11</td>
<td>0.20</td>
<td>0.64</td>
<td>0.06</td>
<td>0.55</td>
<td>0.04</td>
<td>-0.16</td>
<td>0.07</td>
<td>12</td>
<td>0</td>
<td>0</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>278</td>
<td>181</td>
<td>81</td>
<td>100</td>
<td>3</td>
<td>0</td>
<td>0.063</td>
<td>0.000</td>
<td>223</td>
<td>3.11</td>
<td>0.20</td>
<td>0.64</td>
<td>0.06</td>
<td>0.55</td>
<td>0.04</td>
<td>-0.16</td>
<td>0.07</td>
<td>144</td>
<td>0</td>
<td>0</td>
<td>79</td>
<td>1</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>
assignment were split by year, the rate of exclusion from the site of sampling was even lower: no individuals could be excluded from their sampling localities in 2008-09, and only one individual was excluded from its sampling locality in 2009-10 (Table 5.1).

### 5.4.4 Survival (CJS) models

Model averaged estimates of apparent survival were between 0.28 – 0.53 depending on the site, and recapture probability was 0.97 ± 0.03 (Table 5.3). All models described apparent survival better than the global model (model 26 $\Theta_i = 11.34$, Table 5.4). Modelled unconstrained site variation (model 10 $\Theta_i = 5.28$) ranked higher than the constant-only model (model 19 $\Theta_i = 7.86$) indicating survival varied between sites (Table 5.4). The time constant age model (model 15 $\Theta_i = 6.82$) also ranked higher than the constant-only model. The survival rate of adults was greater than that of non-breeders ($\beta(AGE)$ ± S.E. = $-0.47 \pm 0.27$, 95% CI = $-1.00 - 0.05$; breeder $\beta = 0.47 \pm 0.05$, non-breeder $\beta = 0.36 \pm 0.04$). Support for models with age effects that varied over time was limited (models 21 $\Theta_i = 8.89$ and 25 $\Theta_i = 10.52$). Further, there was little support for a model with an effect of sex on survival (model 24 $\Theta_i = 9.90$). The modelled sex effects measured by the beta values suggest there was no meaningful difference in survival rates between males and females ($\beta(SEX)$ ± S.E. = $-0.02 \pm 0.27$, 95% CI = $-0.55 - 0.50$; male $\beta = 0.41 \pm 0.05$, female $\beta = 0.42 \pm 0.04$). Overall, models with specific fire and habitat covariates had the greatest model weights. The combined effects of habitat features (dead shrubs, floristic richness and cover; models 1 – 7, Table 5.4) were clearly the strongest influence on survival. Models that included dead shrubs as a survival covariate had substantial support (Table 5.4); survival was greatest in sites with low dead shrub density ($\beta(DEADSHRUB)$ ± S.E. = $-5.30 \pm 1.83$, 95% CI = $-8.89 - -1.71$). Model combinations of fire and habitat features were also supported (Table 5.4). The main effect of fires indicated an increased incidence of fire had a positive effect on survival ($\beta(FIRES)$ ± S.E. = $0.23 \pm 0.10$, 95% CI = $0.04 - 0.41$). There was less support for survival models that included landscape heterogeneity (model 12 $\Theta_i = 5.43$) and essentially no support for models that included patch area (model 22 $\Theta_i = 9.54$).

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**Table 5.2:** Pairwise site $F_{ST}$ for the eastern chestnut mouse. $F_{ST}$ values below diagonal. Probability values based on 999 permutations are shown above diagonal. All survey years and loci are combined. Non-significant values highlighted in bold.

<table>
<thead>
<tr>
<th></th>
<th>7-2</th>
<th>7-44</th>
<th>7-44B</th>
<th>7-46</th>
<th>7-H</th>
<th>7-I</th>
<th>7-P</th>
</tr>
</thead>
<tbody>
<tr>
<td>7-2</td>
<td>0</td>
<td>0.001</td>
<td>0.001</td>
<td>0.001</td>
<td>0.001</td>
<td>0.001</td>
<td>0.022</td>
</tr>
<tr>
<td>7-44</td>
<td>0.232</td>
<td>0</td>
<td>0.001</td>
<td>0.001</td>
<td>0.001</td>
<td>0.003</td>
<td>0.001</td>
</tr>
<tr>
<td>7-44B</td>
<td>0.152</td>
<td>0.115</td>
<td>0</td>
<td>0.001</td>
<td>0.001</td>
<td>0.001</td>
<td>0</td>
</tr>
<tr>
<td>7-46</td>
<td>0.073</td>
<td>0.142</td>
<td>0.147</td>
<td>0</td>
<td>0.001</td>
<td>0.003</td>
<td>0.347</td>
</tr>
<tr>
<td>7-H</td>
<td>0.287</td>
<td>0.254</td>
<td>0.242</td>
<td>0.230</td>
<td>0</td>
<td>0.001</td>
<td>0.001</td>
</tr>
<tr>
<td>7-I</td>
<td>0.190</td>
<td>0.114</td>
<td>0.153</td>
<td>0.135</td>
<td>0.271</td>
<td>0</td>
<td>0.001</td>
</tr>
<tr>
<td>7-P</td>
<td>0.040</td>
<td>0.132</td>
<td>0.100</td>
<td>0.003</td>
<td>0.213</td>
<td>0.107</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 5.3: Cormack-Jolly-Seber (CJS) and Pradel model averaged parameter estimates presented with unconditional standard error and 95 % confidence interval in parentheses; $\phi =$ apparent survival, $p =$ recapture probability, $f_{1-3}$ = recruitment probability (for 1st, 2nd, and 3rd time interval).

<table>
<thead>
<tr>
<th>Site</th>
<th>$\phi \pm$ S.E.</th>
<th>$p \pm$ S.E.</th>
<th>$f_1 \pm$ S.E.</th>
<th>$f_2 \pm$ S.E.</th>
<th>$f_3 \pm$ S.E.</th>
</tr>
</thead>
<tbody>
<tr>
<td>CJS estimates</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7-2</td>
<td>0.49±0.07 (0.35-0.64)</td>
<td>0.97±0.03 (0.80-1.00)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7-44</td>
<td>0.44±0.09 (0.28-0.61)</td>
<td>0.97±0.03 (0.80-1.00)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7-44B</td>
<td>0.52±0.07 (0.39-0.65)</td>
<td>0.97±0.03 (0.80-1.00)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7-46</td>
<td>0.28±0.06 (0.18-0.43)</td>
<td>0.97±0.03 (0.80-1.00)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7-H</td>
<td>0.33±0.08 (0.20-0.49)</td>
<td>0.97±0.03 (0.80-1.00)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7-I</td>
<td>0.45±0.06 (0.33-0.57)</td>
<td>0.97±0.03 (0.80-1.00)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7-P</td>
<td>0.53±0.10 (0.34-0.71)</td>
<td>0.97±0.03 (0.80-1.00)</td>
<td></td>
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<tr>
<td>Pradel estimates</td>
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<tr>
<td>7-2</td>
<td>0.44±0.07 (0.31-0.57)</td>
<td>0.98±0.02 (0.89-1.00)</td>
<td>0.11±0.31 (0.00-0.98)</td>
<td>3.66±5.74 (-7.59-14.90)</td>
<td>0.01±0.01 (-0.02-0.03)</td>
</tr>
<tr>
<td>7-44</td>
<td>0.29±0.15 (0.09-0.63)</td>
<td>0.98±0.02 (0.89-1.00)</td>
<td>0.13±0.37 (0.00-0.99)</td>
<td>4.29±7.16 (-9.73-18.32)</td>
<td>0.01±0.02 (-0.03-0.04)</td>
</tr>
<tr>
<td>7-44B</td>
<td>0.52±0.11 (0.32-0.72)</td>
<td>0.98±0.02 (0.89-1.00)</td>
<td>0.12±0.33 (0.00-0.98)</td>
<td>4.09±6.56 (-8.78-16.95)</td>
<td>0.01±0.02 (-0.03-0.04)</td>
</tr>
<tr>
<td>7-46</td>
<td>0.32±0.09 (0.18-0.51)</td>
<td>0.98±0.02 (0.89-1.00)</td>
<td>0.14±0.37 (0.00-0.99)</td>
<td>4.47±7.34 (-9.90-18.85)</td>
<td>0.01±0.02 (-0.03-0.04)</td>
</tr>
<tr>
<td>7-H</td>
<td>0.36±0.07 (0.24-0.51)</td>
<td>0.98±0.02 (0.89-1.00)</td>
<td>0.09±0.27 (0.00-0.98)</td>
<td>2.89±4.68 (-6.29-12.06)</td>
<td>0.00±0.01 (-0.02-0.03)</td>
</tr>
<tr>
<td>7-I</td>
<td>0.44±0.07 (0.30-0.59)</td>
<td>0.98±0.02 (0.89-1.00)</td>
<td>0.11±0.31 (0.00-0.98)</td>
<td>3.67±5.85 (-7.79-15.13)</td>
<td>0.01±0.01 (-0.02-0.03)</td>
</tr>
<tr>
<td>7-P</td>
<td>0.47±0.11 (0.27-0.68)</td>
<td>0.98±0.02 (0.89-1.00)</td>
<td>0.16±0.63 (0.00-1.00)</td>
<td>5.31±11.34 (-16.93-27.54)</td>
<td>0.01±0.02 (-0.04-0.05)</td>
</tr>
</tbody>
</table>
Table 5.4: Model summary describing factors affecting survival of the eastern chestnut mouse: Akaike's information criterion for small sample size (AICc), AICc difference ($\Delta$), AICc model weight ($w_i$), parameters (K), $\phi =$ survival; $p =$ recapture probability; sex = male, female; age = breeder or non-breeder; season; site; covariates in parentheses.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>$\Delta$</th>
<th>$w_i$</th>
<th>K</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\phi$(dead shrubs+floristic richness)$p(.)</td>
<td>329.31</td>
<td>0.00</td>
<td>0.141</td>
<td>4</td>
</tr>
<tr>
<td>$\phi$(dead shrubs)$p(.)</td>
<td>330.50</td>
<td>1.19</td>
<td>0.078</td>
<td>3</td>
</tr>
<tr>
<td>$\phi$(dead shrubs+floristic richness+firs$p(.)</td>
<td>330.66</td>
<td>1.35</td>
<td>0.072</td>
<td>5</td>
</tr>
<tr>
<td>$\phi$(dead shrubs+cover)$p(.)</td>
<td>331.04</td>
<td>1.73</td>
<td>0.059</td>
<td>4</td>
</tr>
<tr>
<td>$\phi$(dead shrubs+floristic richness+cover)$p(.)</td>
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<td>339.82</td>
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</tr>
<tr>
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<td>340.65</td>
<td>11.34</td>
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5.4.5 Recruitment (Pradel) models

To estimate recruitment, we modelled apparent survival with unconstrained site effects because the variable ‘site’ was expected to capture all the variation attributed to significant site-level covariates revealed by the CJS modelling. Model averaged estimates of apparent survival were between 0.29 and 0.52, and recapture probability was 0.98 ± 0.02 (Table 5.3). Recruitment was highest in the winter 2009 (W9) to summer 2009 – 2010 (S910) interval and lowest for the summer 2009 – 2010 (S910) – winter 2010 (W10) interval (range 0 – 5.31, Table 5.3). The best supported models of per capita recruitment included age and season and population genetic parameters (H0, pFST, tFST) (models 1 – 4, Table 5.5). We attributed per capita recruitment to the in situ production of offspring, which was highest between winter 2009 (W9) and summer 2009 – 2010 (S910) (non-breeder \( f_1 \pm S.E. = 0.36 \pm 0.09, f_2 = 11.04 \pm 3.86, f_3 = 0.02 \pm 0.02; \) breeder \( f_1 \pm S.E. = 1.71-09 \pm 5.32-07, f_2 = 5.19-08 \pm 1.62-05, f_3 = 8.17-11 \pm 2.55-08 \)). Recruitment rate increased with overall genetic diversity (\( \overline{\text{H0}} \) ± S.E. = 5.50 ± 3.45, 95% CI = -1.27 – 12.27), and decreased with population specific FST (\( \overline{\text{pFST}} \) ± S.E. = -4.18 ± 3.27, 95% CI = -10.58 – 2.22) and temporal FST within each site (\( \overline{\text{tFST}} \) ± S.E. = -0.47 ± 3.97, 95% CI = -8.24 – 7.31) (Table 5.5). When we included site variation in the best Pradel models (models 5 – 8, Table 5.5), the estimates derived from the models changed but there was no difference in AICc weight between the models indicating any combination of genetic covariates with age, season, and site had an equal influence on recruitment. Models that included site-level covariates were unsupported (Table 5.5).

5.5 Discussion

Integrating demographic and genetic analyses improves both our understanding of demographic population processes, and the underlying drivers of spatiotemporal variation in genetic diversity and structure. Our demographic analysis indicated survival rates were influenced by external factors including an increased incidence of fire and specific resources affected by fire (collapsed dead shrub layer, floristic richness, and cover). Recruitment was more strongly explained by site variation than landscape structure, which is consistent with low connectivity between populations, supporting the inference of discrete populations from FST. Site-level fire history is therefore a key factor driving demographic processes in these populations over the period surveyed. Given immigration was rare, apparent survival as predicted in our modelling is likely to be a good estimate of actual survival, where individuals that disappear from the population are attributed to mortality not and emigration. The addition of genetic data improved our demographic inference by revealing reproduction by resident animals was a greater contributor to recruitment than immigration and that the strong genetic structure identified, confirmed populations are largely discrete at the post-fire period of
Table 5.5: Model summary describing factors affecting eastern chestnut mouse recruitment: Akaike’s information criterion for small sample size (AICc), AICc difference (Δi), AICc model weight (wi), parameters (K), $\phi$ = apparent survival; $p$ = recapture probability; $f$ = recruitment probability; age = breeder or non-breeder; season; site; $H_O$ = observed heterozygosity; $p_{FST}$ = population specific genetic differentiation; $t_{FST}$ = temporal FST; covariates in parentheses.

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<td>26</td>
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</table>
this study. The low level of movement between populations suggests that recruitment estimates primarily represent recruitment to the captured age class resulting from locally born individuals. The demographic analyses revealed information about genetic processes that otherwise would have remained unknown or supposition. The genetic site variables are responsive to recruitment patterns: for example, spatial and temporal genetic differentiation reflects the role of recruitment in genetic drift.

5.5.1 Internal population processes: limited immigration, neutral sex effect, age-structured survival

Recruitment by reproduction has been found to be more important than immigration in other disturbed habitats (Pocock et al., 2004, Dooley and Bowers, 1998). Reproduction as major source of recruitment reduces the need for migrants to successfully track suitable habitat within their dispersal distance and is one mechanism by which population recovery can proceed after perturbation (Lindenmayer et al., 2005, Banks et al., 2011a). We propose two plausible models of population dynamics for early successional specialists – Model I ‘colonization model’ where individuals persist in recently burned habitat and move large distances to newly suitable habitat (recruitment due to immigration); and Model II ‘persistence model’ where species are present across the landscape at very low densities but irruptions occur due to increases in reproduction and survival after fire (recruitment due to locally born individuals). Our results do not resolve these processes, however they show that within a few years of recent fire, populations are discrete and exchange few migrants. While populations appear to be isolated during the period of study (i.e. no movement between sampled populations, limited immigration, high population-specific \( F_{ST} \), previous work on this species demonstrates increased genetic connectivity in association with recent fire (Pereoglou et al., 2013). One possibility is that fire promotes movement and colonization of newly suitable burnt habitat, but once established, populations then become relatively isolated until the next fire. We found populations with the highest rates of recruitment were more genetically diverse and were less differentiated from other populations. When recruitment is due to migration, alleles added to the population reduce genetic differentiation between populations. However, our result of spatial genetic structure despite limited immigration suggests populations with higher recruitment potentially experience less genetic drift. Therefore, changes in animal movement over time may be a necessary strategy of inhabiting ephemeral patches of early successional habitat (e.g. Model I followed by Model II as succession proceeds) and genetic diversity (and differentiation between years within populations) is a consequence of these recruitment and survival patterns.

Survival is directly affected by dispersal (Driscoll et al., 2014), and rates can be specific to age classes, sexes, or both. When dispersal is not biased towards either sex, the processes
underpinning survival operate equally on both male and female individuals. For species dependent on early successional habitats, an absence of sex-biased dispersal is an advantageous strategy because greater colonization ability of one sex compared to the other would increase the chance of colonizing newly suitable unoccupied habitat without any potential mates (Pereoglou et al., 2013). As a consequence, sex-biased dispersal is not favored under high demographic stochasticity (Gros et al., 2008) which can be associated with an unpredictable environment. Furthermore, an age-structured population where offspring disperse is beneficial for adults to maximize reproductive potential by retaining access to (temporally) limited resources (e.g. food, refugia, or mates). If immature individuals die or disperse before breeding, then reproductive output is mainly due to resident adults in the source populations (Paradis et al., 1993).

5.5.2 External population processes: fire and landscape structure

In our modelling, site-level habitat quality and landscape-level processes (i.e. disturbance) were more important influences on survival than landscape structure (habitat area and heterogeneity). This would be expected under a Model II scenario where post-fire increases in reproduction and survival are driven by site-level processes including the distribution of critical resources. We found an increased incidence of fire and habitat features associated with fire affected survival in (mainly) predictable ways. Reduced cover and high floristic diversity was associated with a higher survival rate. Cover and floristic richness are indicators of local fire history because both change in expected ways following disturbance; cover increases and floristic richness decreases with vegetation succession in heathland. At a certain threshold, cover and floristic richness can become critical resources.

What constitutes a critical resource is dependent upon a species’ life history and habitat requirements (Morrison et al., 2006). The influence of fire on survival has been linked to the effects of fire on critical resources across multiple taxa. When fire increases the critical resource, increases in survival also occur (Rota et al., 2014). When the critical resource is unaffected by fire, or becomes sub-optimal relative to pre-fire conditions, survival rates remain constant (Banks et al., 2011b, D'Souza et al., 2013, McDonough and Rexstad, 2005). When fire decreases the critical resource, a negative impact of fire on survival has observed (Pardon et al., 2003, Pons et al., 2003).

The negative relationship between survival and density of dead shrubs was surprising despite their function as a critical shelter resource. In heathland a collapsed dead shrub layer is created and maintained by the frequency of fire events (Williams, 1995, Specht, 1981). Reduced survival in populations with a high density of dead shrubs may occur through increased intraspecific competition for shelter sites, or increased mortality through predation by snakes.

Habitat quality also can be measured in terms of landscape structure. At this post-fire period of study, landscape effects on survival and recruitment were not important; models
including landscape structure were relatively unsupported (Table 5.3 and 5.4). In the context of Model I and II, landscape effects are potentially critical during the colonisation phase, but not during the ‘persistence’ phase. For example, if individuals were required to make large-scale movements to colonise suitable habitat and immigration were a significant source of recruits (i.e. Model I), landscape structure should be a strong influence on recruitment because animals would need to traverse unsuitable habitat and colonization would possibly be dependent on patch size (i.e. less chance of successfully colonizing small patches either because they are more difficult to find or because they are already occupied).

5.5.3 Conclusion

We tested the hypothesis that species with genetically structured populations were more likely to have demography influenced by site-level processes than landscape-level processes, because populations that were discrete were likely to be strongly influenced by local resources. Populations appeared isolated, with demographic differences driven by effects of fire history on survival, most likely through impacts on habitat quality. Our modelling suggests that in early successional communities, (i) reproduction is a major source of recruitment and not immigration, (ii) variation in recruitment rate is due to spatial genetic structure and genetic composition of individuals in populations, and (iii) survival rates are strongly influenced by spatial variation in habitat quality as a result of previous fires and to a lesser extent landscape structure. These findings indicate fire provides an important ecological condition for early successional species, and that the importance of fire may be much broader than commonly appreciated for sustaining demographic processes.

5.6 Acknowledgement

We most gratefully acknowledge the Wreck Bay Aboriginal Community and the Wandandian People of the Dharawal and Dhurga language groups on whose lands this study was conducted. We thank Wendy Hartman, Alfred Wellington, Tony Carter, Geoff Kay, Steve Phillips, Marama Hopkins, Nick Dexter, Karen Viggers, Sally Townley, Les Mitchell and Martin Westgate. We also thank Axios Review for referee comments that greatly improved this manuscript. This research was funded by the Norman Wettinall Foundation, MA Ingram Trust, Australian Academy of Science, WV Scott Charitable Trust.

5.7 References


Chapter 6

Conclusion
6.1 Population processes of the eastern chestnut mouse

This thesis is an investigation of the animal population processes occurring in an early successional heathland. The eastern chestnut mouse was used as a case study for this research. For an early successional specialist such as the eastern chestnut mouse, the opportunity to compare processes operating in populations before and/or after disturbance is limited by the unpredictable occurrence of wildfires, the species’ occurrence at low density, and a ‘patchy’ distribution across its geographic range. We know this species responds positively to fire, but we don’t understand the underlying demographic processes involved, nor do we understand the contribution of individual movements, disturbance history, and habitat quality. The research presented here provides new knowledge on the population ecology of the eastern chestnut mouse. This project, for the first time, elucidated mechanisms of population persistence in an early successional heathland through addressing a series of research questions aimed at identifying the resources used for refuge and associated behaviours, predictors of species occurrence, spatial patterns of genetic structure, and drivers of population dynamics in spatially and temporally variable environment. I provide a summary of the previous four research chapters and discuss the mechanisms of population persistence in early successional communities, including the specific role of fire.

Chapter 2 described habitat features and structures selected by the eastern chestnut mouse as refuge sites, and patterns of refuge site fidelity in recently burned heathland. Refuge sites consisted of taller, denser vegetation than randomly selected control sites, and were associated with specific structures including collapsed dead shrubs, Xanthorrhoea and Gymnoschoenus species. There were no differences in the sites selected by males and females. However, there was evidence for a primary–secondary model of refuge use. Primary refuge sites contained a nesting structure (i.e. pad or spherical nest of woven, dried grass) and were the densest sites selected. Seasonal variation in habitat selection and fidelity to sites was attributed to reproductive constraints, intra-specific competition, and environmental conditions. Mice used multiple, rarely occupied refuges, and were mainly solitary although they infrequently ‘shared’ sites without cohabitation. The major finding in Chapter 2 was that refuge sites were highly flammable and would not provide protection from fire. Mice did not select fire-resistant refugia (i.e. rock crevasses or tree roots), or use behaviours associated with fire avoidance (i.e. burrowing). These resource requirements and patterns of use have clear implications for fire management and prescribed burning practices (see ‘The role of fire’ below).

Chapter 3 evaluated the effects of disturbance, landscape structure, and site-level habitat quality on eastern chestnut mouse site occupancy in an early successional ecosystem. This chapter introduced the issue of scale and assessed spatial patterns of landscape suitability and site-level habitat requirements affecting early successional fauna. Landscape configuration was a strong influence on site occupancy; occupancy increased with habitat patch area and decreased...
Chapter 6: Conclusion

with landscape heterogeneity. Resource availability at a local (site-level) scale also was significant. The results affirmed the importance of a collapsed dead shrub layer and indicated the number of dead shrubs increased with burning in the last major wildfire. Although rock crevasses were not identified as refuge sites, rock cover was positively correlated with site occupancy. No predictable patterns of small mammal species co-occurrence were found, contrary to the mammalian secondary succession model. No direct effect of fire was detected. The major finding in Chapter 3 was that fire affected population processes indirectly and site occurrence was a multi-scale course of action. These results have implications for land management including the extent of prescribed fire, clearing or habitat modification, and surrounding land use, and also for experimental design as a guide for survey work targeting populations of the eastern chestnut mouse.

Chapter 4 assessed the effects of landscape variation and recent disturbance history on dispersal by the eastern chestnut mouse. Significant genetic structure was identified, and positive spatial autocorrelation between genotypes was detected up to 2–3 km, indicating dispersal was restricted relative to the overall spatial scale of the study. As predicted, there was no strong evidence for female philopatry and male dispersal. The influence of different habitat- and fire-specific landscape resistance scenarios on genetic connectivity was tested. Recently burned vegetation had greater conductance for gene flow than unburnt habitat, but variation in habitat quality between vegetation types and occupied patches had no effect on gene flow. This was attributed to fire improving habitat suitability for early successional species, and habitat suitability improving genetic connectivity across the landscape. An alternative was that dispersal in burnt areas increased in association with post-fire colonization before returning to levels described under a ‘null landscape’ model. The major finding of Chapter 4 was that fire assisted in structuring populations of an early successional species. Dispersal through unsuitable habitat was possible and the effects of landscape heterogeneity were likely dependent upon the extent of dissimilarity was from a more ‘natural’ state.

Chapter 5 investigated two major components of population growth in the eastern chestnut mouse – survival and recruitment, and how these key demographic parameters vary across the landscape in response to fire history related environmental factors. In this section, demographic and genetic analyses were used to quantify survival, recruitment and immigration rates. Survival varied across sites, with supported models including disturbance history and resources indicative of local fire history (collapsed dead shrubs, cover, floristic richness). Compared to local reproduction, immigration contributed very little to recruitment, suggesting populations are demographically discrete at this post-fire stage. Sites with high recruitment also had higher genetic diversity and lower temporal genetic structure, consistent with reduced genetic drift. The key findings of this chapter suggests a two-phase model of spatial population dynamics, where post-fire colonization is followed by locally driven population dynamics, in which survival rates are influenced by fire-history effects on habitat quality. These results have implications for land
management including the application of fire to maintain critical resources associated with increased survival, and promote genetic connectivity between local populations of species inhabiting post-fire early successional communities by initiating immigration that is otherwise relatively limited.

6.2 Mechanisms of population persistence in an early successional community

The mechanisms used by animals to persist in an early successional ecosystem are discussed in this section. I propose two possible persistence scenarios for early successional species: either (I) individuals are present across the landscape at very low densities but increases in density follow increases in reproduction and survival post-fire (‘persistence model’), or (II) individuals are present in recently burned habitats and move large distances to newly suitable habitat when it becomes available post-fire (‘colonisation model’). The research I have presented in this thesis provides evidence for both potential scenarios. The maintenance of multiple, rarely occupied refuge sites that maximises access to resources that are ‘patchy’ or dispersed, and potentially limited over time is a mechanism underlying the colonisation model of population persistence because refuge sites are likely to be burned by fire, limited by successional changes in vegetation over time, and therefore temporary over longer time scales. The use of existing refuge sites by multiple animals (i.e. inheritance and/or temporally segregated use of refuge sites) to avoid associated costs of seeking suitable new sites in spatially and temporally variable habitat is indicative of the persistence model where population density is (probably) positively associated with the availability of suitable, unoccupied shelter resources. Landscape structure (patch area and landscape heterogeneity) has the potential to mitigate the effects of disturbance for early successional species. A generalist dispersal strategy where animal movement is not sex-biased, or restricted to particular vegetation types or landscape attributes is an indicator of a colonisation model of population persistence because it is the disperser’s ability to follow fire determines whether newly suitable habitat is located. Local reproduction by residents would be expected under a persistence model as an advantageous strategy for increasing population density compared to immigration when the need for migrants to track suitable (available) habitat within dispersal distance in post-fire landscapes can be avoided. In this thesis, I have studied population processes that occur over multiple scales. For example, animal movement, including dispersal and migration, occurs over a landscape scale, whereas equally important mechanisms involving habitat selection, colonization and recruitment occur at a local (site-level) scale. The obvious limitation to the research presented here is that the effects of time and temporal successional changes on refuge site selection and use, predictors of species occurrence, spatial patterns of genetic structure, and drivers of population dynamics currently remain unknown.
6.2.1 The role of fire

Changes to natural fire regimes associated with climate change are expected to result in more frequent disturbance events. Our understanding of the positive aspects of fire-related disturbance is rudimentary and must improve if we seek to conserve biodiversity in early successional environments. Fire can have an indirect effect on population processes in early successional communities. As discussed throughout this thesis, habitat elements created and/or maintained by fire (i.e. a collapsed dead shrub layer, cover, floristic richness, etc.) influence the selection of diurnal refugia, success of site occupancy, and demographic rates. In general, when significant, the direct effect of fire was positive; i.e. fire promotes genetic connectivity between local populations of early successional fauna, and possibly immigration although this later process is unconfirmed. Future research in this subject area might include quantifying the effect of fire regime and landscape structure on the critical resources identified in this thesis, demographic rates, and dispersal strategy of the eastern chestnut mouse.
Chapter 7

Consolidated references
Consolidated References


Chapter 7: Consolidated references


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Chapter 7: Consolidated references


Chapter 7: Consolidated references


Chapter 7: Consolidated references


Pereoglou, F., Population processes in an early successional heathland


Wright, S. (1943) Isolation by distance. Genetics, 28, 139-156.
Appendix 1

Manuscript:

Refuge site selection in recently burned heath

Published, September 2011
Refuge site selection by the eastern chestnut mouse in recently burnt heath

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Abstract

Context. Temporal reduction in shelter is an indirect primary impact of fire. Removal of animal refugia has implications for shelter site selection and fidelity – factors that have been largely overlooked in studies of Australian rodent fauna. This information is critical for guiding species conservation and appropriate land management including prescribed burning practices.

Aims. We sought to determine which features of burnt heath were selected as shelter sites by the eastern chestnut mouse, whether there was sex and/or seasonal variation in shelter site selection and whether we could identify primary refugia.

Methods. We completed a radio-telemetry study to identify diurnal refuge sites and compare habitat attributes with those of a matched set of control sites. We then used habitat features and fidelity parameters to classify refuge site use.

Key results. We found the eastern chestnut mouse selected shelters with the presence of specific structures and had taller, denser vegetation than randomly selected control sites. There were no differences in habitat selection between the sexes. Shelter sites in the non-breeding season had greater vegetation density compared with those used in the breeding season. In the breeding season, the eastern chestnut mouse showed no evidence of increased fidelity to particular refuges. Vegetation density in winter was the best predictor of a primary refuge compared with whether or not an animal returned to a shelter site or the amount of time spent in a shelter site. Mice were ephemeral and non-gregarious in their refuge use. There was some evidence for inheritance of refuge sites from a parent, as well as inter-season shelter site fidelity.

Conclusions. The eastern chestnut mouse selected refugia that had habitat attributes offering maximum protection. Seasonality in refuge site selection is likely to reflect the reproductive and environmental trade-offs in critical resources during different seasons. The maintenance of multiple, rarely occupied shelters by the eastern chestnut mouse is consistent with data for other mammals.

Implications. Fire management should ensure retention of vegetation structure on the ground layer, dense habitat patches in burned areas, and be carefully planned during the winter season to maintain shelter and refuge sites to assist population persistence.

Introduction

The response of small mammal populations to fire has been studied extensively in Australia (Newsome \textit{et al.} 1975; Cockburn \textit{et al.} 1981; Fox 1982; Newsome and Catling 1983; Catling 1986; Thompson \textit{et al.} 1989; Catling 1991; Masters 1993; Letnic 2003; Letnic \textit{et al.} 2004; Lindenmayer \textit{et al.} 2008). A pattern of post-fire irruption followed by decline has been observed for some Australian native rodents (Whelan \textit{et al.} 2002). The eastern chestnut mouse (\textit{Pseudomys gracilicaudatus}) is one example. Existing evidence suggests the species is a pyric specialist with peak population density in recently burnt heathland and a subsequent decline in abundance with time since fire (Fox 1982; Higgs and Fox 1993; Thompson and Fox 1993; Monamy and Fox 2000; Fox \textit{et al.} 2003; Monamy and Fox 2010).

The eastern chestnut mouse occurs at low densities when present, is rare or extinct in many parts of its range (Breed and Ford 2007) and is classified as vulnerable under the Threatened Species Conservation Act 1992 (NSW). Inappropriate fire regimes including fire suppression in areas supporting populations of the eastern chestnut mouse may affect the species’ persistence and viability. However, the mechanisms underlying the species’ fire response are unknown.

Terrestrial small mammals can be affected by fire through direct mortality, and indirectly through changes in resource availability (Whelan \textit{et al.} 2002). Studies of the eastern
chestnut mouse’s dietary requirements indicate the species is a
generalist herbivore with an opportunistic foraging strategy
able to utilise a diverse food resource (Luo and Fox 1994; Luo
et al. 1994). A diverse diet is a basic requirement for rapid
colonisation of recently burnt areas and is an essential attribute
for a fire opportunist to take advantage of all available food
resources (Luo et al. 1994). Given this, it is unlikely that
depletion of the food resource alone would be a determinant of
the species’ fire response.

The role of animal refugia in facilitating population recovery
and persistence after a fire is poorly understood for Australian
rodent fauna. A reduction in available shelter sites is one of the
primary impacts of fire on populations (Newsome and Catling
1983; Friend 1993) and may have multiple consequences
including distributional, demographic and behavioural change
(Sutherland and Dickman 1999). The presence, size and location
of refugia are landscape attributes that may influence the
processes of mortality, colonisation, post-fire survival,
establishment, reproduction and population increase (Whelan
et al. 2002). Daytime refugia and shelter sites are critical for
surviving disturbance events (Brathwaite 1990), environmental
extremes, predation and for providing security while weaning
young (Frank and Layne 1992). Identification of habitat
components that might represent refuges and the question of
how important they are for maintenance of post-fire populations
requires additional study (Keith et al. 2002).

The rate of reappearance after fire is dependent on a
species’ mobility, dispersal capacity, dietary specialisation
and habitat preferences (Keith et al. 2002), including the level
of protection provided by refugia during and after a fire.
An assumption of survival within burnt areas would lead us to
predict rapid reappearance and population growth (Keith et al.
2002). Recruitment from residual animals after disturbance
has been shown to be important (Lindenmayer et al. 2005;
Banks et al. 2011). This suggests refugia may play a critical
role in a species’ ability to survive fire and the subsequent
population response. The identification, distribution and
protection of animal shelter sites and refuges should be an
essential component of conservation strategies in fire-prone
landscapes.

In this paper, we document the results of a radio-telemetry
study of daytime refuge habitat requirements and nest fidelity
of the eastern chestnut mouse. We sought to answer the following
questions:

(i) Does the eastern chestnut mouse preferentially select
shelter sites based on specific habitat attributes? We
expected that mouse-selected shelter sites would be
characterised by denser, taller vegetation than control sites.

(ii) Are there sex differences or seasonal variation in shelter
site selection and fidelity? We hypothesised the female mice
would select shelter sites that offer optimal cover and
protection during summer and would show greater
shelter site fidelity than males. We expected these
differences to be driven by different requirements of the
sexes during the breeding season – care of offspring in
females versus proximity to mates for males. We predicted
there would be no difference between male and female mice
in shelter site selection and fidelity during winter.

(iii) Is there a primary–secondary model of refuge use? We
hypothesised that animals would show increased fidelity
to shelters characterised by particular attributes including
the presence of a mouse-made nesting structure (Wolfe
1970; Klein and Layne 1978; Hartung and Dewsbury
1979). These primary refuges would be used more
frequently and would have habitat attributes that
distinguish them from secondary shelters.

(iv) Does the eastern chestnut mouse share shelter sites? We
expected that individuals would not share shelter sites,
instead likely to be solitary in their nesting habits. The
closely related western chestnut mouse (P. nanus) also has a
dispersed, solitary social organisation (Breed and Ford
2007) and other Pseudomys species have been shown to
engage in agonistic nest defence (Happold 1976).

Identification of small mammal shelter requirements and an
understanding of refuge site fidelity and nesting behaviour could
be used by land managers when designing appropriate burning
regimes or promoting post-fire population recovery. For
threatened species, knowledge of nest requirements
and daytime refuge habitat and use is fundamental for
conservation efforts.

Materials and methods

Study sites

We selected six sites for study in Booderee and Jervis Bay
national parks in south-eastern Australia (Fig. 1). These
adjoining reserves are located ~200 km south of Sydney on the
south coast of New South Wales. We based site selection on
survey data of Townley (2007), Lindenmayer et al. (2008) and a
pilot study indicating the presence of the eastern chestnut mouse
at sufficiently high densities to enable attachment of radio-
transmitters to at least two individuals per site. We classified
study sites as heath (defined by Taws (1997) as vegetation
dominated by shrubs with small narrow leaves), generally less
than 2 m tall and varyingly dominated by Banksia ericifolia and
Sprengelia incarnata, with Allocasuarina distyla, Isopogon
anemonifolius and Hakea teretifolia also being common. Each
of our six field sites had been burnt by wildfire within the last
six years.

Trapping and radio-collaring

We completed trapping and radio-collaring during the 2008–09
summer breeding season (November–March) and the winter
2009 non-breeding season (June–August). We captured
animals using grids of type A Elliot traps open for four
consecutive nights using a bait of rolled oats, peanut butter
and fennel seed. During winter, we insulated traps with non-
absorbent cotton wool and covered them with a plastic sleeve.
Our grid arrangement comprised lines at 20 m intervals with
traps 10 m apart. We provide a summary of field site details,
trapping and radio-collaring data (Table 1).

We assessed the weight, sex, age cohort and breeding
condition of captured animals. We marked mice for permanent
identification using Trovan ID100 implantable transponders
(Microchips Australia Ltd, Melbourne). We selected mice for
radio-collar attachment if they were (i) an adult, (ii) weighed
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Pereoglou, F., Population processes in an early successional heathland

>70 g to ensure collar weight was less than 5% of an individual’s bodyweight, and (iii) not visibly pregnant. We fitted individuals with a single-stage transmitter on a replaceable cable tie weighing 2.5–3.5 g (Sirtrack Limited, Hawkes Bay, NZ) in the field before release at the point of capture. We tracked animals to their diurnal shelter site daily for a period of one month using a Yagi hand-held antenna and a communications specialist R1000 receiver (Sirtrack Limited). Transmission was highly directional at close range allowing us to pinpoint animals to within 1 m². We numbered and permanently marked shelter sites, and recorded location (GPS coordinates).

Assessment of shelter sites
We assessed shelter sites for vegetation density, height and structure. We measured vegetation density with a light meter (in lux) at 20 cm intervals of a 1 m profile (in duplicate) through the centre of the shelter site. We used an umbrella to shade the light meter from direct sunlight to enable assessment to occur in

Table 1. Trapping and radio-collaring site summary

<table>
<thead>
<tr>
<th>Location</th>
<th>Site</th>
<th>Area (ha)</th>
<th>Trap-nights summer</th>
<th>No. of captures</th>
<th>No. of collars fitted</th>
<th>Trap-nights winter</th>
<th>No. of captures</th>
<th>No. of collars fitted</th>
</tr>
</thead>
<tbody>
<tr>
<td>BNP</td>
<td>7–44B</td>
<td>2.40</td>
<td>960</td>
<td>18</td>
<td>4</td>
<td>3</td>
<td>480</td>
<td>10</td>
</tr>
<tr>
<td>BNP</td>
<td>7–1</td>
<td>2.05†</td>
<td>820</td>
<td>17</td>
<td>6</td>
<td>2</td>
<td>400</td>
<td>8</td>
</tr>
<tr>
<td>BNP</td>
<td>7–2</td>
<td>2.00</td>
<td>400</td>
<td>19</td>
<td>4</td>
<td>1</td>
<td>400</td>
<td>13</td>
</tr>
<tr>
<td>BNP</td>
<td>7–46</td>
<td>3.25†</td>
<td>1280</td>
<td>36</td>
<td>7</td>
<td>5</td>
<td>480</td>
<td>7</td>
</tr>
<tr>
<td>BNP</td>
<td>7–H</td>
<td>2.20†</td>
<td>880</td>
<td>20</td>
<td>5</td>
<td>3</td>
<td>400</td>
<td>5</td>
</tr>
<tr>
<td>JNP</td>
<td>7–ST1</td>
<td>2.50</td>
<td>500</td>
<td>7</td>
<td>3</td>
<td>2</td>
<td>500</td>
<td>11</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>14.40</td>
<td>4840</td>
<td>117</td>
<td>29</td>
<td>13</td>
<td>2660</td>
<td>54</td>
</tr>
</tbody>
</table>

Fig. 1. Location of study sites in Booderee and Jervis Bay national parks.
diffuse light conditions on any given day or time of day. We also recorded the maximum height of vegetation and the structure(s) providing the greatest cover. We searched shelter sites for the presence of a mouse-made nest structure. For each shelter site, we also assessed a control site using the identical procedure. We located control sites at a random compass bearing and a random distance between 2 and 20 m from a known shelter site.

Data analysis
We used paired t-tests to determine whether shelter sites differed from controls in vegetation density (estimated as mean lux at 0, 20, 40, 60, 80 and 100 cm), vegetation height and total structure(s) present. We used two-sample binomial tests (Collett 2002) to determine whether mice preferentially selected the presence of structures of different types. To identify effects of sex and/or season in the selection of shelter sites, we used linear mixed models (McCulloch et al. 2008) with the response variables being vegetation height and log-transformed standardised light intensity (as a surrogate for vegetation density, calculated as the proportion of light reaching the ground layer relative to what was available at 1 m). We fitted animal identifier and site as random terms to evaluate individual animal and site variation. We excluded control sites from this analysis.

Using control sites only, we investigated vegetation structure for its effect on standardised light intensity (where standardised light intensity approaching zero would approximate greater ‘cover’). We fitted all possible regression models and ranked them using the Schwarz information criterion (SIC) (Schwarz 1978). The candidate variables were the representative structural categories: Xanthorrhea, buttongrass, dead stems, shrub and no cover.

We considered a primary refuge to be one with a nest structure present. Mouse-made nest structures consisted of finely processed dried grass or sedge woven into either (i) a pad ~10 cm in diameter, or (ii) a sphere ~10 cm in diameter and height with an inconspicuous opening ~2 cm wide. We fitted generalised linear models (GLMs) (McCullagh and Nelder 1989) assuming a Bernoulli response with a logit link function for the probability of occurrence of a nest. The candidate predictors were sex, season, habitat attributes (vegetation density = log-transformed standardised light intensity, vegetation height and structure) and fidelity parameters (re-use, count of fixes standardised by number of radio-tracking days). We ranked all possible models using SIC.

Results
Trapping and radio-tracking
We attached radio-collars to 58 of the 140 individuals of eastern chestnut mouse that we captured. We summarised data on the number of mice captured and radio-collared at each site in each season (Table 1). On average, we tracked each animal 22 ± 1.53 times (mean ± s.e.) to diurnal shelter sites. The overall success rate of radio-tracking individuals for >20 consecutive fixes was 67% with the remaining animals tracked less intensively due to predation, radio-collar loss or signal failure.

Shelter site selection
We identified 453 unique shelter sites from 1300 tracking fixes. On average, each animal had 8 ± 0.5 shelter sites, spent 2.5 ± 0.1 days (total consecutive and non-consecutive fixes) in a shelter site and re-visited shelter sites 0.8 ± 0.1 times (defined as the number of times a mouse returned to a previously identified shelter site). Above ground nest structures were present in 15% of shelter sites. We did not locate any below ground burrow systems.

We found shelter sites had lower lux values (= more dense vegetation) up to 60 cm above the ground (Fig. 2) and taller vegetation with more structure compared with control sites (Table 2). The type of structure present also differed between shelter and control sites with Xanthorrhea, buttongrass and dead stems preferentially selected by the eastern chestnut mouse (Table 3). These structures were significant predictors of decreasing standardised light intensity when we analysed control site data separately (Table 4).

Table 1. Mean (±SE) number of success, test statistic and significance level for differences in height and total number of structures present between paired shelter and control sites

<table>
<thead>
<tr>
<th>Variate</th>
<th>Shelter mean (±SE)</th>
<th>Control mean (±SE)</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height (m)</td>
<td>0.869 ± 0.012</td>
<td>0.785 ± 0.013</td>
<td>4.99</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Total structures</td>
<td>1.589 ± 0.028</td>
<td>1.243 ± 0.023</td>
<td>10.43</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Table 2. Mean (±SE), t-statistics and significance levels for differences in height and total number of structures present between paired shelter and control sites

<table>
<thead>
<tr>
<th>Structure type</th>
<th>Shelter mean (±SE)</th>
<th>Control mean (±SE)</th>
<th>t-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Xanthorrhea</td>
<td>0.496 (±0.358)</td>
<td>0.211 (±0.087)</td>
<td>2.09</td>
<td>0.029</td>
</tr>
<tr>
<td>Buttongrass</td>
<td>0.068 (±0.058)</td>
<td>0.008 (±0.003)</td>
<td>2.12</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Dead stems</td>
<td>0.380 (±0.030)</td>
<td>0.257 (±0.017)</td>
<td>2.13</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Shrub</td>
<td>0.384 (±0.069)</td>
<td>0.696 (±0.213)</td>
<td>2.03</td>
<td>0.031</td>
</tr>
<tr>
<td>No cover</td>
<td>0.255 (±0.053)</td>
<td>0.458 (±0.040)</td>
<td>0.30</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

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Table 4. Multiple regression statistics for a test of the effect of type of structure on standardised light intensity. Analysis excluded shelter sites due to mouse-selection bias

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>s.e.</th>
<th>t-statistic</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-1.25</td>
<td>0.025</td>
<td>-49.98</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Xanthorrhoea</td>
<td>-0.39</td>
<td>0.047</td>
<td>-8.28</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Buttongrass</td>
<td>-1.08</td>
<td>0.205</td>
<td>-5.24</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Dead stems</td>
<td>-0.13</td>
<td>0.044</td>
<td>-2.91</td>
<td>0.004</td>
</tr>
</tbody>
</table>

Irrespective of individual animal and site variation, male and female mice did not differ in the standardised light intensity of sites they selected for sheltering but showed a tendency to choose sites with lower standardised light intensity during winter ($F_{1,88}=9.6$, $P=0.003$; Fig. 3). The height of shelter sites did not differ significantly between sexes or across seasons.

Refuge use and fidelity

We were able to predict a primary refuge (i.e. those scored present for a nest structure) based on log-transformed standardised light intensity and season (Table 5). We found primary refugia were characterised by vegetation that was denser than secondary shelters (i.e. mouse-selected shelter sites that did not have a nest structure present). This relationship was significant in the non-breeding season indicating mice preferentially chose to construct a nest in a shelter site if it comprised very dense vegetation (Table 5). During the breeding season, mice did not appear to be as selective and any given shelter site was equally likely to have a nest structure.

The eastern chestnut mouse was generally a solitary nester. We observed 1165 instances of solitary refuge use. We observed only very occasionally shelter site sharing and confirmed one record of cohabitation. The most common types of sharing we recorded were: (i) where two different mice used the same shelter site during different seasons (mice ‘inherited’ the shelter site from a previous occupant – 14 observations); or (ii) where two different mice used the same shelter site at different times during the same season of radio-tracking (sequential shelter site use – 14 observations; six in summer and nine in winter). We observed a male–female pair of radio-collared mice in the same shelter site on one occasion for 14 contiguous daily fixes during winter. This was the only record of cohabitation. We were unable to determine the genetic relationship (if any) between these two mice. We also recorded seven observations of long-term shelter site fidelity where the same individual was radio-tracked in multiple seasons and used the same shelter sites in both periods. This is potentially more common than recorded here due to the small number of mice we re-collared and radio-tracked during both seasons.

Discussion

Refuge site selection

Selection of appropriate refuge sites represents a substantial investment of time and energy by an animal. Animals spend periods of inactivity in these locations and shelter and raise their young in them. Therefore, the construction of nests and selection of refuge sites should afford the best protection from predation for both adults and offspring to maximise fitness (Stokes 1995). The eastern chestnut mouse preferentially selected refuge sites with particular habitat attributes. We found shelter sites were selected that had taller, denser vegetation compared with the surrounding habitat. Sites with multiple structures, such as Xanthorrhoea, Gymnoschoenus (buttongrass) and collapsed dead shrubs, were also often selected. We suggest these features have a combined effect in providing safety from trampling and predation, insulation against unfavourable climatic conditions, access to foraging areas and protection from aggressive interactions with competitors. For the eastern chestnut mouse, the selection of dense, protected areas for shelter may reflect competitor avoidance. Previous

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Figure 3. Log-scale standardised light intensity (sLI) of male and female eastern chestnut mouse shelter sites (±s.e.) selected during different seasons.

Table 5. Parameters for predicting the presence of a primary refuge. Season refers to the difference between summer breeding and winter non-breeding seasons

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>s.e.</th>
<th>Statistic</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-3.69</td>
<td>0.90</td>
<td>-4.09</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Log10 sLI</td>
<td>-0.634</td>
<td>0.39</td>
<td>-1.61</td>
<td>0.108</td>
</tr>
<tr>
<td>STD count of fixes</td>
<td>0.74</td>
<td>1.25</td>
<td>0.59</td>
<td>0.553</td>
</tr>
<tr>
<td>Season</td>
<td>-3.22</td>
<td>1.42</td>
<td>-2.27</td>
<td>0.023</td>
</tr>
<tr>
<td>Log10 sLI * season</td>
<td>-1.548</td>
<td>0.59</td>
<td>-2.60</td>
<td>0.009</td>
</tr>
<tr>
<td>STD count of fixes * season</td>
<td>3.58</td>
<td>1.86</td>
<td>1.93</td>
<td>0.054</td>
</tr>
</tbody>
</table>
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Refuge site selection by the eastern chestnut mouse

studies indicate competitive exclusion by the swamp rat (Rattus lutreolus) on eastern chestnut mouse access to food resources (Luo et al. 1994; Luo and Fox 1995) and preferred habitat (Higgs and Fox 1993; Morris et al. 2000). In our study, the swamp rat was absent from four of the six study sites. Refugia selected by the eastern chestnut mouse in the two sites where swamp rats were present were not consistently different from those selected in the sites where the swamp rat was absent. From the results of our study, it is impossible to determine the extent of competition for shelter. However, dense cover has been shown to be important for the swamp rat (Catling 1986; Haering and Fox 1995; Monamy and Fox 2000; Fox and Monamy 2007). The height of vegetation and areas of dense cover have been shown to be an important factor in the choice of refuge location for other terrestrial rodent species (Frank and Layne 1992; Stokes 1995; Gray et al. 1998; Wagner et al. 2000). The silky mouse’s (P. apodemoides) preference for low, dense vegetation and the availability of desert banksia (B. ornata) was considered a major influence on the distribution and location of refugia (Cockburn 1981a).

Refuge site use and fidelity

Daytime refuges can include both long-term shelter sites and temporary resting places (Wolff and Hurlbut 1982). Given the multiple functions of a refuge site, we expected to see a primary-secondary model of refuge use. Refuges offering the best protection are likely to be used most frequently and for long periods of time. The acquisition of refugia has a spatial element. To take advantage of dispersed food resources, animals might have many, less frequently used refuge sites (Ward 1978). We found evidence for hierarchical refuge selection. We considered the presence of a nesting structure to be indicative of a primary refuge. The number of days spent in a shelter and whether a shelter site was re-visited during the course of the study were not significant predictors of a primary refuge. However, we did find a seasonal effect, with the density of the vegetation in winter being the best predictor of whether a shelter site would be selected for building a nesting structure. Even though females produced litters during the breeding season, they were no more likely to build nesting structures than males. Any shelter site in the breeding season had an equal likelihood of being a primary refuge. We suggest this may be a result of (i) reproductive constraints including competition for mates, (ii) predator avoidance during the summer months, (iii) competition for foraging resources among females weaning litters, and (iv) an insufficient survey of breeding females because we did not attach radio-collars to visibly pregnant animals. Retaining primary refuge sites over winter is essential for animals to regulate against thermal extremes and ensure access to foraging resources while competing with other adult animals, sub-adults and juvenile offspring from the previous breeding season. Seasonality in shelter use site has been recorded for other rodent species (Madison et al. 1984; Wolton and Trowbridge 1985; Bubela and Happold 1993) and was attributed to environmental factors (i.e. shift in shelter site location dependent on ambient temperature (Madison et al. 1984)) and functionality (i.e. different refuges for weaning litters (Morzillo et al. 2003)) compared with refugia solely for sheltering.

Many mammals defend multiple, rarely occupied refuge sites (Happold 1976; Cockburn 1981a; Wolff and Hurlbutt 1982; Lindemayer et al. 1996; Hall and Morrison 1997; Moro and Morris 2000; Woods and Ford 2000; Morzillo et al. 2003; Sanecki et al. 2006; Hinkelman and Loeb 2007; Ebenesperger et al. 2008). Refuge fidelity and site attachment has links to social organisation and animal behaviour. The eastern chestnut mouse was transient in their refuge use. Our observations indicate the eastern chestnut mouse was most commonly a solitary nester. Solitary sheltering might reflect sparse food resource availability or a territorial social organisation (West and Dublin 1984; Ostfeld 1985). There was some evidence for sharing of refuge sites and long-term fidelity to particular sites. Long-term site fidelity is potentially more common than was possible to record in this study due to the small number of animals we re-collared during both seasons. The most commonly recorded instances of shelter site sharing were temporal segregation or inheritance of a shelter site from a previous occupant. There was only one record of a pair-bond and this was observed during winter. The benefits of refuge site fidelity and defence include: (i) highlighting ownership of, and defence of a shelter site against conspecifics; (ii) reduced parasite burden; (iii) avoiding predators learning patterns of emergence behaviour; and (iv) periodic change in foraging area utilised (Lindemayer et al. 1996). Familiarity with an area and a known location of proven shelter is probably crucial to survival when exploring unknown territory (Gray et al. 1998). Shelter site replacement (occupation by alternate animals) is not necessarily a random event (Haim and Rozenfeld 1995). We propose that shelter sites used by different individuals of the eastern chestnut mouse in different seasons may result from parent–offspring or sibling relationship between animals. Bonds resulting from genealogical relationships (parent–offspring and sibling bonds) are not uncommon for pseudomyine rodents (Happold 1976). The Silky mouse has been recorded from communal burrows in groups comprising a breeding pair with one or more litters of varying developmental stages (Cockburn 1981b). The Hastings River mouse (P. oralis) has high shelter site fidelity (Townley 2000) and there is some evidence to suggest offshore inherited the maternal range (S. Townley pers. comm.). Further research is needed to confirm if this is the case in the eastern chestnut mouse and it would be of interest to determine whether the relationship between animals is a significant determinant of spatial patterns in sheltering.

Prescribed burning practices

Fire management in areas supporting populations of the eastern chestnut mouse should ensure the retention of tall, dense vegetation and structural features in burnt landscapes. We speculate that as time since fire increases, eastern chestnut mouse shelter sites have the potential to become a limiting resource. Vegetation regeneration in heathland would result in a sparse ground layer and in the complete absence of fire we could expect fewer structural components to be available. That is: (i) the current collapsed shrub layer would decompose; (ii) although a long-lived, slow-growing species, the thatched, dead leaves of unburnt Xanthorrhoea would no longer provide
cover at ground level as plants grew taller (Gill and Ingwersen 1976); and (iii) woody species would dominate or eliminate herbaceous plants, increasing in biomass and height (Ingwersen 1977; Specht 1981; Keith et al. 2002). Conversely, immediately after a fire, it is also reasonable to expect shelter sites and refugia to be limiting, particularly following a high intensity burn. In contrast to other Pseudomys species (ash-grey mouse, P. albocinereus (Happold 1976), silky mouse (Cockburn 1981a), smoky mouse, P. fumeus (Woods and Ford 2000), New Holland mouse, P. novaehollandiae (Kemper 1981), and heath rat, P. shortridgei (Taylor and Horner 1972; Happold 1976)) and Fox (1995), we did not find the eastern chestnut mouse to use a below ground burrow complex. Burrows provide a more fire resilient shelter (Happold 1976; Kemper 1981; Friend 1993; Sutherland and Dickman 1999; Whelan et al. 2002). With the complete removal of above ground vegetation, the ability of refugial populations to survive in unburnt patches would be a critical factor affecting population persistence (Friend 1993; Whelan 1995). In a manipulative experiment designed to promote small mammal responses to a simulated fire, there was no effect of a reduction in cover on the eastern chestnut mouse (Fox et al. 2003). However, the spatial scale and structural effect of wildfire is likely to be different from that of experimental clipping, which, for instance, contained intact patches of vegetation within treatment plots (i.e. buttongrass). Further studies are necessary to determine whether the changes in vegetation regrowth after fire affect habitat preferences of shelter sites and refugia.

Assuming the occurrence of fire in heathland is important for retention of habitat features selected by the eastern chestnut mouse for refugia, appropriate timing of prescribed burning practices may be important. Within mouse-selected refuge sites, those with denser vegetative cover were used for over-wintering. These shelters were significantly more likely to have a nest structure present. The eastern chestnut mouse builds an above ground surface nest comprising dried sedge or grassy material woven into a pad or spherical structure. These are highly flammable refuges. Protection from fire by such a shelter would be limited and the likelihood of direct mortality by fire would be very high. The eastern chestnut mouse nest structure resembles that of the eastern bristle bird (Dasynornis brachypterus); a co-occurring heathland species, which has also been found absent immediately after wildfire from sites that were previously occupied (Lindemayer et al. 2009). The only other Pseudomys species known exclusively to build an above ground grass nest is the western chestnut mouse (P. nanus), which is also now extinct from the southern part of the species’ historical range and is rare or extinct throughout current distribution (Strahan 1995; Breed and Ford 2007). Management practices that allow burning during winter months would remove valuable primary refuge sites and may result in the post-fire residual eastern chestnut mouse population expending greater energy to re-establish over-wintering nesting structures at a cost of reduced foraging capacity.

Conclusions

The eastern chestnut mouse preferentially selects relatively taller, denser vegetation (up to 1 m) with structural features present at the ground layer for refuge. Refugia are highly flammable and do not provide protection from fire. These shelter site requirements have implications for land management and prescribed burning practices. There is some evidence for a primary–secondary model of refuge use. Primary refuge sites had a nesting structure present and were the more dense shelter sites selected by the eastern chestnut mouse. Any shelter had an equal likelihood of being a primary or secondary refuge during the summer breeding season but dense vegetation was the best predictor of a primary refuge for over-wintering animals. There are likely to be several reasons for this seasonal aspect of shelter site use including reproductive constraints and intra-specific competition for reproductive resources in the summer breeding season and environmental constraints including regulation against thermal extremes in the absence of huddling behaviour in winter. The maintenance of multiple, rarely occupied shelters is consistent with data for other mammals and is likely to be the result of territorial defence, access to dispersed resources and predator avoidance. The eastern chestnut mouse is mostly solitary in its sheltering habits but there is some evidence for short-term sharing, temporal segregation in the use of the same sites, or familial inheritance in the longer time frame.

Acknowledgements

We most gratefully acknowledge the Wreck Bay Aboriginal Community and the Wandandian People of the Dharkal and Dhurga language groups on whose lands this study was conducted. For valuable field assistance, advice and discussions, we thank Wendy Hartman, Alfred Wellington, Tony Carter, Geoff Kay, Steve Phillips, Marama Hopkins, Nick Dexter, Karen Viggers, Sally Townley, Les Mitchell and Martin Westgate. This research was funded by the Norman Wettenhall Foundation and the MA Ingram Trust and conducted under The Australian National University Animal Experimentation Ethics Committee protocol C.RE.49.08, NSW National Parks and Wildlife Service Scientific Licence S12690 and Booreree National Park Permit BDR08/00009.

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Rattus

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Wildlife Research

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Appendix 2

Manuscript:

Site occupancy of an early successional specialist

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Landscape, fire and habitat: which features of recently burned heathland influence site occupancy of an early successional specialist?

Felicia Pereoglou · Christopher MacGregor · Sam C. Banks · Jeff Wood · Fred Ford · David B. Lindenmayer

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Abstract
Context Multiple ecological drivers generate spatial patterns in species’ distributions. Changes to natural disturbance regimes can place early successional habitat specialists at an increased risk of extinction by altering landscape patterns of habitat suitability.

Objectives We developed a series of hypotheses to evaluate the effects of landscape structure, fire history, and site-level habitat quality on site occupancy by an early successional specialist, the eastern chestnut mouse (Pseudomys gracilicaudatus).

Methods We obtained eight years of monitoring data from 26 sites in recently burned heathland in southeast Australia. We used generalised linear models to determine which explanatory variables were related to occupancy. We also explored predictability in patterns of small mammal species co-occurrence.

Results Landscape structure (patch area, landscape heterogeneity) was strongly related to site occupancy. Site occupancy was associated with dead shrubs in the understory and rock cover on ground layer, but was not directly influenced by recent or historical fire. Contrary to contemporary ecological theory, we found no predictable species associations in our early successional community.

Conclusions We recommend surveys take account of landscape configuration and proximity to suitable habitat for optimal results. Fire regimes expected to promote eastern chestnut mouse population growth should encourage the retention of critical habitat features rather than be based on temporal rates of successional stages. For management to adequately account for post-disturbance patterns in early successional communities, a species-by-species, multi-scaled approach to research is necessary.

Keywords Fire · Succession · Heathland · Patch area · Landscape heterogeneity · Habitat specialist

Introduction
Early successional communities are the starting point for recovery after major disturbance. These communities are comprised of residual individuals, colonising opportunists and habitat specialist species (Connell
and Slatyer 1977; Swanson et al. 2011). Understanding the ecological processes operating in early successional communities is important, given these ephemeral habitats are confined to the variable length of time between a disturbance, and re-establishment of the later successional stages of community composition (Swanson et al. 2011). Estimating the duration of the early successional community is difficult as it is related to the type of ecosystem and is likely to fluctuate within ecosystems of the same type (Bradstock et al. 2012); for example, years for heathlands (Keith et al. 2002) compared to decades or even centuries in some forests (McCarthy et al. 1999). This time frame is likely to vary geographically (Velle and Vandvik 2014), and be dependent on the type and frequency of disturbance events (e.g. Sousa 1979; Delmoral and Bliss 1993; Rossi et al. 2007; Gill and Allan 2008).

Heathland communities often occur in the early successional stage of regeneration after disturbance. In Australia, heathlands are one of the most fire-prone and flammable ecosystems (Williams 1995; Keith et al. 2002). Following disturbance, these heathlands can accumulate sufficient plant biomass for fire ignition every 2 years (Williams 1995) and reach a mature to senescent phase after 25–50 years (Specht 1981). The compositional dynamics of heathland are primarily driven by the fire regime. High fire frequency (i.e. every 2 years) can reduce a heathland to a sedgeland by eliminating woody shrubs and allowing herbaceous species to dominate (Williams 1995). Long intervals between fires (i.e. greater than 20 years) will produce closed scrubs with diminished understory floristic richness (Williams 1995; Keith et al. 2002). Heathlands generally occur as patches of various sizes within a heterogeneous landscape (Williams 1995).

Fire occurs over multiple spatial and temporal scales, with variable impacts on biodiversity and key ecosystem processes that are strongly site- and species-specific (Pickett and White 1985; Turner et al. 1998; Whelan et al. 2002). For small mammals, patterns of population responses to fire have been studied over multiple decades (Newsome et al. 1975; Masters 1993; Letnic et al. 2013). Small mammals are associated with a range of fire frequencies; from high (e.g. heath rat (Pseudomys shortridgei), Cockburn et al. 1981; eastern chestnut mouse (P. gracilicaudatus), New Holland mouse (P. novahollandiae), Fox 1982) to low (e.g. desert mouse (P. desertor), Letnic and Dickman 2005; brown antechinus (Antechinus stuartii), bush rat (Rattus fuscipes), swamp rat (R. lutreolus), Lindenmayer et al. 2008a; silky mouse (P. apodemoides), Di Stefano et al. 2011). Changes to fire regimes can reduce habitat suitability for some species (e.g. Fox 1982; Baker et al. 2010).

Contingent upon a species’ location along the continuum, increased fire frequency may improve population viability. For early successional species, fire suppression can lead to population extinction through habitat degradation and impaired demographic processes (Hutto 2008; Templeton et al. 2011). For example, with the re-introduction of fire, Templeton et al. (2011) showed isolated patches could transition into a stable metapopulation with concomitant changes in the amount and patterns of animal movements across the landscape. Furthermore, fire-specialist fauna have been shown to occur with increasing likelihood as spatial proximity to fire, or fire severity increases (Hutto 2008), and have positive population growth rates in habitat created by fire (Rota et al. 2011). For early successional heathland specialists, the local physical conditions that are associated with their presence are likely to be in a continual state of change. The ability to reverse population declines for these species is complicated by the unpredictable, spatially and temporally variable nature of their habitats. However, whether fire plays a positive role in species occurrence and assists in maintaining habitat suitability in early successional communities is poorly understood.

Research across multiple spatial scales is necessary for identifying the processes underlying species’ responses in patchy and temporally-dynamic communities (Levin 1992; Thornton et al. 2011). Most theoretical and empirical research in disturbance ecology has focussed on site-level disturbance history (e.g. time since fire). However, multiple ecological drivers together generate spatial patterns in species’ distributions (Turner 2005). For instance, research in landscape ecology has a strong focus on landscape pattern variables such as patch size and landscape heterogeneity, as well as site-level habitat quality (Burel and Baudry 2003). Here, we tested the effects of landscape patterns on spatial processes by integrating fire history [sensu landscape legacy (Turner 2005) or ecological memory (Peterson 2002)], with classic landscape ecology themes of patch size and landscape
Appendix 2: Manuscript – Site occupancy

Pereoglou, F., Population processes in an early successional heathland heterogeneity, as well as community ecology themes of interspecific interactions. We investigated landscape patterns of habitat suitability across multiple spatial scales using a species described as an early successional specialist, the eastern chestnut mouse (*Pseudomys gracilicaudatus* Gould 1845). Specifically, we assessed a series of hypotheses relating to the perceived importance of fire history, landscape, community and site-level habitat features influencing site occupancy in an early successional heathland (Fig. 1).

**Hypothesis 1 (fire history)** We predicted occupancy was positively related to the distribution of the most recent fire, positively related to a high incidence of fires, and negatively related to the years since last fire (Fig. 1). Recent fire creates suitable habitat for early successional specialists (Monamy and Fox 2000). Therefore, with either a recent fire or an increased incidence of fire at a site, post-fire recruitment by residual survivors should offset the potential for local extinction.

**Hypothesis 2 (site-level habitat quality)** We predicted occupancy was positively related to understory floristic richness, the number of dead shrubs in the understory, and live vegetative cover on the ground layer (Fig. 1). The distribution of species after disturbance is dependent on the availability of suitable local habitats, and has been linked to shelter (Fox et al. 2003; Robinson et al. 2013), food (Luo and Fox 1996; Vieira and Briani 2013), and breeding resource requirements (Banks et al. 2005b; Watson et al. 2012). The floristic richness of early successional heathland provides a varied diet for an opportunistic generalist herbivore like the eastern chestnut mouse (Luo et al. 1994). Dense vegetation on the ground layer and a collapsed dead shrub layer are significant components of the species’ diurnal shelter requirements (Pereoglou et al. 2011).

**Hypothesis 3 (interspecific interactions)** We predicted eastern chestnut mouse site occupancy was negatively related to swamp rat (*Rattus lutreolus*) occurrence, but was not influenced by the occurrence of the bush rat (*R. fuscipes*) or brown antechinus (*Antechinus stuartii*) (Fig. 1). After a disturbance, species are added to the community assemblage when their specific habitat requirements are met (habitat accommodation model; Fox 1982). Species replacement is a result of subsequent competitive interactions that occur with time since fire or vegetation succession (Fox et al. 2003). The swamp rat is the only one of the co-occurring species that is similar to the eastern chestnut mouse in its resource requirements and has also been shown to be competitively superior (Higgs and Fox 1993).

**Hypothesis 4 (landscape context)** We predicted site occupancy was positively related to heathland patch area and negatively influenced by landscape

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**Fig. 1** Conceptual diagram showing the predicted effects of explanatory variables on eastern chestnut mouse site occupancy; black arrows indicate a positive effect, white arrows indicate a negative effect, grey arrows indicate no effect.
heterogeneity (Fig. 1). The probability of species occurrence in a habitat patch varies as a function of patch size (MacArthur and Wilson 1967) with a species’ area sensitivity being greater when the intervening matrix is inhospitable (Prugh et al. 2008). The eastern chestnut mouse is considered a heathland habitat specialist (Fox 1982) but there has been no study of how habitat availability and heterogeneity influences the species’ local distribution across a landscape.

Materials and methods

Study species

The eastern chestnut mouse is an endemic Australian murid rodent. It has a disjunct distribution along the east coast of Australia (inset Fig. 2) and is absent throughout much of its range. The species inhabits heathland in southern Australia and has been recorded in woodland in the northern parts of its range (Fox 2008). Usually reported at low density, populations peak in abundance post-fire before declining as vegetation regenerates (Fox 1982). Threats to the viability of populations of the species are thought to include fire suppression, loss of heath habitat, and predation (Fox 2008). A summarised description of the eastern chestnut mouse and the co-occurring small mammal species with which it is expected to have competitive interactions is provided (Table 1; a full version of species’ descriptions available in Appendix S1).

Study area and survey design

Booderee National Park is a ~6500 ha reserve located in the Jervis Bay region, approximately
200 km south of Sydney, Australia (Fig. 2). Booderee National Park is characterised by natural heterogeneity in vegetation with six broad vegetation types (forest, rainforest, woodland, heathland, shrubland and sedgeland) identified in previous vegetation surveys (Taws 1997) (Fig. 2).

Monitoring heathland sites (n = 26) began in 2003 as part of a long-term study on the effects of fire on vertebrate biota (see Lindenmayer et al. 2008a). Site monitoring was conducted annually during the summer months for the period 2003–2011. Sites comprised a single 100 m transect with: (i) a black plastic drift fence connecting 380 mm deep x 300 mm diameter pitfall traps at 0 and 20 m, 40 and 60 m, and 80 and 100 m; (ii) large wire cage traps (30 x 30 x 60 cm) placed at 0 m and 100 m with four small wire cage traps (20 x 20 x 50 cm) at 20 m intervals between; and (iii) ten aluminium box traps (Elliott Scientific Equipment, Australia) placed every 10 m along the transect line from 0 to 90 m (Fig. 3). We baited wire cage traps and aluminium box traps with rolled oats and peanut butter. Effort varied

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Table 1: Summarized description of the eastern chestnut mouse and co-occurring small mammal species

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat</th>
<th>Average adult weight (grams)</th>
<th>Mating system</th>
<th>Litter size</th>
<th>Breed in season of birth</th>
<th>Lifespan (years)</th>
<th>Diet</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Heathland</td>
<td>34 (male), 20 (female)</td>
<td>S</td>
<td>8–10 No</td>
<td>1 (male)</td>
<td>8–10</td>
<td>Insectivorous</td>
<td>Fox and Archer (1993), Crowther and Braithwaite (2002), Crowther, and Braithwaite (2008)</td>
</tr>
</tbody>
</table>

Fig. 3: Layout of a site transect and the location of vegetation plots. Diagram is not to scale.

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Pereoglou, F., Population processes in an early successional heathland
between sites and survey years, but on average, we opened traps for three consecutive nights each survey year. We checked all traps daily during the trapping period and recorded species, sex, age class, trap number and trap type. Animals were marked to identify recaptures within a single survey year trapping period before release at the point of capture.

Vegetation was sampled during the survey years of 2004/05, 2006/07, 2007/08, and 2009/10 in two 20 × 20 m plots located at the 20–40 m and 60–80 m sections of each transect (Fig. 3). We counted the number of dead shrubs (where a shrub was defined as single woody plant either multi-stemmed at the base or, if single stemmed, <2 m tall; dead shrubs, Table 2), the number of understory plant species present (floristic richness, Table 2), and visually estimated the understory (<2 m) percent live cover of all plant species combined (cover, Table 2). Values were averaged across the two vegetation plots. Percent rock cover, bare ground and regenerating shrubs in the ground layer were visually estimated in four 1 × 1 m sub-plots nested within the larger vegetation plot, values were averaged (Table 2).

Fire history data was extracted from GIS layers available for Booderee National Park using ArcGIS version 9.2 (ESRI 2009). At each site, for each survey year, we calculated the number of years elapsed since the last fire (years since fire, Table 2), and counted the number of fires affecting the site since fire mapping began in the mid-1950s (previous fires, Table 2). Sites were scored with a 0 or 1 to indicate whether they were burned in the most recent major fire in December 2003 (burned 2003, Table 2). 80 % of heathland sites were burned in the 2003 fire.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Mean</th>
<th>SE</th>
<th>Min</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>Survey year</td>
<td>2003–2010/11 (n = 9)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site</td>
<td>Unique site identifier (n = 26)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Effort</td>
<td>Total number of traps open × total number of nights traps were open</td>
<td>63.30</td>
<td>2.09</td>
<td>0</td>
<td>138</td>
</tr>
<tr>
<td>Species associations</td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Eastern chestnut mouse</td>
<td>Eastern chestnut mouse captures (new animals + recaptures)</td>
<td>0.63</td>
<td>0.11</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>Bush rat</td>
<td>Bush rat captures (new animals + recaptures)</td>
<td>2.78</td>
<td>0.28</td>
<td>0</td>
<td>24</td>
</tr>
<tr>
<td>Swamp rat</td>
<td>Swamp rat captures (new animals + recaptures)</td>
<td>0.45</td>
<td>0.10</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>Brown antechinus</td>
<td>Brown antechinus captures (new animals + recaptures)</td>
<td>1.89</td>
<td>0.16</td>
<td>0</td>
<td>11</td>
</tr>
<tr>
<td>Fire history</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Burned 2003</td>
<td>Site burned (1) or not (0) in the December 2003 fire</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of previous fires</td>
<td>Count of previous fires recorded at each site</td>
<td>4.54</td>
<td>0.12</td>
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<td>9</td>
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<tr>
<td>Years since fire</td>
<td>Number of years elapsed since the last fire at each site</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Site-level habitat quality</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dead shrub</td>
<td>Count of dead shrubs&lt;sup&gt;a&lt;/sup&gt;</td>
<td>28.10</td>
<td>3.25</td>
<td>0</td>
<td>270</td>
</tr>
<tr>
<td>Floristic richness</td>
<td>Number of understory species&lt;sup&gt;a&lt;/sup&gt;</td>
<td>13.09</td>
<td>0.46</td>
<td>4.5</td>
<td>26.50</td>
</tr>
<tr>
<td>Percent cover</td>
<td>Percent live cover of all understory species combined&lt;sup&gt;a&lt;/sup&gt;</td>
<td>85.44</td>
<td>1.79</td>
<td>15</td>
<td>100</td>
</tr>
<tr>
<td>Percent rock</td>
<td>Percent rock cover in ground layer&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.24</td>
<td>0.39</td>
<td>0</td>
<td>24.38</td>
</tr>
<tr>
<td>Percent bare</td>
<td>Percent cover of bare ground in ground layer&lt;sup&gt;b&lt;/sup&gt;</td>
<td>17.41</td>
<td>2.12</td>
<td>0</td>
<td>81.88</td>
</tr>
<tr>
<td>Percent regenerating vegetation</td>
<td>Percent cover of regenerating vegetation in ground layer&lt;sup&gt;b&lt;/sup&gt;</td>
<td>16.71</td>
<td>2.63</td>
<td>0</td>
<td>100</td>
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<tr>
<td>Landscape structure</td>
<td></td>
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</tr>
<tr>
<td>Patch area</td>
<td>Number of hectares of contiguous patch of vegetation of type i</td>
<td>88.59</td>
<td>8.74</td>
<td>0.93</td>
<td>362.20</td>
</tr>
<tr>
<td>Landscape heterogeneity</td>
<td>Number of vegetation types in 500 m radius of site</td>
<td>4.00</td>
<td>0.07</td>
<td>2</td>
<td>6</td>
</tr>
</tbody>
</table>

Summary statistics calculated for data pooled over sites and survey years
<sup>a</sup> Average of data measured in two 20 × 20 m plots
<sup>b</sup> Average of data measured in four 1 × 1 m subplots
Landscape structure was measured from GIS layers of the vegetation mapping of Taws (1997) available for Booderee National Park, using ArcGIS version 9.2 (ESRI 2009). As a measure of landscape heterogeneity, we determined the number of vegetation types within a polygon of 500 m radius around each site (landscape heterogeneity, Table 2). A 500 m radius was chosen because the closest sites were 1 km apart. We calculated the area of the mapped polygon of heathland within which a site was located (patch area, Table 2). Landscape heterogeneity and patch area were fixed for the study period.

Statistical analyses

We used Spearman’s rank correlation (Conover 1999) to identify redundant variables.

We explored the individual significance of the explanatory variables (Table 2; Fig. 1) using a series of univariate hierarchical generalised linear models (HGLMs; Lee et al. 2006) with an over-dispersed Poisson distribution and logarithm-link function. Our model response variable, site occupancy, was the total number of eastern chestnut mouse captures across trap nights at each site. We fitted each explanatory variable individually in separate models that included site as a random term to account for variation among sites, and survey year as a fixed effect (except where site occupancy was predicted by years since the last fire, survey year was fitted as a random term). We calculated effort as the total number of traps open at each site multiplied by the total number of nights that traps were open within a survey year and we included the log of effort as an offset variable to account for unequal survey effort between sites and survey years (Table S1).

To check for possible interrelationships between the effects of the explanatory variables, we also fitted generalized linear models (GLMs; McCullagh and Nelder 1989) for all possible subsets of the set of potential explanatory variables (Table 1; Fig. 1). We evaluated the fits using Schwarz information criterion (SIC; Schwarz 1978) and Akaike’s information criterion (AIC; Burnham and Anderson 2002). Complex fixed effects models are computationally much easier to fit using GLMs. Terms that did not contribute anything useful in the HGLMs might be retained, but it was very unlikely we would omit a term that was important. We also looked for an indirect effect of fire via other explanatory variables by testing whether the apparent effect of fire was removed when another explanatory variable was included in our models, and in turn fitting a model to test whether that variable was significantly affected by fire. Based on the explanatory variables identified in the GLM of all subsets and the univariate HGLMs, we then fitted a multivariate HGLM using the predictors from the ‘best’ model.

Finally, we fitted the captures of other small mammals (bush rat, swamp rat and brown antechinus) as dependent variables in a series of separate models to determine whether the eastern chestnut mouse responded differently compared to sympatric species in relation to fire history, landscape structure and site-level habitat quality.

Results

We completed a total of 14,812 trap nights and made 1346 captures (including 366 recaptures) of the eastern chestnut mouse and co-occurring terrestrial small mammal species.

Correlation between explanatory variables

We found a low level of correlation between explanatory variables (Table 3). Variable pairs with the highest levels of correlation included patch area and landscape heterogeneity, previous fires and landscape heterogeneity, years since last fire and burned 2003, and bush rat and effort. The landscape structure variables represented different effects and were not so highly correlated that inclusion together substantially reduced the reliability of the further modelling. The extent of the 2003 fire meant insufficient fire ages were available to model a time since fire effect on occupancy so we removed years since fire from further analysis and retained the binary variable.

Fire history

Although the eastern chestnut mouse was only observed on burned sites, the direct effect of burning in 2003 was not significant. This partly reflects the small number of heathland sites that were not burned in the most recent fire. Whether a site was burned in 2003 had a positive effect on eastern chestnut mouse site occupancy when the percent rock cover on the
Table 3  Correlation matrix showing Spearman’s rank correlation coefficients for explanatory variables

<table>
<thead>
<tr>
<th>Variable</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
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<th>13</th>
<th>14</th>
<th>15</th>
<th>16</th>
</tr>
</thead>
<tbody>
<tr>
<td>Effort</td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>Eastern chestnut mouse</td>
<td>-0.10</td>
<td>1</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Bush rat</td>
<td>0.59</td>
<td>-0.18</td>
<td>1</td>
<td></td>
<td></td>
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<td>Brown antechinus</td>
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<tr>
<td>Burned 2003</td>
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<td>-0.29</td>
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<td>Number of previous fires</td>
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<td>0.01</td>
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<td>Dead shrub</td>
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<td>-0.10</td>
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<td>Percent cover</td>
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<td>-0.07</td>
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<td>Percent bare</td>
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<td>0.08</td>
<td>-0.12</td>
<td>0.05</td>
<td>-0.03</td>
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<td>Percent regenerating vegetation</td>
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<td>-0.15</td>
<td>-0.04</td>
<td>-0.02</td>
<td>0.10</td>
<td>0.19</td>
<td>-0.29</td>
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<td>Landscape heterogeneity</td>
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<td>0.10</td>
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<td>-0.32</td>
<td>-0.67</td>
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</table>

Correlated variables ± >0.5 are bold
Appendix 2: Manuscript – Site occupancy

Table 4  Ten best generalized linear models from fitting all possible subsets of explanatory variables

<table>
<thead>
<tr>
<th>ΔSIC</th>
<th>ΔAIC</th>
<th>Model terms</th>
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<tr>
<td>0</td>
<td>1.22</td>
<td>Survey year + percent rock + burned 2003</td>
</tr>
<tr>
<td>1.37</td>
<td>0</td>
<td>Dead shrub + survey year + percent rock + burned 2003</td>
</tr>
<tr>
<td>2.44</td>
<td>1.07</td>
<td>Survey year + percent regenerating vegetation + percent rock + burned 2003</td>
</tr>
<tr>
<td>3.17</td>
<td>1.80</td>
<td>Survey year + percent rock + percent bare + burned 2003</td>
</tr>
<tr>
<td>3.84</td>
<td>2.47</td>
<td>Survey year + percent cover + percent rock + burned 2003</td>
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<tr>
<td>4.09</td>
<td>2.72</td>
<td>Survey year + floristic richness + percent rock + burned 2003</td>
</tr>
<tr>
<td>4.16</td>
<td>2.79</td>
<td>Survey year + percent rock + brown antechinus + burned 2003</td>
</tr>
<tr>
<td>4.40</td>
<td>3.03</td>
<td>Survey year + percent rock + patch area + burned 2003</td>
</tr>
<tr>
<td>4.41</td>
<td>3.04</td>
<td>Survey year + percent rock + bush rat + burned 2003</td>
</tr>
<tr>
<td>4.45</td>
<td>3.08</td>
<td>Survey year + percent rock + burned 2003 + landscape heterogeneity</td>
</tr>
</tbody>
</table>

ΔSIC and ΔAIC are the differences in SIC and AIC for the given models from the value for the optimal model.

Fig. 4  Conceptual diagram showing the modelled effects of explanatory variables on eastern chestnut mouse site occupancy; black arrows indicate a positive effect, white arrows indicate a negative effect, broken line represents indirect effect.

The number of dead shrubs in the understory had a weak positive effect on eastern chestnut mouse site occupancy (Fig. 4). An exponential increase in the number of dead shrubs in the understorey was associated with a small increase in eastern chestnut mouse captures per 100 trap nights (Fig. 5a). As an indirect effect of fire, we found the number of dead shrubs significantly increased with burning in 2003. Percent rock cover on the ground layer positively influenced eastern chestnut mouse site occupancy in burned sites (Table 4). Understory floristic richness and percent cover did not affect eastern chestnut mouse site occupancy, nor did the percent bare ground or regenerating shrubs in the ground layer. We accepted $H_2$, habitat features of the understory and ground layer influence eastern chestnut mouse site occupancy (Table S2; Fig. 4).
Species associations

We found a negative effect of bush rat abundance on eastern chestnut mouse site occupancy (Fig. 4). There was no significant influence of swamp rat or brown antechinus abundance on eastern chestnut mouse site occupancy. When we included the occurrence of the bush rat, swamp rat and brown antechinus as fixed terms in a model together, no species had a significant influence on eastern chestnut mouse site occupancy (Table S2). Hence, $H_3$ was rejected, as co-occurring small mammal species did not influence eastern chestnut mouse site occupancy as predicted (Table S2; Fig. 4).

We found direct effects of fire history and landscape structure for the sympatric small mammal species. Burning in the 2003 fire had a strong negative effect on both swamp rat and brown antechinus site occupancy estimates (Table S2). A weak negative effect of patch area on brown antechinus and swamp rat site occupancy indicates a potential sensitivity to landscape heterogeneity (Table S2).

Landscape structure

Landscape heterogeneity had a strong negative effect on eastern chestnut mouse site occupancy (Fig. 4), with the number of captures per 100 trap nights decreasing significantly as habitat diversity increased (Fig. 5b). To a lesser extent, eastern chestnut mouse site occupancy was affected by patch area (Fig. 5c). Hence, we accepted $H_4$, landscape structure affected eastern chestnut mouse site occupancy (Table S2; Fig. 4).

‘Best’ model for predicting eastern chestnut mouse site occupancy

When significant explanatory variables determined from the univariate HGLMs and all subsets regression were included in a single model, burned 2003 and percent rock cover were the only variables whose coefficients were not significantly different from zero (Table 5).
Discussion

Importance of landscape structure versus site-level habitat selection

Our study tested the importance of key themes of ecological theory from disturbance ecology (site-level disturbance history), landscape ecology (site-level habitat quality and landscape patterns) and community ecology (interspecific interactions) on the distribution of an early successional species in a fire-prone environment. A key finding from our study was that site occupancy was strongly influenced by landscape (i.e. broad-scale landscape structure, hypothesis 4), and to a lesser extent, elements within the landscape (i.e. resource availability at a site-level, hypothesis 2) (Fig. 4). Large heathland habitat patches, a less heterogeneous intervening habitat matrix, and the presence of dead shrubs indicated a greater likelihood of sites being occupied by the eastern chestnut mouse. This reflects the species’ known shelter resource requirements and presumed habitat specialisation.

The basic principle of landscape ecology is that the spatial organization of the environment controls ecological processes (Burel and Baudry 2003). Species respond to patch-level variables because they are important predictors of distribution and abundance (Prugh et al. 2008; Thornton et al. 2011). Habitat specialists that inhabit patchy terrestrial landscapes could be expected to occur predominantly in large habitat patches of the preferred vegetation type and this was the case in our study. Large habitat patches can support higher rates of occupancy compared to smaller ones for species in disturbed landscapes (Thomas et al. 1992; Banks et al. 2005a). For early successional species, large habitat patches may facilitate post-fire population recovery as a result of both population expansion from within the fire boundary (Banks et al. 2011) and colonisation of individuals from outside the fire boundary (Watson et al. 2012).

Properties of the matrix surrounding habitat patches are also important (Prugh et al. 2008). The surrounding landscape influences patch dynamics and the networks of exchange that exist between habitat patches, facilitating the processes of recolonization (Pickett and White 1985; Burel and Baudry 2003). Therefore, species in isolated patches should have a lower probability of persistence (Turner 1989). In our study, patches were less likely to be occupied as landscape heterogeneity increased. Movement through peripheral habitat can result in direct mortality through predation, or indirectly influence survival through increased competition for sub-optimal resources (Higgs and Fox 1993; Chesson 2000). As other vegetation communities replace heathland, or late seral stage heath replaces early successional communities, species that track suitable environmental conditions may become locally extinct (Templeton et al. 2011). For example, to avoid eastern chestnut mouse extinction, early successional heathland would need to become available close to an extant local population or alternatively, fire itself would need to improve conditions suitable for dispersal (e.g. Templeton et al. 2011; Banks et al. 2013). Analysis of eastern chestnut mouse genetic data supports the latter proposal that recently burned vegetation has greater conductance for gene flow than unburnt habitat (Pereoglou et al. 2013). The interaction between dispersal processes and landscape pattern influences the temporal dynamics of populations (Turner 1989).

The capacity of individuals of a population to leave one patch to colonize another similar patch is an essential process of landscape dynamics after disturbance (Burel and Baudry 2003). Conservation must emphasise management of existing habitats and creation of new habitats within colonising distance (Thomas 1994).

Species distribution and abundance patterns are influenced by fine-scale features of the environment with which they interact most directly (Thornton et al. 2011). Within-patch habitat attributes such as dead shrubs were important predictors of site occupancy and were positively associated with the most recent major wildfire (Fig. 4). This demonstrates that site occupancy of early successional specialists can be facilitated indirectly through the role of fire in creating or maintaining critical habitat features and is indicative of the eastern chestnut mouse preference for sheltering in the collapsed dead shrub layer in recently burned heath (Pereoglou et al. 2011). Habitat features expected to provide shelter have been correlated with animal density for other Pseudonys species—e.g. Xanthorrhoea skirt for the heath rat P. shortridgei (Di Stefano et al. 2011), presence of Banksia ornata shrubs for the silky mouse P. apodemoides (Cockburn 1981), and rock cover for the Hastings river mouse P. oralis (Townley 2000). Rock cover was also identified in our modelling as an influence on eastern chestnut

Pereoglou, F., Population processes in an early successional heathland
mouse occupancy. However, unlike the Hastings river mouse, rock crevasses have not previously been identified as a shelter resource or a preferred micro-habitat, so the reasons for this result remain unclear. The variable rock cover may be confounded with fire history because sites that were not burnt in the 2003 fire had no rock cover.

The level of floristic and structural complexity in regenerating communities has been linked to small mammal species assemblages, and underpins assumptions on species occurrence in successional ecosystems (Catling 1991; Masters 1993; Monamy and Fox 2010). In our study, floristic richness as well as the amount and type of cover were not significant predictors of eastern chestnut mouse site occupancy (Fig. 4). Our result is consistent with other investigations, which have uncovered strong species- and site-specific variation in habitat preferences (see also Cockburn 1978; Di Stefano et al. 2011).

Fire history as a predictor of site occupancy for an early successional specialist

Natural disturbances leave legacies that persist for decades to centuries and integrating this history with current understanding of landscape patterns and processes remains an important goal of landscape ecology (Turner 2005). A key finding of this study was that eastern chestnut mouse site occupancy was not directly affected by fire history (hypothesis 1) (Fig. 4). Potential explanations for an absence of direct fire history effects are two-fold. First, by comparison with the common co-occurring small mammal species which showed negative responses to fire, the ability to endure disturbance seems to be a necessary trait amongst habitat specialists (Hutto 2008). In another study, where researchers experimentally simulated the effects of fire, populations of the eastern chestnut mouse were also unaffected (Fox et al. 2003). Individuals of the eastern chestnut mouse that survive after fire could be considered ‘biological legacies’ (sensu Franklin et al. 2000). In another investigation in our study region, eastern bristlebirds (Dasyornis brachypterus) that persisted in burned sites also were considered to be survivors of a pre-fire fauna (Lindenmayer et al. 2009).

Secondly, the effects of fire history were either captured by, or confounded with other variables. Eighty percent of heathland sites were burned in the 2003 fire, and it is possible that fire history and vegetation type were confounding one another in our analyses. Research that replicates equal numbers of burned and unburned heathland sites may show a different result. We have shown fire to indirectly affect eastern chestnut mouse site occupancy by creating critical habitat features used for diurnal refugia. Therefore, the effects of fire may have been captured entirely by the variable dead shrub. Finally, we may simply not have measured enough fire attributes to model in our analyses. For example, fire regimes are possibly more important than fire history in predicting species occurrence and we were unable to distinguish the relative effects of fire frequency, season and severity (Whelan 1995; Keith et al. 2002).

Species interactions and the habitat accommodation model

The habitat accommodation model (Fox 1982) has been shown to be a poor predictor of ecological patterns in relation to fire in other systems (Letnic et al. 2004; Driscoll and Henderson 2008; Di Stefano et al. 2011). The absence of predictable sympatric small mammal species effects on eastern chestnut mouse site occupancy (Fig. 4) suggested competitive exclusion was not the strongest biological mechanism structuring the small mammal community as predicted in a mammalian secondary succession (Fox 1982). There was some indication that site occupancy of the eastern chestnut mouse increased in the absence of the bush rat but this effect disappeared when all co-occurring species were modelled together. In other studies, the departure from theoretical predictions has been attributed to various processes including the absence of competitors (Catling 1986; Di Stefano et al. 2011), rapid recovery of vegetation (Lindenmayer et al. 2008b, 2009) and correlation with alternative explanatory variables (Letnic et al. 2004; Driscoll and Henderson 2008). However, in situ survival of individuals during a fire event probably has a greater influence on population persistence after fire (Lindenmayer et al. 2005; Banks et al. 2011) compared to relative thresholds of habitat suitability. Therefore, it seems unrealistic to expect theoretical models to accurately forecast species assemblages, as they are likely to vary with the complexities of disturbance regimes, spatial patterns of landscape continuity, site-level habitat features, and the interactions among these factors.
Conclusions

Our study evaluates the effects of disturbance, spatial patterns of landscape structure and site-level habitat features on species occupancy in an early successional community. We found a positive effect of heathland patch area and a negative effect of landscape heterogeneity on site occupancy by the eastern chestnut mouse. Eastern chestnut mouse site occupancy also was associated with habitat features, such as a collapsed dead shrub layer, that may be created by burning. We found recent fire and the effect of multiple fires per se did not have a strong influence on eastern chestnut mouse site occupancy. We recommend surveys targeting the species take account of landscape configuration for optimal results. Furthermore, fire regimes expected to promote eastern chestnut mouse population growth should encourage the retention of critical habitat features rather than be based entirely on temporal rates of successional stages. We confirmed the general importance of the multi-level approach to landscape ecology studies, as our study species responded to landscape, patch, and within-patch variables (Thornton et al. 2011). Our work suggests that a multi-scaled approach to investigations of site occupancy should be taken to ensure species- and site-specific resource requirements are identified and that the impacts of changes to disturbance regimes on these resources can be effectively evaluated.

Acknowledgments

We most gratefully acknowledge the Wreck Bay Aboriginal Community and the Wandanian People of the Dharawal and Dhurga language groups on whose lands this study was conducted. Mason Crane, Damien Michael, Rebecca Montague-Drake, and Sachiko Okada provided fieldwork assistance. This project is part of a major study in Booderee National Park funded by the Australian Research Council, the Department of Environment and Water Resources and the Department of Defence.

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Appendix 3

Manuscript:

Landscape genetics in a disturbance-prone environment

Published, March 2013
Landscape genetics of an early successional specialist in a disturbance-prone environment

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Abstract

Species that specialize in disturbed habitats may have considerably different dispersal strategies than those adapted to more stable environments. However, little is known of the dispersal patterns and population structure of such species. This information is important for conservation because many postfire specialists are at risk from anthropogenic changes to natural disturbance regimes. We used microsatellite markers to assess the effect of landscape variation and recent disturbance history on dispersal by a small mammal species that occupies the early seral stage of vegetation regeneration in burnt environments. We predicted that a postfire specialist would be able to disperse over multiple habitat types (generalist) and not exhibit sex-biased dispersal, as such strategies should enable effective colonization of spatially and temporally variable habitat. We found significant differentiation between sites that fitted an isolation-by-distance pattern and spatial autocorrelation of multilocus genotypes to a distance of 2–3 km. There was no consistent genetic evidence for sex-biased dispersal. We tested the influence of different habitat- and fire-specific landscape resistance scenarios on genetic distance between individuals and found a significant effect of fire. Our genetic data supported recently burned vegetation having greater conductance for gene flow than unburnt habitat, but variation in habitat quality between vegetation types and occupied patches had no effect on gene flow. Postfire specialists must evolve an effective dispersal ability to move over distances that would ensure access to early successional stage vegetation. Natural disturbance and natural heterogeneity may therefore not influence population genetic structure as negatively as expected.

Keywords: dispersal, fire, habitat heterogeneity, landscape resistance

Received 6 July 2011; revision received 20 October 2012; accepted 4 November 2012

Introduction

Dispersal behaviour and landscape configuration are primary determinants of population genetic structure (Bowler & Benton 2005; Baguette & Van Dyck 2007). The landscape matrix can facilitate or impede movement of organisms between populations (Taylor et al. 1993; Lindenmayer & Fischer 2006; Fahrig 2007) with dispersal behaviour influencing spatial patterns in abundance (Fahrig & Paloheimo 1988) and habitat selection (Morris 1992). Recently, landscape genetics research has contributed to our understanding of population connectivity in relation to landscape elements (Manel et al. 2003; Storfer et al. 2010). However, threatened species with habitat preferences for disturbed environments are not well represented in the population genetics literature. The ecological requirements of these specialist species suggest that their patterns of dispersal and demography differ considerably from species that utilize more stable environments and that this is likely to be revealed in patterns of genetic diversity and structure.
In conjunction with landscape data, spatial genetic information can identify habitat variables that maintain connectivity among populations or serve as barriers to animal movements (Scribner et al. 2005). Current research on landscape connectivity has focussed on the influence of ‘habitat breaks’ (i.e. anthropogenic landscape fragmentation; Gauffre et al. 2008; Macqueen et al. 2008; Spear & Storfer 2008; Pavlacky et al. 2009), natural barriers (e.g. rivers, mountains and topography; Spear et al. 2005; Murphy et al. 2010) or a combination of both (Cushman et al. 2006; Perez-Espona et al. 2008; Short Bull et al. 2011). There is limited information on the effect of natural disturbance such as wildfire, naturally heterogeneous landscapes or natural variation in habitat suitability on patterns of genetic diversity, population structure and gene flow.

Fire is a major form of natural disturbance (Turner et al. 1998). Different fire regimes produce distinct landscape patterns and species arrays (Bond & Keeley 2005). Population recovery and persistence in postfire environments are influenced by fire regimes and their effects on landscape features including patch isolation and connectivity (Clarke 2008). With altered fire regimes and increased fire occurrence being a likely impact of climate change (Williams et al. 2001; Flannigan et al. 2008; Steffen et al. 2009), our understanding of how fire events influence biota is a critical contemporary environmental issue. Fire playing a positive role in maintaining habitat suitability is an effect that is plausible for postfire specialist fauna and those that colonize early successional ecosystems, but one that is not well studied.

In this study, we examined the population genetic structure of the eastern chestnut mouse (Pseudomys gracilicaudatus Gould 1845), a threatened small mammal endemic to the east coast of Australia and dependent on regular fire. We addressed a series of hypotheses relating to the dispersal strategy of a postdisturbance specialist mammal, including the following:

1 Fire/burned areas will promote gene flow. Several studies have shown that fire affects genetic structure through environmental changes that cause demographic variation such as population expansion (including colonization) or decline and variation in connectivity (Templeton et al. 2001; Schrey et al. 2010, 2011; Templeton et al. 2011). For species that specialize in early seral stage, postdisturbance habitats, we expect a reduction in genetic structure in recently burned areas. This is because fire increases the area of suitable habitat, so small and relatively isolated prefire populations will expand and individuals will disperse to colonize newly suitable habitat. Population expansion, increased connectivity between existing populations and colonization of new areas (particularly with a large number of colonists) are expected to weaken genetic structure (Wade & McCauley 1988; Templeton et al. 2001; Excoffier et al. 2009). Our prediction may be incorrect if the number of individuals colonizing newly suitable habitat after fire is very small and ongoing migration in subsequent generations is rare (Wade & McCauley 1988). However, our hypothesis was that the former prediction would hold.

2 Natural habitat heterogeneity will not restrict gene flow. Habitat suitability has been considered as a correlate of ‘conductance’ to dispersal across a landscape, on the assumption that environmental types that rank poorly by occupancy or abundance criteria will also be poor for dispersal (Wang et al. 2008; Spear et al. 2010). The eastern chestnut mouse has a naturally patchy distribution within our study area due to very specific requirements for vegetation type and fire history (Pereoglou et al. 2011). Habitat suitability is thus spatially patchy and temporally dynamic. We predicted that an effective dispersal strategy to access and colonize suitable habitat under such dynamic environmental conditions would be one in which dispersal is possible across all landscape types and is not restricted by perceived habitat preferences.

3 Dispersal will not be strongly sex biased. Male-biased dispersal is common among mammals (Greenwood 1980) and occurs in other small mammal species that occur in our study area, including the brown antechinus (Antechinus stuartii) and the bush rat (Rattus fuscipes; Cockburn et al. 1985; Peakall et al. 2003). However, we predicted a lack of strong sex bias in dispersal for an early seral specialist. Modelling suggests that strong sex-biased dispersal is not favoured under high demographic stochasticity (Gros et al. 2008). After fire, dispersal by eastern chestnut mice is likely to be associated with colonization of newly suitable habitat, and greater colonization ability by males compared with females would be disadvantageous in that it would increase the likelihood of settling in unoccupied habitat with no potential mates.

Methods

Study species

Pseudomyine rodents provide some of the best examples of fire specialist fauna (Catling & Newsome 1981) due to their rapid establishment and early breeding after fire, rapid population increase and ability to maintain viable breeding populations from first colonization.
The eastern chestnut mouse is an early seral specialist that colonizes heathland habitat, peaking in abundance postfire before declining over time as vegetation regenerates (Fox 1982; Monamy & Fox 2000; Fox et al. 2003). It has a disjunct distribution along the east coast of Australia and occurs at low density throughout much of its range. The species was considered extinct in southern Australia until 2002 when it was discovered in the Jervis Bay region (Meek & Triggs 1997). This area now supports the only contemporary population of the eastern chestnut mouse south of Gosford, New South Wales (33°23′S, 151°18′E) and is arguably the most isolated population of the species in eastern Australia.

The eastern chestnut mouse is an annual summer breeder capable of producing multiple litters of one to five (usually three) offspring (Fox 2008). The species lives for <2 years in wild populations (Watts & Kemper 1989). Early development is rapid, which contrasts with a slow growth rate to reach maturity (Fox & Kemper 1982). Adults show significant sexual dimorphism (Fox & Kemper 1982) and attain average weights of 90 g for males and 75 g for females (Fox 2008). Little is known about social organization and behaviour in this species.

Radio-tracking data suggest that adult eastern chestnut mice are solitary, territorial and maintain female home ranges of 0.5–1 ha and up to 4 ha for males (F. Pereoglou unpublished data).

**Study area and sampling**

We collected tissue from 26 sites surveyed between 2008 and 2010 in Booderee National Park, located approximately 200 km south of Sydney, Australia (Fig. 1). We genotyped 287 individual animals, and sample sizes ranged from 1 to 58 mice per site (Fig. 1). We used two approaches to survey the study area. Initial site selection was randomly stratified by vegetation type and consisted of a single 100-m transect. Each transect comprised the following: (i) a black plastic drift fence connecting 380 mm deep × 300 mm diameter pitfall traps at 0–20, 40–60 and 80–100 m; (ii) large wire cage traps (30 × 30 × 60 cm) placed at 0 and 100 m with four small wire cage traps (20 × 20 × 50 cm) at 20 m intervals between; and (iii) ten aluminium box traps (Elliot Scientific Equipment, Australia) placed every 10 m along the transect line from 0 to 90 m. Data on the number of transects in each vegetation type, the number with eastern chestnut mouse captured and the corresponding occupancy estimates are given in Table S1 (Supporting information). We then chose five transects and selected an additional four sites for intensive grid trapping to sample sufficiently high densities of the eastern chestnut mouse to allow for population genetic analyses. We classified all grid sites as dry heath (Taws 1997), and each had been burned by wildfire in December 2003. Our grid arrangement comprised lines at 20 m intervals with traps 10 m apart covering an area ranging from 1 to 3 ha (1.9 ± 0.19 ha). Transect sites were surveyed annually during the eastern chestnut mouse breeding season (November–February), and grid sites were surveyed twice each year, during the breeding season and also during the nonbreeding season (June–August). We opened traps for three or four consecutive nights (31 548 trap nights in total) and baited with rolled oats, peanut butter and fennel seed. We assessed captured animals for weight, sex, age cohort

![Study area and distribution of survey sites. Solid symbol indicates site with eastern chestnut mouse presence, and the number of genotyped individuals is provided above symbol. Hollow symbol indicate sites with no eastern chestnut mouse captures.](image-url)
and breeding condition and collected a 2-mm ear biopsy that is stored in 100% ethanol.

**DNA extraction, PCR amplification and genotyping**

We extracted DNA from ear tissue using the method of (Bruford et al. 1988) and re-suspended the DNA pellet in 100 μL of TE buffer (10 mM Tris and 0.1 mM EDTA). We genotyped samples at 10 microsatellite loci (Moro & Spencer 2003; Table S2, Supporting information). Microsatellite PCRs with a total volume of 30 μL contained 10× buffer (Qiagen), 200 μM dNTPs, 1.8 mM MgCl₂, 0.5 μL BSA, 4 pmoles reverse primer, 1.5 pmoles forward-tailed primer, 2.5 pmoles fluorescent end-labelled M13 primer sequence (Schuelke 2000), 0.2 units Taq polymerase (Qiagen) and 1.5 μL template DNA. We ran all reactions on a thermal cycler (Applied Biosystems Inc.) with initial denaturation of 94–95 °C for 3 min, then cycled using PCR conditions described in Table S2 (Supporting information), followed by a final extension step of 72 °C for 10 min. We ran the PCR products on an ABI 3130 (Applied Biosystems Inc.) automated sequencer with the LIZ 500 size standard. We ran negative controls in PCRs and in each sequencer run to check for contamination. We used GeneMapper version 3.7 (Applied Biosystems Inc.) to score each locus for each sample.

**Genetic data analysis**

We used the genotype matching function of MSTools (Park 2001) to identify identical genotypes. Duplicate genotypes were re-labelled if the corresponding capture records were consistent with multiple captures and samples from the same individual (e.g. due to temporary marking or tag loss). We ran analyses separately for each survey year. Survey years included a 12-month period from the beginning of the eastern chestnut mouse breeding season in September to August of the following year (September–August 2008–2009 and September–August 2009–2010).

**Population genetic summary statistics.** We excluded locations from the population-level analyses if sites had <10 individuals genotyped. We calculated standard population genetic summary statistics for all loci and sites including the number of alleles, observed and expected heterozygosities and \( F_S \) using GENEALEx version 6.3 (Peakall & Smouse 2006). We tested for departures from Hardy–Weinberg (H–W) equilibrium using FSTAT (Goudet 2001).

**Population subdivision and isolation by distance (IBD).** We used AMOVA to estimate population subdivision and calculated pairwise values of \( F_{ST} \) for all sites where sample sizes were >10 individuals. We used Mantel tests to test for isolation by distance on pairwise \( F_{ST} \) between sites (\( F_{ST}/1 - F_{ST} \) vs. log geographic distance). Unless otherwise stated, all permutational tests were performed 999 times, and analyses were completed using GENALEX.

To further investigate the spatial pattern of genetic structure, we calculated the spatial autocorrelation (\( r \)) of pairwise multilocus genetic distances (GD) over a set of geographic distance classes (Smouse & Peakall 1999). We calculated pairwise multilocus GD according to the methods of Smouse & Peakall (1999) and tested the null hypothesis of no spatial genetic pattern (\( r = 0 \)) against the alternative that spatial autocorrelation was positive at some distances and negative at others (\( r \neq 0 \)). For each survey year (2008–2009 \( n = 172 \), 2009–2010 \( n = 141 \)), we ran two different analyses. In the first analysis, we selected 500-m distance classes up to 5 km. The second was a finer-scaled analysis, where we investigated spatial autocorrelation at 50-m intervals up to 250 m (i.e. fine-scale structure within sampling sites). The choice of distance classes primarily relates to our sampling scheme, where the first (coarse-scaled) distance classes were larger than our sampling sites, so we were testing differences between spatial autocorrelation among individuals within sites (0–500 m) and at increasing distances between sites. The finer-scaled analysis focussed on testing for spatial clustering of similar genotypes within the scale of our sampling grids. We used 999 permutations with a bootstrap re-sampling procedure run 1000 times to estimate the 95% confidence interval.

We used the programs Structure version 2.3 (Pritchard et al. 2000) and GENELAND version 3.2.4 (Guillot et al. 2005) to complement our other analyses of population structure with the specific aim of testing whether our samples could be clustered into spatially discrete subpopulations (parameters in Appendix S1, Supporting information).

We used the program GSTe v2 (Foll & Gaggiotti 2006) to estimate effects of landscape variables on population-specific \( F_{ST} \). For this analysis, we restricted data set to nine sites with the greatest sample sizes, from which a mean of 28 individuals was sampled (SD = 16). All of these sites were within areas burnt in 2003, so we were unable to test for effects of fire history. However, we tested for effects of vegetation heterogeneity with variables representing the proportion of heath (the most preferred vegetation type) within 200 and 500 m buffers, as well as sample size (as a proxy for local population density) and \( X \) and \( Y \) coordinates to test for broad spatial gradients in the strength of genetic structure (e.g. an east–west peninsula effect). For this
analyses, we pooled individuals from both years within the same sites. Many individuals were sampled in both years, and previous analyses showed no major differences in the patterns detected in either year.

**Sex-biased dispersal.** To test the hypothesis that genetic structure and corresponding philopatry are not sex biased, we used two approaches. First, we used the heterogeneity test of Smouse et al. (2008) to compare the spatial autocorrelation $r$-values of males and females. We assessed spatial autocorrelation at two scales: 500-m distance classes up to 5-km and 50-m distance classes up to 250 m. If there was a sex bias, for the philopatric sex we expected declining correlations of $r$-values with increasing distance if the null hypothesis of $r = 0$ was not correct. If both sexes showed a similar pattern of decline, we expected the $r$-values in the first distance class would be largest for the philopatric sex (Smouse et al. 2008). We focussed on the first distance class because if one sex remains relatively philopatric (such that relatives are spatially clustered), any differences in spatial autocorrelation between the sexes are expected to be most apparent in this class (Banks & Peakall 2012). We used 999 permutations with a bootstrap re-sampling procedure run 1000 times to estimate the 95% confidence interval. Sample size differed by survey year: 2008–2009 male $n = 79$, female $n = 90$ and 2009–2010 male $n = 65$, female $n = 76$. Second, we used a set of one-sided biased dispersal tests in FSTAT (Goudet et al. 2002). We permuted these tests 10 000 times to compare the estimated metrics including mean corrected assignment index, variance of corrected assignment index, $F_{ST}$, $F_{IS}$ and $H_{S}$ between male and female animals. Sample size differed by survey year: 2008–2009 $n = 160$ animals in 12 sites and 2009–2010 $n = 132$ animals in 10 sites. Sites without adequate sample sizes of both sexes were excluded from analysis in FSTAT.

**Landscape resistance.** We used partial Mantel tests in a causal modelling framework to analyse the influence of habitat on gene flow and to determine the extent to which possible landscape resistance models explained the spatial pattern of GD between individuals. We created a matrix of GD based on the same genetic distance measure used for the spatial autocorrelation analysis described above (Smouse & Peakall 1999). We produced landscape resistance surfaces representing different hypotheses about the difficulty in traversing different habitat types using CIRCUTSCAPE version 3.5 (McRae & Shah 2009). CIRCUTSCAPE uses circuit theory (McRae & Beier 2007; McRae et al. 2008) to predict connectivity in heterogeneous landscapes and allows for multiple pathways of gene flow rather than a single corridor with user-defined dimensions. We used the pairwise source/ground modelling mode to calculate connectivity between genotype point locations with habitat data specifying per cell conductance values, an eight-neighbour cell connection and calculations based on average conductance.

We assigned conductance values to raster cells in ArcGIS version 9.2 (ESRI 2009) representing hypotheses about the influence of distance, fire and vegetation type on genetic connectivity (Fig. 2; Table 1).

1 Distance: Our first hypothesis and simplest model was a test of isolation by distance across a uniform-resistance terrestrial landscape (Wright 1943). We did not use the classic Euclidean distance measure as it was inappropriate to represent straight line distances, given the study area was a peninsula and the coastline and ocean create a substantial barrier for a terrestrial small mammal. Therefore, in our null model, we assumed movement could occur in any direction, all raster cell values were equal in conductance, and the only limit to gene flow was that imposed by the coastline and ocean.

2 Fire: Our second hypothesis was that fire promotes genetic connectivity for fauna that specialize in early successional ecosystems. We expected to find a positive effect of fire (i.e. a relative negative effect of unburnt areas) because it resets the vegetation succession creating suitable habitat for postfire specialist species (Monamy & Fox 2000). Residual survivors become responsible for postperturbation population recovery (Turner et al. 1998; Banks et al. 2011) potentially following burned vegetation to recolonize and reproduce. Because causal modelling provides only significance tests and does not yield estimates of resistance from which we could assess the effect of fire, we took the approach of testing a series of models covering what we considered to be the range of plausible conductance values of fire (Table 1).

3 Vegetation type: Our third hypothesis was that for species with spatially and temporally variable habitat requirements, movement across unsuitable vegetation types would need to occur to access newly created habitat patches postfire. In our study, the eastern chestnut mouse was highly habitat specific in occurrence across a landscape characterized by a heterogeneous mosaic of vegetation types. Therefore, we took two approaches to test the influence of vegetation type on genetic connectivity: first we classified vegetation types as habitat vs. nonhabitat based on whether they were occupied or not and parameterized the models according to the range of plausible conductivity values (with the conductance value of habitat ranging from equal to nonhabitat...
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up to 1000 times greater than nonhabitat); and second, we considered conductivity was proportional to habitat quality as assessed by the percentage of sites of each vegetation type that were occupied (Table 1).

We proposed nine alternative landscape models (Table 1) that we tested against the ‘null landscape’ isolation-by-distance hypothesis. We used Mantel and partial Mantel correlations as the test statistics for causal modelling, including (i) simple Mantel tests between genetic distance and landscape resistances; (ii) partial Mantel tests between genetic distance and landscape resistances, partialling out the effects of the null model; and (iii) for those landscape resistance scenarios for which (ii) was significant, partial Mantel tests between genetic distance and the null model, partialling out the effects of the landscape resistance models. We conducted Mantel and partial Mantel tests using the ECODIST package (Goslee & Urban 2007) in R version 2.7 (R Development Core Team 2008) with 10 000 randomizations. To infer an effect of a landscape resistance scenario on dispersal, we expected (i) and (ii) to be significant, and we expected (iii) to be nonsignificant if that scenario ‘correctly’ explained population connectivity in our study population (Cushman et al. 2006). As an alternative statistical test of the effect of landscape resistance after accounting for the ‘null’ model, we used multiple regression on distance matrices (MRDM; Lichstein 2007).

Results

Population genetic summary statistics

Genotype proportions deviated from H–W expectations in 2008–2009 at locus 7D12 in site 7-P and in 2009–2010 at locus 9A8 in site 7-L, locus 10G6 in site 7-46 and locus 1A7 in site 7-95. Locus 6D4 showed consistent significant departures from HWE (in sites 7-44B, 7-2 and 7-H in 2008–2009 and at 7-44B, 7-46 and 7-M in 2009–2010) and was removed from subsequent analyses. With the
null hypothesis. The number of samples (n), the number of alleles (Na), observed heterozygosity (HO), expected heterozygosity (HE), and Fis for each site averaged across loci ± standard error. The exception of locus 6D4, the departures from H–W expectations in our data set were not beyond the false error rate for multiple testing (i.e. seven of 130 tests were likely to be significant) nor were they consistent across sites or years. Overall, we identified between three and six alleles per locus. Genetic diversity across sites ranged from 0.499 to 0.652 in 2008 to 2009 and 0.415 to 0.632 in 2009 to 2010, with observed heterozygosity averaged across sites greater than expected in both survey years (Table 2).

### Population subdivision and spatial genetic structure

We found significant genetic differentiation among sites across the study area (2008–2009 FST = 0.161, P = 0.001; 2009–2010 FST = 0.195, P = 0.001; Table S3, Supporting information) and an effect of isolation by distance. Euclidean distance (log-scale geographic distance) was a significant predictor of FST between sites (2008–2009 Mantel r = 0.703, P = 0.007; 2009–2010 Mantel r = 0.377, P = 0.044 r = 0.377, P = 0.044; Fig. 3).

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**Table 1** Raster cell values used to create resistance landscapes

<table>
<thead>
<tr>
<th>Model</th>
<th>Hypothesis</th>
<th>Cell conductance values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Null</td>
<td>All habitat types exert the same level of permeability to gene flow</td>
<td>All cells = 1</td>
</tr>
<tr>
<td>Firemodel1</td>
<td>Areas burnt in the 2003/2004 fire are twice as permeable to gene flow as unburned habitat</td>
<td>Burnt areas = 2</td>
</tr>
<tr>
<td>Firemodel2a</td>
<td>Areas burnt in the 2003/2004 fire are 10 times as permeable to gene flow as unburned habitat</td>
<td>Burnt areas = 10</td>
</tr>
<tr>
<td>Firemodel2b</td>
<td>Areas burnt in the 2003/2004 fire are 100 times as permeable to gene flow as unburned habitat</td>
<td>Burnt areas = 100</td>
</tr>
<tr>
<td>Firemodel2c</td>
<td>Areas burnt in the 2003/2004 fire are 1000 times as permeable to gene flow as unburned habitat</td>
<td>Burnt areas = 1000</td>
</tr>
<tr>
<td>Vegmodel3†</td>
<td>Vegetation types where mice have been captured twice as likely to facilitate gene flow</td>
<td>Cells in heathland, woodland and sedgeland = 2</td>
</tr>
<tr>
<td>Vegmodel4†</td>
<td>Vegetation types where mice have been captured 10 times as likely to facilitate gene flow</td>
<td>Cells in other vegetation types = 1</td>
</tr>
<tr>
<td>Vegmodel5†</td>
<td>Vegetation types where mice have been captured 100 times as likely to facilitate gene flow</td>
<td>Cells in heathland, woodland and sedgeland = 100</td>
</tr>
<tr>
<td>Vegmodel6†</td>
<td>Vegetation types where mice have been captured 1000 times as likely to facilitate gene flow</td>
<td>Cells in other vegetation types = 1</td>
</tr>
</tbody>
</table>

Water was assigned a value of zero.

†Cell values were estimated from unpublished annual monitoring data (refer to Table S1, Supporting information).

**Table 2** Population genetic parameters for the eastern chestnut mouse

<table>
<thead>
<tr>
<th>Site</th>
<th>n</th>
<th>Na</th>
<th>HO</th>
<th>HE</th>
<th>FIS</th>
<th>n</th>
<th>Na</th>
<th>HO</th>
<th>HE</th>
<th>FIS</th>
</tr>
</thead>
<tbody>
<tr>
<td>7-44</td>
<td>8</td>
<td>2.9 ± 0.2</td>
<td>0.597 ± 0.093</td>
<td>0.589 ± 0.028</td>
<td>0.005 ± 0.134</td>
<td>24</td>
<td>3.2 ± 0.2</td>
<td>0.585 ± 0.048</td>
<td>0.551 ± 0.042</td>
<td>-0.075 ± 0.055</td>
</tr>
<tr>
<td>7-46</td>
<td>38</td>
<td>3.8 ± 0.3</td>
<td>0.610 ± 0.069</td>
<td>0.567 ± 0.058</td>
<td>-0.070 ± 0.037</td>
<td>11</td>
<td>3.0 ± 0.2</td>
<td>0.524 ± 0.068</td>
<td>0.500 ± 0.044</td>
<td>-0.029 ± 0.073</td>
</tr>
<tr>
<td>7-95</td>
<td>2</td>
<td>3.1 ± 0.3</td>
<td>0.528 ± 0.078</td>
<td>0.471 ± 0.065</td>
<td>-0.112 ± 0.037</td>
<td>18</td>
<td>3.1 ± 0.2</td>
<td>0.530 ± 0.069</td>
<td>0.526 ± 0.052</td>
<td>-0.002 ± 0.069</td>
</tr>
<tr>
<td>7-2</td>
<td>23</td>
<td>3.3 ± 0.2</td>
<td>0.579 ± 0.038</td>
<td>0.556 ± 0.039</td>
<td>-0.048 ± 0.031</td>
<td>17</td>
<td>3.3 ± 0.2</td>
<td>0.572 ± 0.024</td>
<td>0.569 ± 0.028</td>
<td>-0.021 ± 0.055</td>
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<tr>
<td>7-H</td>
<td>23</td>
<td>3.4 ± 0.3</td>
<td>0.499 ± 0.058</td>
<td>0.452 ± 0.055</td>
<td>-0.093 ± 0.040</td>
<td>21</td>
<td>2.9 ± 0.2</td>
<td>0.415 ± 0.055</td>
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<td>0.032 ± 0.055</td>
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<td>7-I</td>
<td>19</td>
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<td>14</td>
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<td>0.473 ± 0.060</td>
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<td>0.652 ± 0.067</td>
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<td>8</td>
<td>2.8 ± 0.2</td>
<td>0.621 ± 0.062</td>
<td>0.520 ± 0.048</td>
<td>-0.203 ± 0.077</td>
</tr>
<tr>
<td>Mean</td>
<td>3.2 ± 0.1</td>
<td>0.576 ± 0.025</td>
<td>0.538 ± 0.018</td>
<td>-0.069 ± 0.027</td>
<td>3.0 ± 0.1</td>
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<td>0.511 ± 0.016</td>
<td>-0.070 ± 0.025</td>
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</table>
At a broad scale, we detected positive and significant spatial autocorrelation in distance classes up to 2 km (Fig. 4A, B). At distances exceeding 3–3.5 km, pairwise multilocus genotypes were less similar than those assigned to distance classes at random. At a fine scale, the within-site distribution of genotypes was significant and positively autocorrelated up to 200–250 m (Fig. 4C, D).

We did not identify discrete, spatially segregated, genetic populations above the scale of sampling grids using the clustering methods. Structure did identify the presence of three groups in both years. However, it could not assign individuals to a population with >90% confidence (Table S5, Supporting information). Further, these groups did not correspond to spatially discrete clusters of individuals, and we found that samples from a particular site included a mixture of individuals from different structure groups (Appendix S2 and Figure S1, Supporting information). GENECLAND identified seven groups in 2008–2009 and eight in 2009–2010. Individuals were assigned to clusters that reflected population subdivision based on pairwise $F_{ST}$, suggesting field sites

Fig. 4 Correlograms indicating spatial autocorrelation of pairwise multilocus genetic distances over 5 km (A) 2008–2009, (B) 2009–2010; and over 250 m (C) 2008–2009, (D) 2009–2010. Broken lines represent the 95% CI for the null hypothesis of a random distribution of genotypes. Error bars represent the 95% CI around $r$ for a specific distance class.
Sex-biased dispersal

We found some evidence that spatially proximal females were more genetically similar than males in one of our analyses in on year of sampling; however this pattern was inconsistent. We did not find strong evidence for heterogeneity between correlograms for males and females. In 2008–2009, female r-values were significantly greater than males in the 0- to 50-m distance class according to the $T_2$ test ($T_2 = 4.182$, $P = 0.033$) but not in the 0- to 500-m distance class ($T_2 = 0.001$, $P = 0.977$). However, the bootstrap 95% CIs of the r values, a more conservative test (Banks & Peakall 2012) for males and females overlapped (Table S6, Supporting information). In 2009–2010, female r-values were not significantly greater than males in the 0- to 50-m distance class ($T_2 = 0.087$, $P = 0.751$), but they were in the 0- to 500-m distance class ($T_2 = 14.258$, $P = 0.001$). This was the only spatial autocorrelation value test of sex-biased dispersal to be supported by the conservative bootstrap 95% CI overlap test (Table S6, Supporting information). There were no consistent biological patterns in the other distance class comparisons in either survey year (Table S6, Supporting information). None of the sex-biased dispersal tests in $F_{ST}$-est provided evidence for female philopatry and male dispersal, and none of the test statistics were significant in either survey year (Table S7, Supporting information). The test statistics were conflicting in regard to expectations of male-biased dispersal (e.g. $F_{ST}$, $F_{IS}$ and $H_{O}$; Table S7, Supporting information). The lack of apparent sex-biased dispersal may be attributed to small sample sizes used in these analyses. However, given that sex-biased dispersal can be detected with similar sample sizes in species where this is a prevailing life-history strategy, such as Antechinus species (Banks & Peakall 2012), our results are likely due to biological reasons discussed in the next section.

Landscape resistance

1 Simple Mantel tests between genetic distance and landscape resistances. All of the simple Mantel tests were significant (Table 3). Both the null model and the alternate resistance landscapes explained variation in genetic distance between individuals. However, when the models were ranked based on Mantel r, only Firemodell performed better than the null model.

2 Partial Mantel tests between genetic distance and landscape resistances, partialling out the effects of the null model. We found significant effects of the fire models 1, 2a, 2b and 2c (conductance across burned habitat was twice, 10, 100 and 1000 times greater than unburned habitat, respectively; Table 1) after accounting for variation in genetic distance explained by the null landscape. After we accounted for the null model, the partial correlations of the vegetation models (with increases in relative conductivity of preferred habitat to other vegetation types and with conductance parameterised to reflect the distribution of capture records and habitat preferences) with genetic distance were nonsignificant (Table 3).

3 Partial Mantel tests between genetic distance and the null model, partialling out the effects of the landscape resistance models. Of the landscape resistance scenarios that explained a significant component of the variation in genetic distance between individuals when the null model was partialled out (the four fire models: Table 1), the null model was nonsignificant after Firemodell was accounted for (Table 3). This model featured a conductance of recently burned habitat twice that of unburned habitat. The null model explained a significant component of the variation in genetic distance even after the remaining fire models (Firemodell 2a–c, featuring relatively higher conductance values of burned habitat: Table 1) were fitted (Table 3). This suggests that the latter models potentially overestimate the relative conductivity of burnt habitat.

Discussion

Our study provides support for a ‘generalist’ dispersal strategy, which would be advantageous for a species that prefers ephemeral habitat, conditional on spatial and temporal variability. We found significant genetic differentiation between sites that followed an isolation-by-distance pattern and significant spatial autocorrelation between genotypes, indicating dispersal was restricted relative to the overall scale of the study. However, we did not find strong evidence for dispersal to be male-biased and limited to only one sex. Our data suggested no effect of heterogeneity in heterogeneous
native vegetation on genetic structure, despite strong habitat selection for specific vegetation types, and there was evidence for a positive effect of fire in promoting connectivity.

**Landscape connectivity and gene flow**

For a pyric specialist species with preference for early successional stage vegetation, we predicted fire would promote gene flow and enhance connectivity because following burned vegetation would potentially lead dispersers to unoccupied suitable habitat. While we identified significant genetic differentiation between populations, we found no evidence for discrete structure above the level of sampling sites (i.e. broad spatial population groupings or clusters), suggesting that a model of isolation by distance is an appropriate interpretation of this system. The population-specific $F_{ST}$ analysis in GESTE provided no evidence for genetic structure being influenced by the distribution of preferred and nonpreferred habitat (vegetation heterogeneity). Consistent with this finding, landscape genetics analyses of the relationships between pairwise individual GD and a set of landscape resistance scenarios did not support an effect of vegetation-mediated habitat suitability on spatial genotypic patterns. This suggests that occupancy and abundance are not appropriate surrogates for landscape permeability to movement in disturbance-adapted species (Spear et al. 2010). However, these analyses did support an increased relative permeability of burnt landscapes over unburnt landscapes, suggesting that fire promotes connectivity in this species. The support for increased permeability of burnt relative to unburnt habitat came from simple Mantel tests

<table>
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<th>Matrix 1</th>
<th>Matrix 2</th>
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<th>P-value</th>
<th>MRDM</th>
<th>P-value</th>
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<td>0.157</td>
<td>&lt;0.001</td>
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<td>(2) Partial Mantel tests between genetic distance and landscape resistances, partialling out the effects of the null model</td>
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GD = pairwise multilocus genetic distance. Data for both survey years are combined. Significance levels from multiple regression on distance matrices (MRDM) are included for comparison.
of interindividual genetic versus landscape resistance distances, in which Firemodel1 (Table 1), where the conductance of recently burned habitat was twice that of unburned habitat, had the strongest simple Mantel correlation (Table 3). Although our Mantel correlations were not high (maximum $r = 0.229$), we expected that geographic correlations with individual multilocus distances to be ‘messier’ than population-based distances as the latter do not include intrapopulation (interindividual) variation. Further, partial Mantel tests and MRDM identified this model as being significantly associated with genetic distance after accounting for a ‘null’ landscape model. This model that satisfied the classic causal modelling criteria for acceptance (Cushman et al. 2001) was Firemodel1 (Table 1), in which the conductance of recently burned habitat was twice that of unburned habitat. Landscape resistance scenarios in which recently burned habitat had a conductance 10-, 100- or 1000-fold greater than unburned habitat were significant after accounting for the null model, but the null model was also significant after these models were accounted for. This suggests that these latter models overstate the relative conductance value of recently burned habitat and that Firemodel1 is a reasonably accurate representation of the resistance landscape for the studied population. While this finding was consistent with our prediction for this species, and with other lines of evidence (the observed heterozygosity excess in both years is consistent with increased dispersal and admixture of populations that were likely to have been considerably smaller and more isolated before the 2003 fire), we do interpret the partial Mantel and MRDM analyses with some caution, as recent simulation work has shown that these tests can, under some circumstances, have unacceptable error rates for the significance of spatially structured explanatory variables (Jaquery et al. 2011; Guillot & Rousset 2012). Statistical caveats aside, we discuss the implications of fire for connectivity in postfire specialists below.

Potentially, fire promotes connectivity for early successional specialist fauna in two ways. First, fire improves habitat suitability for such species, and habitat suitability improves landscape conductance to gene flow. Where long-term fire suppression occurred in a previously fire-maintained ecosystem, Templeton et al. (2001) observed a significant increase in dispersal and colonization rate of new patches by collared lizards after re-initiation of burning. The increase in dispersal was attributed not to the fire itself but to the change in structure of the intervening habitat matrix and opening of the understorey (Templeton et al. 2001). For example, burned areas may not be an impediment to movement as long as some structure, native plant regeneration or patches of remnant vegetation are present.

A postfire-collapsed shrub layer may even provide cover and protection facilitating movement (Spear et al. 2005). Spear & Storfer (2010) found gene flow was maintained across burned areas and suggested movement was facilitated by biological legacies (sensu Franklin et al. 2000) in the form of downed trees and debris. For dispersing individuals of the eastern chestnut mouse, a fire boundary of unburned habitat or late successional stage vegetation might be a greater deterrent to movement than the burnt landscape (i.e. habitat cues can assist directional movement; Bowler & Benton 2005). Under this scenario, the underlying mechanism for persistence of postfire specialist fauna may be the disperser’s ability to follow fire in an attempt locate suitable habitat.

Second, an alternative explanation is that the resistance landscape for dispersal by the eastern chestnut mouse is not static and that dispersal is increased dramatically in burnt areas in association with colonization immediately after the fire and then returns to levels described under a ‘null landscape’ model. Genetic signals of recent (but not current) dispersal scenarios can persist for a number of generations (Landguth et al. 2012). Under this scenario, fire causes substantial mortality but also results in rapid colonization of newly created early successional habitat by residual survivors and thus increased gene flow over the immediate short-term postfire. Once the empty territories have been colonized, there is no longer any reason for higher dispersal across burnt areas. Our data do not distinguish these two explanations.

For species with spatially and temporally variable habitat requirements, we predicted natural habitat heterogeneity would not restrict gene flow because dispersal would still need to occur through landscapes that do not meet specific habitat requirements. A heterogeneous cover of native vegetation types is unlikely to restrict gene flow because dispersal is still possible through landscapes that are considered inappropriate when conditional on perceived habitat preferences. Although the eastern chestnut mouse has specific habitat requirements including early successional stage heathland vegetation, we found genetic connectivity across the study area was not limited by vegetation type and that other native vegetation communities interspersed throughout heathland did not restrict movement. While barriers to dispersal may funnel movement in one direction (Gustafson & Gardner 1996), dispersal through unfavourable habitat has been recorded for many species (Ruscoe et al. 1998; Mossman & Waser 2001; Selonen & Hanksi 2004; Gauffre et al. 2008; Macqueen et al. 2008). Selectivity for preferred habitat during dispersal has also been recorded for other species (Lorenz & Barrett 1990; Baur & Baur 1992;
Schultz 1998; Lindenmayer & Peakall 2000; Banks et al. 2005), indicating the effect (or not) of habitat heterogeneity on gene flow is likely to be strongly species specific and/or site specific. A species’ capacity for movement through heterogeneous landscapes is likely to depend on whether heterogeneity is provided by indigenous vegetation of varying composition (as demonstrated in our study) or by small, remnant patches of native vegetation interspersed with anthropogenic modified landscapes (i.e. agricultural land, non-native forest plantations, built environments, etc.).

Population genetic structure and dispersal behaviour

A generalist dispersal strategy (i.e. one where movement is not restricted to particular vegetation types or landscape attributes) is advantageous for a species that prefers ephemeral habitats that are less predictable and more variable in temporal and spatial dispersion of resources (Lee et al. 1981). For small mammals in relatively stable environments, dispersal is often restricted (Peakall et al. 2003; Kraaijeveld-Smit et al. 2007; Macqueen et al. 2008; Gardner-Santana et al. 2009). Temporal instability of habitat quality may enhance effective dispersal and/or increase dispersal propensity (Gauffre et al. 2008). For example, a dispersal strategy with movement restricted to neighbouring habitat patches would be ineffective for the eastern chestnut mouse to take advantage of recently burned heathland and access early successional stage vegetation. While there is not a clear relationship between dispersal distance and the scale of genetic spatial autocorrelation, the scale of positive autocorrelation that we identified (2–3 km; Fig. 4) is similar to the movement patterns of other pseudomyine mice. The smoky mouse Pseudomys fumeus and eastern pebble-mound mouse P. patrius have both been observed to make minimum movements >600 m and 1 km, respectively, in a single night (Ford 2003, 2008). The sandy inland mouse P. hermannsburgensis is capable of dispersing very large distances (>16 km; Dickman et al. 1995), suggesting the eastern chestnut mouse may be physiologically capable of much longer dispersal subject to landscape constraints.

Given that colonization is limited by the dispersal-limited sex, a generalist dispersal strategy that includes an absence of sex-biased dispersal would be beneficial for a postfire specialist species to access available high-quality but unoccupied habitat. Our results show no obvious evidence for sex bias in dispersal by the eastern chestnut mouse. This indicates that both sexes disperse or that our data set was not large enough to discern the philopatric sex. Whether a low, or temporally inconsistent, level of sex-biased dispersal occurs and was not detectable in our genetic data is difficult to determine. However, clear genetic signals of sex-biased dispersal were detected using similar sample sizes for two other species that also occur in this landscape (or are closely related to species in this landscape), the agile antechinus (Antechinus agilis) and the bush rat (Rattus fuscipes; Peakall et al. 2003; Banks et al. 2005; Banks & Peakall 2012). These species are not postfire specialists. So whatever the absolute level of dispersal by male and female eastern chestnut mice, the evidence suggests that the relative strength of sex bias in dispersal is weaker in the eastern chestnut mouse than in other small mammals studied in this region. The lack of a signal of sex-biased dispersal (a consistent significant difference in pairwise spatial autocorrelation of male and female animals) suggests an atypical mammalian structure exists (Gardner-Santana et al. 2009). This is because male-biased dispersal in mammals is considered an effective mechanism for inbreeding avoidance (Greenwood 1980; Bowler & Benton 2005). Eastern chestnut mouse dispersal behaviour may have evolved as a response to acquisition of suitable habitat rather than inbreeding avoidance, and therefore, it is an advantageous strategy for both sexes to be capable of dispersal. An interesting area for future research would be to investigate whether patterns of sex-biased dispersal differ between colonization and migration (between existing populations) dispersal events, a point raised by Wade & McCauley (1988). There is evidence that the tendency of one sex or another towards dispersal may be unpredictable and dependent on habitat quality or landscape pattern (Banks et al. 2005). For example, in the Australian bush rat Rattus fuscipes, sex-biased dispersal was absent in populations studied in south-eastern Australian forest (Kraaijeveld-Smit et al. 2007), but distinct female philopatry was found in fragmented rainforest in Queensland (Macqueen et al. 2008). Further research into eastern chestnut mouse dispersal behaviour should be replicated over multiple study areas before we are able to confirm the mechanisms postulated above.

Conclusion

Landscape resistance was a better predictor of genetic structure in the eastern chestnut mouse population than isolation by distance alone. Genetic connectivity was provided by burnt habitat, indicating fire may play a positive role in structuring populations of some species. Dispersal was possible through unsuitable habitat, and any effect of landscape heterogeneity is likely to depend on whether heterogeneity is provided by indigenous vegetation or by anthropogenic modified landscapes. We postulate that a generalist dispersal strategy – where movement is not restricted to particular vegetation types, landscape attributes or sex biased – is
advantageous for a species that prefers ephemeral habitat conditional on spatial and temporal variability.

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F.P., S.B., J.W., F.F. and D.L. designed the research; F.P., C.M., J.W., D.L. and S.B. performed the research; F.P., J.W. and S.B. analysed data; F.P., S.B. and D.L. wrote the manuscript; F.F., C.M. and J.W. provided editorial comment on the manuscript.

Data accessibility
Appendix S2 (Supporting information) includes an Excel file with separate worksheets containing the genotypes and locations of individuals sampled in 2008/2009 and 2009/2010, as well as a combined genotypes sheet. Also included are the locations of each sampling site, the recent fire history and vegetation characteristics of the landscape around each site, and a sheet containing pairwise genetic distances between individuals, Euclidean geographic distances and the resistance distances corresponding to each model of landscape resistance (Table 1).

Supporting information
Additional supporting information may be found in the online version of this article.

Appendix S1 Methods for Structure and GENELAND analyses.
Appendix S2 Results for Structure and GENELAND analyses.
Table S1 Number of sites surveyed, sites with eastern chestnut mouse captures, and occupancy by vegetation type.
Table S2 PCR conditions and characteristics of microsatellites.
Table S3 Pairwise site Fst for the eastern chestnut mouse (Fst for 2008–2009 below the diagonal, 2009–2010 above).
Table S4 Results of clustering analysis in GENELAND.
Table S5 The number of individuals assigned to each population cluster in GENELAND.
Table S6 Results of sex-biased spatial autocorrelation analysis for both survey years.
Table S7 Results of sex-biased dispersal test for both survey years using FSTAT.
Fig. S1 Number of population clusters identified using Structure.
Fig. S2 Estimates of population-specific Fst (HPDIs) from GESTE. The 95% highest posterior density intervals of GESTE population-specific Fst estimates (x-axis) for the nine populations with the largest sample sizes (y-axis).

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Appendix 4

Supporting information for

Chapter 3 Site occupancy
Appendix 4. Supporting Information for Chapter 3 Site occupancy

Landscape, fire and habitat: which features of recently burned heathland influence site occupancy of an early successional specialist?


Appendix S1: Study species

Eastern chestnut mouse (*Pseudomys gracilicaudatus*)

The eastern chestnut mouse is an endemic Australian murid rodent. It has a disjunct distribution along the east coast of Australia and is absent throughout much of its range. The Jervis Bay region supports the most southerly contemporary population of the species (Meek and Triggs 1997). Usually reported at low density, the eastern chestnut mouse has been recorded in grassy open woodland to open dry sclerophyll forest, but is more often found in heathland (Fox 2008) where populations peak in abundance post-fire before declining over time as vegetation regenerates (Fox 1982). Threats to the viability of populations of this species’ are thought to include fire suppression, loss of heath habitat, and predation (Fox 2008).

The eastern chestnut mouse is an annual summer breeder capable of producing multiple litters of one to five (usually three) offspring (Fox 2008). Early development is rapid which contrasts with a slow growth rate to reach maturity (Fox & Kemper 1982). Adults show significant sexual dimorphism (Fox & Kemper 1982) and attain average weights of 90 g for males and 75 g for females (Fox 2008). The species’ lifespan is less than two years in wild populations (Watts & Kemper 1989). Studies of the eastern chestnut mouse dietary requirements indicate it is a generalist herbivore, opportunistic in foraging and less specialised in food selection than any other species within the genus (Luo et al. 1994). The eastern chestnut mouse is terrestrial, mostly nocturnal, and individuals select diurnal refuges associated with the presence of specific structures including grass trees (*Xanthorrhoea* spp.), buttongrass (*Gymnoschoenus* sp.), collapsed dead stems, and areas of tall, dense vegetation (Pereoglou et al. 2011). The eastern chestnut mouse is transient and non-gregarious in its use of shelter sites (Pereoglou et al. 2011). Little is known about social organisation and behaviour. Radio-tracking data suggests that adults of the eastern chestnut mouse are solitary and territorial, with females having a home range of 0.5 – 1 ha and up to 4 ha for males (Pereoglou et al. unpublished data).

Bush rat (*Rattus fuscipes*)

The bush rat is a common and widespread terrestrial murid rodent that occurs throughout many parts of eastern Australia (Watts & Aslin 1981). The species can be found in many
different habitats and is widespread in eucalypt forest and areas where there is a dense understory (Breed and Ford 2007). Weights in excess of 200 g have been recorded for adult animals (Lunney 2008a). Bush rats are capable of breeding all year round under favourable (wet) conditions, but births predominantly occur in late spring and summer with litter size ranging from one to seven (average five) (Watts and Aslin 1981). Multiple litters can be produced in the breeding season, with animals born early attaining sexual maturity in the same season, and all animals capable of breeding in the following spring (Watts and Aslin 1981). Mortality occurs after breeding and the average lifespan of most animals is one year (Watts and Aslin 1981); few individuals (< 5%) survive to breed a second year (Robinson 1987). The bush rat has an omnivorous diet of fungi, seeds, fruit, plant tissue and arthropods (Warneke 1971). The species is nocturnal but not strictly territorial; home ranges can overlap (Lunney 2008a) with male territories being larger than those of females (Watts and Aslin 1981).

Swamp rat (*R. lutreolus*)

The swamp rat is a native murid rodent distributed over coastal and sub-coastal south-eastern Australia (Lunney 2008b). The species occurs predominantly in heathland and sedgeland (Braithwaite 1982), and prefers areas of wet, dense cover (Lunney 2008b). Adult animals attain an average weight of approximately 200 g (Lunney 2008b). Breeding occurs in summer (Watts and Aslin 1981). Like its congener, the bush rat, the swamp rat is capable of breeding year around provided conditions are favourable. Females can produce multiple litters of three to five young in a single season, and offspring born early are able to breed in the season of their birth (Lunney 2008b). Longevity is also probably similar to the bush rat, being mostly annual. The swamp rat is a specialist herbivore whose main diet consists of grasses and sedges (Watts and Aslin 1981). The species shelters in burrows or builds above-ground nests in waterlogged areas (Lunney 2008b). The swamp rat is partially diurnal and moves through runways constructed in dense vegetation (Watts and Aslin 1981). Male home ranges are larger than non-overlapping female ranges, and individuals exhibit territorial social behaviour throughout much of the year (Lunney 2008b). The swamp rat is immediately and adversely affected by fire due to the species’ dependence on dense cover (Lunney 2008b) and relatively specialised diet (Braithwaite 1982).

Brown antechinus (*Antechinus stuartii*)

The brown antechinus is a small dasyurid marsupial, widespread in forest and heathland throughout its coastal distribution from southern Queensland to southern New South Wales, Australia (Crowther 2002). The brown antechinus is mostly terrestrial although it also can be arboreal depending on the habitat. High density populations are found in areas with thick ground cover and abundant logs (Crowther and Braithwaite 2008). Adult males and females
attain average weights of 35 g and 20 g, respectively. Mating occurs in winter, and females typically have 8 – 10 pouch young. Multiple paternity is common (Kraaijeveld-Smit et al. 2002), with most litters being sired by two or three males. All males die at the end of a two-week mating season, although some females may survive to breed in a second year (Crowther and Braithwaite 2008). The brown antechinus is an opportunistic insectivore (Fox and Archer 1984). Ranging behaviour is probably similar to the agile antechinus (A. agilis), with males covering an area three times greater than that of females (Dickman 2008). Individuals nest communally, usually in hollow logs of tree trunks. Male-biased post-natal dispersal occurs in summer and individuals may continue to move between communal nests prior to the breeding season (Cockburn and Lazenby-Cohen 1992).
Table S1: Ratio of eastern chestnut mouse captures to recaptures across vegetation type and survey years. The number of sites surveyed is provided in parentheses.

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<td>15:5 (169)</td>
<td>3:3 (109)</td>
<td>28:13 (107)</td>
<td>69:18 (110)</td>
<td>43:16 (106)</td>
<td>6:2 (51)</td>
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A Site establishment was impeded by wildfire
B Some sites were trapped more than once during the survey year
C Some sites were unable to be surveyed due to flooding
D Some sites were not surveyed due to logistical reasons

Table S2: Hierarchical generalised linear model parameters and results summary

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### Appendix 4: Supporting information

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### Site-level habitat quality

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### Appendix 4: Supporting information

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### Landscape context

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Appendix 5

Supporting information for

Chapter 4 Landscape genetics
Appendix 5: Supporting Information for Chapter 4

Landscape genetics of an early successional specialist in a disturbance-prone environment
F. Pereoglou, S. C. Banks, C. MacGregor, F. Ford, J. Wood and D. B. Lindenmayer

Appendix S1 (Methods for Structure and Geneland analyses)

In STRUCTURE, we ran five iterations of eight possible models (K=1-8) to obtain an average probability value for each model. We used the default parameter settings (admixture model, allele frequencies correlated) with a 200000 burn-in period and 1000000 MCMC repetitions after burn-in.

In GENELAND, we performed five independent runs with 100000 MCMC iterations (thinning=100) allowing K to vary from 1 to 20. We used a spatial model with 100 m error on coordinates and correlated allele frequencies. We inferred K from the modal value of the run with the highest likelihood.

Appendix S2 (Results for Structure and Geneland analyses)

The estimated logarithm of likelihood for data analysed in STRUCTURE was highest for K = 3 in both years (Fig. S1). When individuals were assigned to population clusters using probability values > 0.90, only 22 (2008-09) and 19 (2009-10) individuals could be assigned to a cluster, with the remaining 87 % of animals not able to be assigned. When a more stringent reclassification was applied using probability values > 0.95, no animals could be assigned to a population cluster in either survey year. This suggests that the three clusters identified in each year were not demographically discrete groups.

Using a spatial model in GENELAND, nine clusters were inferred in 2008-09 and eight in 2009-10 (Table S1). Individuals were not uniformly distributed to each of the identified population clusters (Table S2) and there was no spatial separation between populations, with individuals trapped at one site belonging to one or more populations. None of the probability levels upon which the assignments were made were greater than 90 % suggesting that the spatial model was also unable to detect demographically discrete groups corresponding to spatially segregated regions.
Table S1: Number of sites surveyed, sites with eastern chestnut mouse captures, and occupancy by vegetation type. Unpublished annual monitoring data (see Lindenmayer et al. 2008)

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<th>Vegetation type</th>
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<th>Occupancy (%)</th>
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Table S2: PCR conditions and characteristics of microsatellites. Number of alleles, expected heterozygosity estimated across sites combined over years

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<td>61 – 51</td>
<td>60</td>
<td>40</td>
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</tr>
<tr>
<td>9A8</td>
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<td>0.3998</td>
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<td>60</td>
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<td>66 – 60</td>
<td>45</td>
<td>35</td>
<td>5</td>
<td>0.6697</td>
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<td>1A7</td>
<td>94</td>
<td>66 – 60</td>
<td>45</td>
<td>35</td>
<td>4</td>
<td>0.6626</td>
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<tr>
<td>10G6</td>
<td>94</td>
<td>66 – 60</td>
<td>45</td>
<td>35</td>
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<td>0.6523</td>
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Table S3: Pairwise site Fst for the eastern chestnut mouse (Fst for 2008-09 below the diagonal, 2009-10 above). All loci are combined. na indicates sites that were excluded from analysis. Non-significant values highlighted in bold

<table>
<thead>
<tr>
<th></th>
<th>7-2</th>
<th>7-44</th>
<th>7-44B</th>
<th>7-46</th>
<th>7-95</th>
<th>7-H</th>
<th>7-I</th>
<th>7-M</th>
<th>7-P</th>
</tr>
</thead>
<tbody>
<tr>
<td>7-2</td>
<td>na</td>
<td>0.106</td>
<td>0.062</td>
<td>0.016</td>
<td>0.269</td>
<td>0.273</td>
<td>0.183</td>
<td>0.027</td>
<td></td>
</tr>
<tr>
<td>7-44</td>
<td>0.244</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>na</td>
</tr>
<tr>
<td>7-44B</td>
<td>0.190</td>
<td>0.119</td>
<td>0.136</td>
<td>0.126</td>
<td>0.246</td>
<td>0.264</td>
<td>0.185</td>
<td>0.089</td>
<td></td>
</tr>
<tr>
<td>7-46</td>
<td>0.095</td>
<td>0.094</td>
<td>0.167</td>
<td>0.058</td>
<td>0.249</td>
<td>0.248</td>
<td>0.187</td>
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</tr>
<tr>
<td>7-95</td>
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<td>na</td>
<td>na</td>
<td>na</td>
<td>na</td>
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<td>0.170</td>
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<td>7-H</td>
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<td>0.200</td>
<td>0.256</td>
<td>0.223</td>
<td>0.360</td>
<td>0.162</td>
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<tr>
<td>7-I</td>
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<td>0.097</td>
<td>0.119</td>
<td>0.229</td>
<td>0.268</td>
<td>0.200</td>
<td></td>
<td></td>
</tr>
<tr>
<td>7-M</td>
<td>Na</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>na</td>
<td>0.138</td>
<td></td>
</tr>
<tr>
<td>7-P</td>
<td>0.065</td>
<td>0.099</td>
<td>0.101</td>
<td>0.006</td>
<td>na</td>
<td>0.192</td>
<td>0.087</td>
<td>na</td>
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</tr>
</tbody>
</table>
Table S4: Results of clustering analysis in GENELAND. The value of K estimated for each of the five runs is presented with log-scale likelihood in decreasing ranked order.

<table>
<thead>
<tr>
<th></th>
<th>2008-09 Likelihood</th>
<th>K</th>
<th>2009-10 Likelihood</th>
<th>K</th>
</tr>
</thead>
<tbody>
<tr>
<td>-4684.793342</td>
<td>9</td>
<td>-4201.876479</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>-4718.412455</td>
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<td>-4248.043092</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>-4929.102147</td>
<td>8</td>
<td>-4299.593687</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>-5011.304671</td>
<td>9</td>
<td>-4330.276253</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>-5163.609895</td>
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<td>-4492.967675</td>
<td>8</td>
<td></td>
</tr>
</tbody>
</table>

Table S5: The number of individuals assigned to each population cluster in GENELAND.

<table>
<thead>
<tr>
<th></th>
<th>2008-09 cluster</th>
<th>n</th>
<th>2009-10 cluster</th>
<th>n</th>
</tr>
</thead>
<tbody>
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<td>1</td>
<td>3</td>
<td>1</td>
<td>44</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>12</td>
<td>2</td>
<td>36</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>1</td>
<td>3</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>16</td>
<td>4</td>
<td>40</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>33</td>
<td>5</td>
<td>1</td>
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<td>6</td>
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<td>7</td>
<td></td>
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<td>7</td>
<td>6</td>
<td>7</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>57</td>
<td>8</td>
<td>3</td>
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</tr>
<tr>
<td>9</td>
<td>23</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
**Appendix 5: Supporting information**

Table S6: Results of sex-bias spatial autocorrelation analysis for both survey years. Male and female genetic correlation ($r$), upper (Ur) and lower (Lr) bootstrap 95% confidence limit for $r$, $p$-value for test $r > 0$ ($Pr$), T2 and probability ($P$) of sex-bias at spatial scales of up to 250 m and 5 km. Distance class in metres

<table>
<thead>
<tr>
<th></th>
<th>Female</th>
<th>Male</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Dist. class</td>
<td>$r$</td>
</tr>
<tr>
<td>2008-09</td>
<td>Fine-scale correlograms</td>
<td></td>
</tr>
<tr>
<td>0-50</td>
<td>0.246</td>
<td>0.196</td>
</tr>
<tr>
<td>50-100</td>
<td>0.145</td>
<td>0.103</td>
</tr>
<tr>
<td>100-150</td>
<td>0.117</td>
<td>0.067</td>
</tr>
<tr>
<td>150-200</td>
<td>0.053</td>
<td>-0.099</td>
</tr>
<tr>
<td>200-250</td>
<td>0.088</td>
<td>0.006</td>
</tr>
<tr>
<td>Coarse-scale correlograms</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0-500</td>
<td>0.130</td>
<td>0.110</td>
</tr>
<tr>
<td>500-1000</td>
<td>0.063</td>
<td>0.028</td>
</tr>
<tr>
<td>1000-1500</td>
<td>0.002</td>
<td>-0.035</td>
</tr>
<tr>
<td>1500-2000</td>
<td>0.028</td>
<td>0.005</td>
</tr>
<tr>
<td>2000-2500</td>
<td>-0.003</td>
<td>-0.027</td>
</tr>
<tr>
<td>2500-3000</td>
<td>0.010</td>
<td>-0.014</td>
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<tr>
<td>3000-3500</td>
<td>-0.061</td>
<td>-0.079</td>
</tr>
<tr>
<td>3500-4000</td>
<td>-0.028</td>
<td>-0.054</td>
</tr>
<tr>
<td>4000-4500</td>
<td>-0.042</td>
<td>-0.095</td>
</tr>
<tr>
<td>4500-5000</td>
<td>-0.132</td>
<td>-0.160</td>
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<tr>
<td>2009-10</td>
<td>Fine-scale correlograms</td>
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<tr>
<td>0-50</td>
<td>0.191</td>
<td>0.126</td>
</tr>
<tr>
<td>50-100</td>
<td>0.202</td>
<td>0.158</td>
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<tr>
<td>100-150</td>
<td>0.206</td>
<td>0.149</td>
</tr>
<tr>
<td>150-200</td>
<td>0.088</td>
<td>0.023</td>
</tr>
<tr>
<td>200-250</td>
<td>-0.377</td>
<td>0.000</td>
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<tr>
<td>Coarse-scale correlograms</td>
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<td></td>
</tr>
<tr>
<td>0-500</td>
<td>0.182</td>
<td>0.154</td>
</tr>
<tr>
<td>500-1000</td>
<td>0.082</td>
<td>0.034</td>
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<tr>
<td>1000-1500</td>
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<td>-0.009</td>
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<tr>
<td>1500-2000</td>
<td>0.091</td>
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<tr>
<td>2000-2500</td>
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<tr>
<td>2500-3000</td>
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<td>-0.043</td>
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<tr>
<td>3000-3500</td>
<td>-0.061</td>
<td>-0.086</td>
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<tr>
<td>3500-4000</td>
<td>-0.065</td>
<td>-0.097</td>
</tr>
<tr>
<td>4000-4500</td>
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<td>-0.104</td>
</tr>
<tr>
<td>4500-5000</td>
<td>-0.058</td>
<td>-0.084</td>
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</table>
Table S5: Results of sex-biased dispersal test for both survey years using FSTAT. Dispersing sex expected to have lower mean of assignment index and $F_{ST}$, greater variance of assignment index, $F_{IS}$ and $H_{S}$ compared to the philopatric sex

<table>
<thead>
<tr>
<th>Survey year</th>
<th>Test</th>
<th>Male</th>
<th>Female</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>2008-09</td>
<td>Mean corrected assignment index</td>
<td>-0.079</td>
<td>0.068</td>
<td>0.318</td>
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<tr>
<td></td>
<td>Variance of corrected assignment index</td>
<td>4.149</td>
<td>3.374</td>
<td>0.155</td>
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<tr>
<td></td>
<td>$F_{ST}$</td>
<td>0.097</td>
<td>0.093</td>
<td>0.525</td>
</tr>
<tr>
<td></td>
<td>$F_{IS}$</td>
<td>-0.025</td>
<td>-0.069</td>
<td>0.164</td>
</tr>
<tr>
<td></td>
<td>$H_{S}$</td>
<td>0.540</td>
<td>0.545</td>
<td>0.630</td>
</tr>
<tr>
<td>2009-10</td>
<td>Mean corrected assignment index</td>
<td>-0.198</td>
<td>0.170</td>
<td>0.154</td>
</tr>
<tr>
<td></td>
<td>Variance of corrected assignment index</td>
<td>4.405</td>
<td>3.891</td>
<td>0.304</td>
</tr>
<tr>
<td></td>
<td>$F_{ST}$</td>
<td>0.086</td>
<td>0.128</td>
<td>0.154</td>
</tr>
<tr>
<td></td>
<td>$F_{IS}$</td>
<td>-0.014</td>
<td>-0.006</td>
<td>0.483</td>
</tr>
<tr>
<td></td>
<td>$H_{S}$</td>
<td>0.548</td>
<td>0.516</td>
<td>0.074</td>
</tr>
</tbody>
</table>

Figure S1. Number of population clusters identified using STRUCTURE. Data is mean posterior probability ($\text{LnP(D)}$) ± standard error based on 1000000 MCMC repetitions. Solid symbol is 2008-09 survey year ($K = 3$); hollow symbol is 2009-10 survey year ($K = 3$).
Figure S2. The 95% highest posterior density intervals of GESTE population-specific $F_{ST}$ estimates (x-axis) for the nine populations with the largest sample sizes (y-axis).