The effects of different forestry practices on two native rodent species, the swamp rat (*Rattus lutreolus*) and the long-tailed mouse (*Pseudomys higginsi*)


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Chapters 2 to 5 are modified as original research articles for peer-reviewed journals.

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Statement of Co-Authorship

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Statement of Ethical Conduct

The research associated with this thesis abides by the international and Australian codes on animal experimentation. All research was conducted with the approval of the University of Tasmania Animal Ethics Committee (approval permits A9923, A10504, A11389) and the Department of Primary Industries and Water, Parks and Wildlife (permits FA 8098, FA9075, FA10047, FA10176); and with permission from Forestry Tasmania to conduct mammal trapping in State Forest.

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Abstract

Forest fragmentation, modification and loss can have a range of negative impacts on wildlife, including reduced foraging opportunities, increased competition for resources, loss of habitat connectivity and restricted dispersal, and increased predation risk due to removal of habitat cover. Harvesting practices such as clearfelling (clearcutting) in native forests typically remove all standing mature forest elements, resulting in large tracts of land with little vegetation cover and altered biodiversity. An alternative practice, aggregated retention, was developed with the objectives to 'lifeboat' species and processes, retain and enhance structural complexity and improve connectivity within the landscape, by retaining patches of unlogged forest within 'islands' and surrounding 'edges' in the harvested matrix. Although this practice has been successful in retaining biodiversity and mature forest species for some taxa, there have been relatively few studies on small ground mammals, particularly in the Southern Hemisphere, and very little attention has been given to landscape connectivity.

The main aim of this thesis was to determine the effects of different forestry practices (clearfelling, unlogged native forest and aggregated retention treatments) in wet eucalypt forest in Tasmania on two native rodent species: the swamp rat (*Rattus lutreolus*), a cover-dependent species, and the long-tailed mouse (*Pseudomys higginsi*), a habitat generalist. The first part of this project involved a field investigation of rodent abundances, demographics and habitat use (Chapter 2). The distinctly different responses of the two species to each practice, particularly within aggregated retention, then prompted investigations into physiological responses of both species (Chapter 3), and the genetic (Chapter 4) and behavioural (Chapter 5) implications of forestry practices on the cover-dependent swamp rat.

A major field study examining rodent abundances (Chapter 2) showed that the cover-dependent swamp rat declined with increasing disturbance among the three treatments, with abundance highest in unlogged forest, lowest in clearfelled and intermediate in aggregated retention. These responses to disturbance were also seen in the different habitat types created within aggregated retention sites, with lowest abundances in the harvested matrix, highest in the forested edges and intermediate in the forested islands. There was also a significant positive relationship between swamp

rat abundance and lower strata vegetation cover in harvested areas. In contrast, the abundance of the long-tailed mouse was not significantly different among treatments nor within the different habitat types in aggregated retention sites and there were no clear relationships with vegetation cover. The abundance results indicated that swamp rats were highly sensitive to harvesting while long-tailed mice were resilient and able to persist in harvested areas. Interestingly, the physiological data (blood profiles and body condition, Chapter 3) did not reflect this result, with no indication of stress responses nor differences in general condition in swamp rats, while long-tailed mice showed poorer body condition in clearfelled sites compared to unlogged sites. Long-tailed mice may only inhabit harvested areas out of necessity rather than showing resilience to disturbed habitats. Swamp rats were rarely found in harvested areas and may be minimising physiological impacts by preferentially residing in forested areas. Alternatively, populations may be experiencing elevated physiological stress in both harvested and unlogged sites due to fragmentation of the latter by minor roads.

Habitat fragmentation can impede movement of animals between suitable habitat, restricting dispersal and gene flow, and resulting in population differentiation. Analyses of swamp rat genetic samples (Chapter 4) from aggregated retention and unlogged sites revealed no evidence of inbreeding, but increased relatedness in aggregated retention island patches, which is most likely due to restricted dispersal across the 'hostile' harvested matrix. Surprisingly, analyses also revealed that swamp rats do not easily move across unpaved, narrow (< 10 m) and seldom-used roads. While harvesting may result in immediate and large-scale changes to suitable habitat, roads may pose a longer-term hindrance to dispersal.

Swamp rats prefer dense vegetation cover (Chapter 2), although the importance of ground-level structural cover and overhead visual cover was not clear from the field trial. Therefore, captive behavioural trials (Chapter 5) were run to test habitat cover preferences by swamp rats using ground-level structural cover and 1 m high overhead (visual) cover in low risk (dark) and high risk (light) conditions. There were no clear preferences for different densities of structural or visual cover. However, the walls of the experimental arena (essentially a type of structural cover, perhaps analogous to

large logs) were preferred over the centre area of the arena, regardless of cover density or risk conditions for both structural and visual cover types.

This thesis highlights the importance of using multiple disciplines (ecology, physiology, genetics, and behaviour) to investigate anthropogenic disturbances on wildlife. Despite persistence within the harvested matrix, long-tailed mice showed decreased body condition, which may have longer-term health and reproductive consequences. Additionally, while swamp rat populations appear to be thriving in unlogged forests, population differentiation is occurring due to the presence of unpaved, narrow, and seldom-used roads acting as dispersal barriers. It also confirmed that the practice of aggregated retention as an alternative to clearfelling is beneficial for small ground-dwelling mammals for the objective of life-boating, but may not be providing landscape connectivity as there are some restrictions for dispersal of cover-dependent species, at least over the short-term.

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CHAPTER 1: General introduction

Examples of native wet *Eucalyptus* forest harvesting in southern Tasmania. The top photo shows a clearfell, burn and sow site; the bottom photo shows a partially harvested (aggregated retention) site.

Anthropogenic habitat disturbance is a significant threat to biodiversity worldwide (Fahrig 2003; Foley *et al.* 2005). Habitat fragmentation, loss and modification can result in a decrease or degradation of habitat quality and quantity for associated species (Bender *et al.* 1998; Newell 1999). The impacts of habitat disturbance on populations, species and communities are often immediately observable, with a rapid decline in abundance and species richness (Andren 1994; Laurance 1997). Other impacts may be less obvious, but equally important for long-term species persistence. For example, habitat fragmentation may result in a patchy landscape of suitable habitat patches in a 'hostile' matrix, consequently reducing dispersal by cover-dependent or less mobile species, and thus negatively impacting breeding systems and gene flow (Banks *et al.* 2005; Lancaster *et al.* 2011). Furthermore, habitat modification can alter ecosystem processes and microclimates (e.g. edge effects; Saunders *et al.* 1991) and inter-species interactions (e.g. increased competition and predation risk; Crino *et al.* 2011), resulting in a more 'stressful' environment for individuals (Suorsa *et al.* 2004; Johnstone *et al.* 2012).

In disturbed landscapes, species persistence often relies on the ability of populations to retain functional, reproductively viable groups (Saunders *et al.* 1991; Turner 1996). In ecological studies, faunal species and community responses to disturbances are often measured through abundance or presence/absence metrics. These data are vital for assessing the persistence of populations or species that are vulnerable to disturbance. For example, abundance monitoring can provide information on ongoing persistence or loss of populations within the disturbed area (Hossack *et al.* 2012), which are of particular interest where species of high conservation value are likely to be affected (IUCN 2001). Furthermore, where capture-mark-recapture methods are used, demographic and reproductive data can be collected (e.g. sex ratios, age disparities; Spencer *et al.* 2005; Martin & Handasyde 2007; Flynn *et al.* 2011). However, in some cases, these traditional metrics can fail to detect crucial information about a species, particularly the associated health and reproductive impacts of persisting within a disturbed landscape (Wikelski & Cooke 2006). Therefore, this thesis aimed to evaluate the impacts of anthropogenic habitat disturbance on native mammal species using a multi-disciplinary approach. Ecological, physiological, genetic and behavioural studies were employed to provide a comprehensive assessment of species' responses to habitat modification in a production forestry landscape.

1.1 Native forest harvesting

Harvesting of native forests has been a contentious issue globally and locally. Native forests provide habitat for a great diversity of taxa, but are often managed for forest harvesting practices or converted into agricultural or urban land uses (FAO 2010). Forests that are managed for native forest harvesting are typically regenerated into stands of similar pre-harvesting tree species. A widespread method of forest harvesting over the past few decades has been clearfelling (also known as clearcutting), which involves the removal of virtually all standing trees and vertical structures within the site (coupe). Clearfelling of mature forests results in a relatively quick transformation from an uneven-aged forest, supporting a diverse range of late-seral and cover-dependent biota, into an area with few biological and structural legacies (Lindenmayer & Franklin 2002). Over the longer-term, the regenerating forest is typically even-aged, and lacking the biological legacies and diversity of habitats found in forests regenerating following natural disturbances such as wildfire (Franklin *et al.* 1997). As a consequence, forests regenerating following clearfelling may not provide suitable habitat for forest-dependent species (Niemela *et al.* 1993; Carey & Johnson 1995; DeMaynadier & Hunter 1995).The stark visual contrast between unlogged native forest and clearfelled forest (which in some cases is burnt post-harvest to stimulate tree seed germination) has resulted in strong, and often emotive, social responses (Ford *et al.* 2009), and has culminated in a demand for alternatives which will retain mature forest biological values.

1.2 Alternatives to clearfelling

One of the biggest challenges land managers face in any system, is adapting management strategies to meet the continued demand for natural resources while preserving biodiversity values (and thus minimising environmental and social concerns). Over the past few decades, forest managers have been seeking alternative silvicultural practices in an effort to improve biodiversity and aesthetic outcomes and thus conduct practices using an environmentally sustainable and socially acceptable approach (Gustafsson *et al.* 2012). In the 1990's, 'variable retention' (also now known as 'retention forestry') was developed by Franklin *et al.* (1997) as an alternative to clearfelling. The main premise was to emulate, as far as possible, natural disturbances

like wildfire, by harvesting in a manner which results in mosaics of young and old forests with structural complexity, within a relatively small area (in comparison to clearfelling). The three main ecological objectives of variable retention are to (1) 'lifeboat' species and processes, (2) enhance structural complexity, and (3) improve connectivity within the landscape. Franklin *et al*. (1997) proposed three different practices to achieve these outcomes: dispersed retention, aggregated retention, and mixed retention. Dispersed retention retains individual trees as standing structural features throughout the harvested coupe (Fig. 1.1b). In contrast, aggregated retention involves retaining stands or patches of trees within the harvested matrix as isolated 'island' aggregates and/or along the coupe boundary as 'edge' aggregates (Fig. 1.1c). Mixed retention, as the name implies, is a combination of both dispersed retention and aggregated retention.

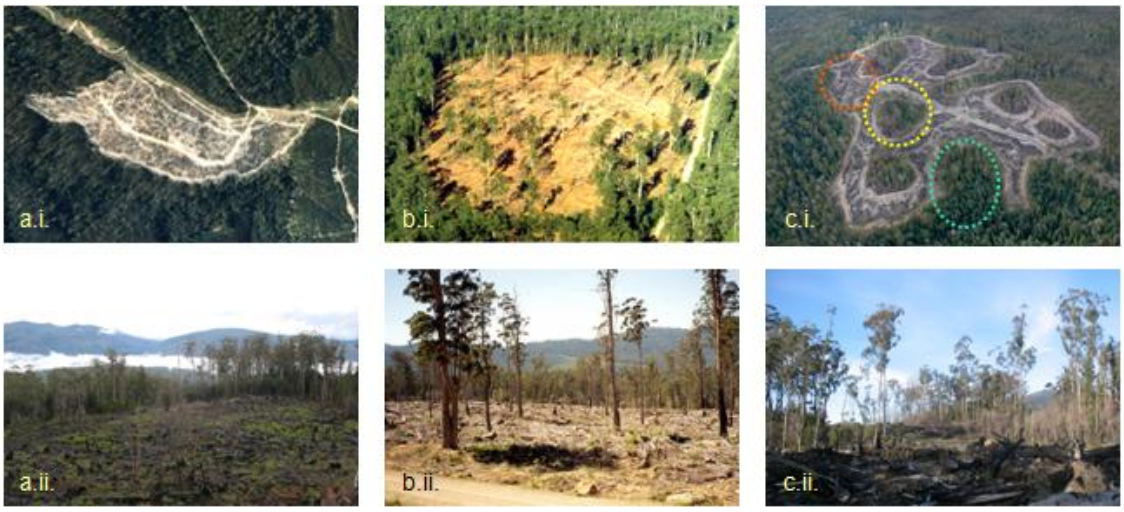

Fig. 1.1 Aerial and ground photos of three coupes that have been harvested using (a) clearfelling (b) dispersed retention, and (c) aggregated retention. All sites are from wet *Eucalyptus* forests in southern Tasmanian State Forests. Clearfelling (or clearfell, burn and sow, CBS) in Tasmanian wet forests involves removing virtually all standing structural features, burning the remaining debris, and sowing locally collected *Eucalyptus* seeds; these photos show a post-regeneration burn site. Dispersed retention retains individual standing trees within the harvested matrix (note that this method is not used in Tasmania); these photos show sites pre-regeneration burn. Aggregated retention involves retaining patches of unlogged forest as 'islands' (e.g. in the yellow circle; the ground photo shows the same island aggregate) within the harvested matrix (e.g. orange circle) or as 'edges' on the coupe boundary (e.g. green circle); these photos show coupes post-regeneration burn. Aerial and bii photos courtesy of Forestry Tasmania.

Variable retention has been trialled and put into practice (as operational coupes) in many different systems worldwide over the past two decades (Lindenmayer *et al.* 2012). While this is a relatively short period of time when considering the lifespan of mature forests (e.g. *Eucalyptus regnans* stands have been dated at > 500 years; Wood *et al.* 2010), over the short-term many taxa are showing responses that are beneficial in comparison to clearfelling (Rosenvald & Lohmus 2008; Gustafsson *et al.* 2010; Baker & Read 2011). These benefits have predominantly focussed on evaluating the first two objectives of variable retention: (1) lifeboating and (2) structural enrichment. In terms of lifeboating (i.e. maintaining species within a site), variable retention has been successful for some taxa, including those dependent on mature forest elements such as old growth standing trees and coarse woody debris (Lazaruk *et al.* 2005; Hyvärinen *et al.* 2009). Therefore, the second objective of variable retention, structural enrichment, often enables the retention of late-seral species and as such is intrinsically linked to the first objective of lifeboating.

Structural features such as coarse woody debris (CWD) and standing trees and stags (also known as snags) are crucial for providing habitat for many plant and animal species (Sverdrup-Thygeson & Ims 2002; Koch *et al.* 2008; Djupström *et al.* 2012). However, during clearfelling, the quantity and/or quality of CWD can be reduced (Grove & Stamm 2011) and most standing features are typically removed. Variable retention not only contributes to the preservation of CWD and standing trees and stags at the time of harvest (particularly in aggregated retention), but by retaining trees of mixed age classes within the harvested matrix, it also provides future CWD and hollow-bearing trees. Coarse woody debris provides a substrate for many species of fungi and bryophytes (Ódor *et al.* 2006), and is vital for the persistence of taxa such as saproxylic beetles which inhabit CWD and subsequently aid in its decomposition (Grove 2002). Furthermore, CWD is an important habitat component for some small ground-dwelling mammals (Vanderwel *et al.* 2010), and there is evidence that within harvested sites, the presence of CWD is maintaining late-seral mammal species (Fauteux *et al.* 2012). Within systems that use post-harvest regeneration burns (e.g. wet *Eucalyptus* forests), CWD retained in the unburnt patches (in aggregated retention) may provide essential habitat for many taxa. Standing trees and stags within the harvested matrix provide habitat for hollow-dependent fauna (e.g. birds and mammals; Cawthen & Munks 2011) and bark-dependent fauna (e.g. arthropods; Halaj *et al.* 2009).

Despite the wide attention variable retention has received, particularly over the last few years (see reviews by Rosenvald & Lohmus 2008; Gustafsson *et al.* 2010; Baker & Read 2011; Gustafsson *et al.* 2012; Lindenmayer *et al.* 2012), there are still large gaps in our knowledge of the effects of these practices on biodiversity. The three largest gaps that I have identified are (1) long-term impacts, (2) landscape connectivity, and (3) Southern Hemisphere systems. Until research trials or commercially-harvested coupes have been in place for longer time frames, direct studies investigating the longer-term impacts of variable retention are not possible. Improvement in landscape connectivity is the one of the major objectives of variable retention, but has largely been unexplored. Landscape connectivity in the context of variable retention implies the ability of individuals and propagules to disperse effectively through the variable retention areas. The scale at which this is assessed obviously differs dependent on what species or taxa are being investigated. For example, assessing the impact of variable retention on a large carnivore that moves up to 10 km per day is not feasible for coupe-scale studies. However, there are still many options to investigate this objective, but to my knowledge, one only study has directly investigated landscape connectivity (Chan-McLeod & Moy 2007).

There has been a clear dominance of Northern Hemisphere studies of variable retention, particularly in North America. Rosenvald & Lohmus (2008) conducted the largest review of variable retention to date, examining 214 studies, but excluded the Southern Hemisphere and Asia due to the paucity of published studies (as they were only able to locate three: Dignan *et al.* 1998; Yoshida *et al.* 2005; Vergara & Schlatter 2006). While the intervening years have produced an increase in published studies from Southern Hemisphere systems (e.g. Baker *et al.* 2009; Gates *et al.* 2009; Lefort & Grove 2009; Lencinas *et al.* 2009; Lindenmayer *et al.* 2010; Law & Law 2011; Lencinas *et al.* 2011; Neyland & Jarman 2011), there are still many taxa that have not been investigated including groups that are likely to be impacted by loss of mature forest habitat such as hollow-dependent non-flying fauna, bryophytes, and ground-dwelling mammals.

1.3 Variable retention in Tasmania: what we do and don't know

In Tasmania, a number of different alternative silvicultural systems were trialled in *Eucalyptus* forests of southern Tasmania in the Warra Silvicultural Systems Trial (Warra SST) (Neyland *et al.* 2012). These included aggregated retention (ARN), dispersed retention, clearfell with understorey islands, and clearfelling (clearfell, burn and sow, CBS) harvesting practices. The trials were established in 1997, with ARN ranking the highest of the four practices for the majority of mature-forest biodiversity measures such as ground-beetles and vascular plants (Baker & Read 2011), while dispersed retention was ranked second in most categories. Aggregated retention retains patches of unlogged and unburnt forest ('aggegates') within and adjacent to the harvested matrix (in Tasmanian wet *Eucalyptus* forests, the harvested matrix is burnt and sown in a similar process to CBS), while dispersed retention retains single trees. Dispersed retention was considered more dangerous for forestry workers in Tasmania's tall *Eucalyptus* forests (often over 50 m high, with crown characteristics making directional felling difficult) and as a result, ARN has been adopted as a standard harvesting practice in old growth Tasmanian wet *Eucalyptus* State Forests with the first coupes harvested in 2004 (although clearfelling is also still practised in the majority of wet regrowth forests). However, not all taxonomic groups have been represented in the Tasmanian ARN studies to date, and one of these groups that are likely to be affected by forest harvesting is small ground-dwelling mammals.

Small ground-dwelling mammal populations are susceptible to forest harvesting and disturbances for a number of reasons. Where home ranges are small (< 5 ha), disturbances at the scale of forest harvesting (typically 30 to 50 ha in Tasmanian wet *Eucalyptus* forests) are likely to have severe implications for individuals and populations, such as dispersal barriers, increased edge effects, and reduced access to resources. Where patches of habitat ('islands') are isolated, the island size and characteristics, edge effects and degree of isolation (i.e. matrix characteristics) may all play a role in determining the impact on a particular species (MacArthur & Wilson, 1967).

Isolated patches of forest within a 'hostile' matrix can have implications for dispersal between islands, resulting in higher relatedness and increasing the likelihood of

inbreeding (Peakall & Lindenmayer 2006). The impact of edge effects can be amplified due to an increase in the edge to forest ratio, particularly in isolated patches (Mills 1995). Where habitat cover is removed, small mammals may be more susceptible to predation near edges due to increased visibility by predators (Kotler *et al.* 1991). Food sources such as fungi and seedlings can be altered as a result of disturbance (Jacobs & Luoma 2008), and while some mature-forest species may be able to exploit the changes in resources, the boom may be temporary and thus abundance of the dependent species may also be short-lived (Sullivan *et al.* 1999). If individuals persist beyond initial disturbance but subsequently avoid open areas, then population density may increase in the remaining preferred habitat, resulting in increased intra- and inter-species competition for resources (Abramsky *et al.* 1979). The decreases in habitat and resource availability and quality, and increases in predation threat may then result in a more stressful environment, with long-term health and reproductive implications (Wikelski & Cooke 2006).

1.4 Native small ground-dwelling mammals of Tasmanian wet forests

Five small ground-dwelling species of mammals have been recorded in Tasmanian wet *Eucalyptus* forests: three carnivorous marsupials (dusky antechinus, swamp antechinus, white-footed dunnart) and two rodents (swamp rat, long-tailed mouse). In this thesis, I have focussed on the native rodent species as we were unlikely to obtain sufficient sample sizes of the three marsupial species for a population study (J. McEvoy pers. comm.; Rounsevell *et al.* 1991). The two native rodent species are both common and widespread throughout Tasmania and are sympatric in wet *Eucalyptus* forests. However, they differ in their habitat associations, making the investigation into their responses to harvesting all the more appealing.

The swamp rat, *Rattus lutreolus* Gray 1841, is a common and widespread native rodent species found throughout south-eastern Australia, including an endemic Tasmanian sub-species, *R.l. velutinus* Thomas 1882. The long-tailed mouse, *Pseudomys higginsi* Trouessart 1897, is an endemic species found throughout Tasmania. The swamp rat and long-tailed mouse share similar life expectancies (1 to 2 years; Green 1967; 1968), breeding and reproductive cycles (spring/summer, 1-3 litters; Green 1967; Stoddart &

Challis 1991), and diets (predominantly stem and leaf material, Driessen 1987). The swamp rat weighs approximately 95 to 124 g (Monamy 1995a), while the long-tailed mouse has been reported to weigh only 60 to 66 g (Monamy 1995c). They occupy many of the same vegetation types but appear to differ in habitat requirements, which has been attributed to competition between the species and their size disparity (Luo *et al.* 1998; Monamy & Fox 1999).

The swamp rat occupies many different habitat types (e.g. coastal heath, dry and wet sclerophyll forests), but within these areas it almost exclusively inhabits areas with dense vegetation cover (Fox & Monamy 2007). Despite the swamp rats' widespread distribution across Tasmania, and south-eastern Australia, it is vulnerable to habitat disturbance due to its dependence on dense habitat cover (Monamy 1995b; Monamy & Fox 2000). When disturbances such as wildfire occur, the swamp rat disappears from those areas and will not recolonise until vegetation cover reaches a certain density threshold (Fox *et al.* 2003). As a result, this species is regarded as a habitat specialist, and is likely to be negatively affected by harvesting practices that remove large areas of vegetation cover. The loss of cover is likely to expose swamp rats to increased predation risk (and mortality) and potential dispersal barriers (thus impeding immigration and emigration). In ARN, the patches of retained unlogged forest within the harvested matrix may benefit cover-dependent species such as swamp rats, and provide a 'lifeboat' for population persistence.

Despite being a common and widespread species across Tasmania, few studies have been conducted on long-tailed mice. Stoddart & Challis (1991; 1993) investigated their habitat associations, morphology and breeding cycles, and the growth and development of young mice in field and laboratory studies. Monamy (1995c) also studied habitat use of long-tailed mice in wet *Eucalyptus* forests. Within these same forests, Monamy & Fox (1999) and Luo *et al*. (1998) investigated competition between long-tailed mice and swamp rats as a result of observed microhabitat partitioning. They concluded that female swamp rats were dominant and inhabited the densest vegetation, then male swamp rats and finally long-tailed mice which were out-competed due to their smaller size. These were the last published studies of long-tailed mice, leaving quite a big gap in our knowledge of their ecology. However, their use of many different habitats and their ability to inhabit both densely and sparsely vegetated

microhabitats indicates that long-tailed mice fall on to the 'generalist' side of the habitat specialist-generalist groupings.

1.5 Using a multi-disciplinary approach for assessing responses to habitat disturbance

Studies investigating the impacts of habitat disturbance on wildlife often focus on a single approach. For example, species abundance is a common method for measuring disturbance impacts on populations. However, where multi-disciplinary methods are used, it is possible to gain a greater understanding of underlying mechanisms for population responses (Wikelski & Cooke 2006). For example, long-term studies of fluctuating snowshoe hare populations have been explained not only by predator abundance, but also by sublethal stress effects of predators on prey, and maternal stress on reproductive success and offspring fitness (Sheriff *et al.* 2011). These types of multidisciplinary approaches are also being applied in habitat disturbance studies. For example, a study of forest fragmentation showed that population decline of the small mammal, *Antechinus agilis*, may be a result of declining health (high parasite load and anaemia) related to greater environmental stress living in fragments than unfragmented habitats (Johnstone *et al.* 2012). In this thesis, I have adopted a multi-disciplinary approach to investigate habitat disturbance on native rodents in a forestry landscape. Initially, I used traditional ecological methods such capture-mark-recapture to provide abundance data and demographic profiles, and vegetation surveys to collect habitat surveys which allowed me to create a broad-scale overview of rodent responses to different forestry practices. This subsequently led me to key areas of interest from both the species perspective and the applied conservation perspective. These additional areas of interest were investigated using physiological health metrics, genetic techniques, and a captive behavioural trial. The reasoning for using each of these methods is detailed below.

1.5.1 Long-term stress and health responses

Short-term stress responses by an individual are typically beneficial as they allow non-essential physiological and behavioural functions to shut down in order to deal with a stressor (Romero 2004). For example, an encounter with a predator increases the release of stress hormones, initiating the 'fight or flight' response (Sapolsky *et al.* 2000). However, where stressors are increased or prolonged (i.e. long-term), they can become detrimental to the health of an individual, resulting in reduced condition, reproductive output and immunocompetence (Dhabhar & McEwen 1997; Sapolsky *et al.* 2000; Charbonnel *et al.* 2008). Long-term stress can impair an individual's ability to mount a short-term stress response, thus affecting its ability to evade lethal encounters (Cyr *et al.* 2009). The health effects of long-term stress can even be passed on from parents to offspring, thus affecting the long-term fitness of a population (Sheriff *et al.* 2010; Love *et al.* 2012). Through stress response indicators such as stress hormones and leukocyte profiles, and health metrics such as body condition indices and erythrocyte analysis, the longer term health and fitness of populations can be assessed.

1.5.2 Population genetics and landscape connectivity

While individuals or populations may be able to persist in remnant habitat patches after anthropogenic disturbance, if the surrounding matrix is uninhabitable or too dangerous to use, then restricted emigration and immigration may occur (Peakall *et al.* 2006). Reduced landscape connectivity due to anthropogenic fragmentation can lead to restricted gene flow and increased relatedness and may have long-term implications for the persistence of species within a landscape (Frankham *et al.* 2002). Over the past few years, the use of genetic analyses to identify population responses to habitat fragmentation and degradation has been growing rapidly (Storfer *et al.* 2010). Microsatellite DNA markers are the most commonly used tool to investigate population genetics and can inform us about population structure at multiple scales. They can detect inbreeding within populations, relatedness between isolated populations, and gene flow over the larger landscape (Peakall *et al.* 2006; Macqueen *et al.* 2008; Lancaster *et al.* 2011).

1.5.3 Examining habitat requirements through behavioural studies

Where species have specific habitat requirements, modifications to the habitat within their home range may result in reduced population size, and, over time, the loss of local populations (Bender *et al.* 1998; Wayne *et al.* 2006). However, by providing essential habitat features within a disturbed environment, populations may be able to utilise the modified area. For example, by retaining mature hollow-bearing trees within a harvested coupe, hollow-dependent fauna such as possums are able to persist in the modified landscape (Cawthen & Munks 2011). Where habitat requirements are unclear, captive behavioural studies of wild-caught individuals can be conducted to determine habitat preferences.

1.6 Aims of thesis

The primary aim of this thesis was to determine the effects of an alternative forestry practice, aggregated retention, on native rodent populations and to compare these effects with those from traditional clearfelling and native unlogged forest. The use of multi-disciplinary techniques in this project provide not only a snapshot of rodent population persistence or loss by using abundance and demographic measures, but allows the assessment of the potential longer-term implications of aggregated retention through health metrics and gene flow, and provides a clearer understanding of habitat associations through behavioural responses to different habitat covers. This thesis is not only relevant to forest managers, but also to land managers interested in the effects of habitat fragmentation and loss, particularly where isolation of remnant habitat may occur, and in mitigating these effects. At the same time, this thesis aims to improve our knowledge of the ecology of a relatively unknown species, the long-tailed mouse, and to build on previous studies of a more widespread, but cover-dependent habitat specialist, the swamp rat.

1.6.1 Chapters and specific research questions:

Chapter 2: Rodent abundance and habitat associations. How do different forestry practices affect the abundance and sex ratios of a cover-dependent species and a habitat generalist species?

Chapter 3: Are physiological stress indicators and health impacts higher in native rodents living in disturbed habitats than in undisturbed habitats?

Chapter 4: Do harvesting practices and forestry roads create barriers to gene flow for a cover-dependent species?

Chapter 5: Do swamp rats have preferences for different types of habitat cover (ground-level structure and overhead visual cover)?

Chapter 6 provides a synthesis of the four experimental chapters, discusses these implications, assesses the success of variable retention objectives, and details suggestions for future work.

Each of the four data chapters are written as papers for peer-reviewed journals. For this reason, there is some repetition in the introduction and methods sections, as well as slight inconsistencies in format and style associated with specific journal requirements. All references have been formatted in one style for the ease of the reader.

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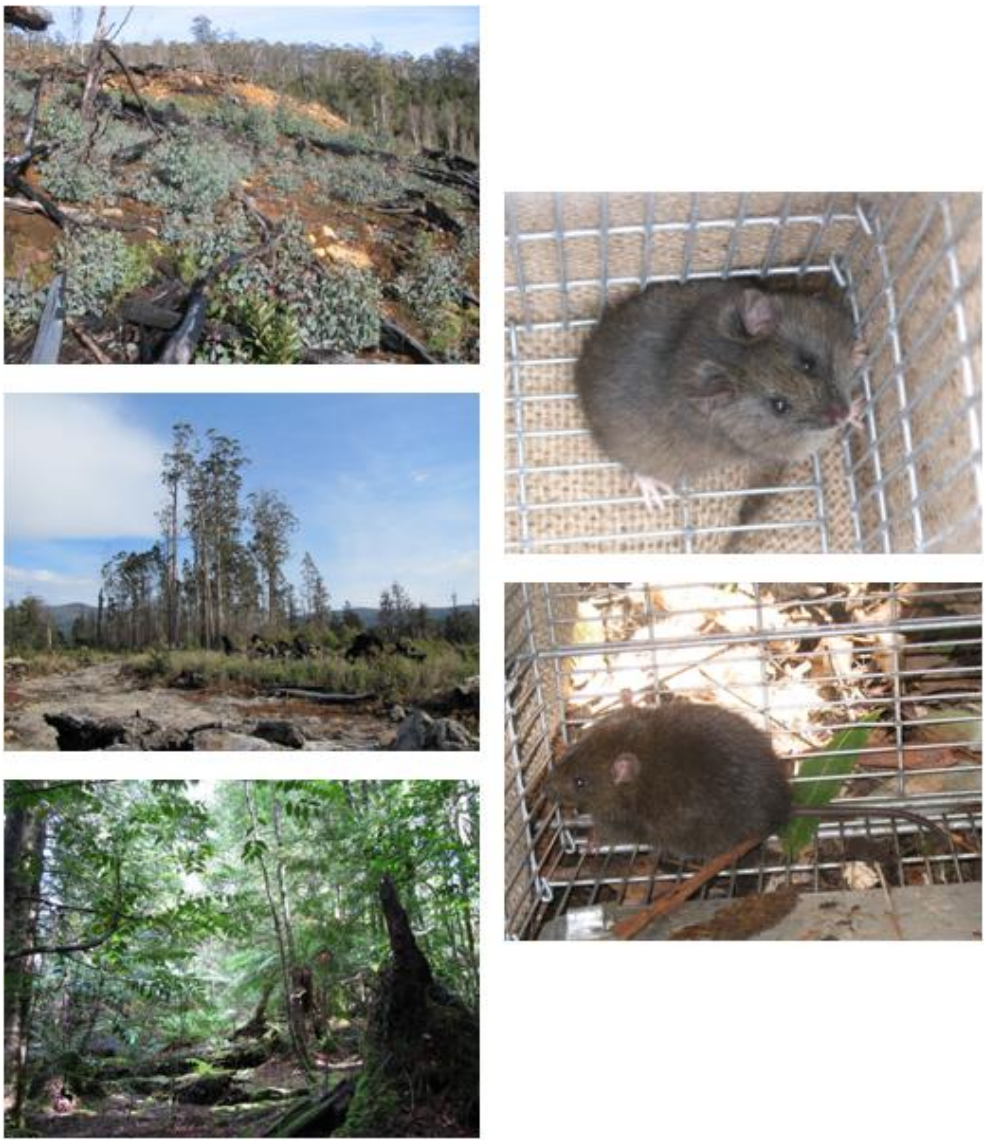
CHAPTER 2: Short-term responses of native rodents to aggregated retention in old growth wet *Eucalyptus* forests

Stephens H.C., Baker S.C., Potts B.M., Munks S.A., Stephens D. & O'Reilly-Wapstra J.M. (2012) Short-term responses of native rodents to aggregated retention in old growth wet *Eucalyptus* forests. *Forest Ecology and Management* **267**, 18-27



From top to bottom: on the left, a clearfell burn and sow coupe, an aggregated retention coupe showing an island aggregate, and an unlogged site; on the right, a large male long-tailed mouse (*Pseudomys higginsi*), and a female swamp rat (*Rattus lutreolus*).

Abstract

Aggregated retention (a type of variable retention) is a silvicultural practice that is being implemented in forests worldwide as an alternative to traditional clearfelling (clearcutting) practices. Aggregated retention retains patches of unlogged forest within the harvested matrix. It has been proposed that it retains biodiversity values better than clearfelling, although, to date, there has been limited research on small mammal responses to this practice, especially in southern hemisphere systems.

This study determined whether aggregated retention provided a 'lifeboat' for two native rodent species; the habitat specialist, cover-dependent swamp rat (*Rattus lutreolus velutinus*), and the habitat generalist, long-tailed mouse (*Pseudomys higginsi*), in wet *Eucalyptus* forests. We compared their abundances in three forestry treatments (clearfell, burn and sow, unlogged native forest and aggregated retention (including edges, islands and harvested matrix) over three trapping periods (one- to three-years post-burn), and assessed the effect of habitat cover (vegetation) on rodent abundances.

The cover-dependent swamp rat was found in highest abundance in unlogged forest, intermediate in aggregated retention and lowest in clearfelling. Within aggregated retention, there was a trend for decreasing swamp rat abundance with increasing disturbance within the different habitat types (highest abundance in edges, intermediate in islands, lowest in harvested matrix). The generalist long-tailed mouse, was found in equal abundance across all forestry treatments and habitat types. Island size within aggregated retention coupes had no effect on the presence of either species. Sex ratios did not differ between forestry treatments or habitat types for either species, although swamp rats showed female dominance irrespective of treatment or habitat type. Within harvested areas, a high percentage understorey cover was an important predictor of swamp rat abundance.

Our results demonstrate that aggregated retention provides a lifeboat for cover-dependent small mammals in comparison to traditional clearfelling practices. The habitat cover provided by the retained forest allows populations to persist in connected and isolated patches within production landscapes. Vegetation density at the lower strata appears to be an important determinant for recolonisation in harvested areas.

2.1 Introduction

Unmanaged native forests exist as mosaics of early, mid and late-successional stands that contain a high level of structural diversity, providing habitat for a wide range of species (Berg *et al.* 1994; Lindenmayer & Franklin 2002). However, where native forests are part of production landscapes, traditional harvesting methods such as clearfelling (or clearcutting) are commonly practiced, resulting in even-aged stands lacking mature forest elements and stand structural complexity. Variable retention silviculture (or green-tree retention, retention forestry) was developed to retain structural complexity at the coupe scale to achieve visual (social), ecological (e.g. maintenance of biodiversity) and economic goals in production forest landscapes (Franklin *et al.* 1997). The main biodiversity-related objectives of variable retention are to provide 'lifeboating' for species and processes (retention of species, populations or processes post-disturbance), structural and functional enrichment of the forest regenerating after harvesting, and to improve connectivity in the landscape by reducing gaps between unlogged forest elements (Franklin *et al.* 1997).

A review of variable retention by Rosenvald & Lohmus (2008) compared the responses of different taxa to clearfelling and variable retention. Species richness and abundance showed either a positive or equal response to variable retention compared to clearfelling. Variable retention reduced harvest-related losses of populations or individuals in the majority of studies and lifeboating was particularly successful for ectomycorrhizal fungi, epiphytic lichens and small ground-dwelling mammals. However, most studies examining the biodiversity impacts of variable retention silvicultural systems compared to clearfelling have focused on forests in North America (particularly the Pacific Northwest) and Europe (Rosenvald & Lohmus 2008). In the Southern Hemisphere there have been few studies examining variable retention silvicultural systems (Vergara & Schlatter 2006; Baker *et al.* 2009; Lefort & Grove 2009; Lencinas *et al.* 2009; Lindenmayer *et al.* 2010), leaving considerable gaps in our knowledge of these systems within this region.

Aggregated retention is a form of variable retention where patches of intact forest are retained within a harvested coupe (or stand, cutblock) (Franklin *et al.* 1997). This silvicultural practice has recently been adopted as a standard practice for harvesting

(retaining contiguous and/or free-standing patches) in the majority of old growth wet *Eucalyptus* forests on Tasmanian public land (State Forest) to achieve ecological, economic and social goals (Forestry Tasmania 2009). However, there are still relatively few studies which have examined the effects of aggregated retention on biodiversity values in *Eucalyptus* forests (Baker & Read 2011) and only one has measured the responses of ground mammals (Lindenmayer *et al.* 2010). Small ground-dwelling mammals are an ideal taxonomic group for assessing the impacts of different forestry practices, since they can occupy different habitat niches. For example, habitat generalists occupy a wide range of habitat types and hence may be more adaptable to various levels of disturbance (Andren, 1994), whereas habitat specialists require particular habitat features (e.g. dense vegetation, structural cover) which make them more sensitive to disturbances, showing decreases in abundance and slower population recovery (Recher *et al.* 2009). Furthermore, the limited home range size of small mammals make them susceptible to reduced landscape connectivity, resulting in disrupted dispersal and breeding systems (Banks *et al.* 2007) and altered sex ratios (Martin & Handasyde 2007; Flynn 2011).

In this current paper, we examine the effects of aggregated retention on two sympatric ground-dwelling native rodents in Tasmania. The swamp rat (*Rattus lutreolus velutinus* Thomas 1882) and long-tailed mouse (*Pseudomys higginsi* Trouessart 1897) are both relatively common in old growth wet *Eucalyptus* forests in Tasmania and share similar diets (Driessen 1987) and breeding cycles (Norton 1987a; Stoddart & Challis 1991). The swamp rat is considered a habitat specialist as it is cover-dependent (Fox & Monamy 2007). Although less is known about the long-tailed mouse, we considered it to be a habitat generalist, as it is found in most habitats throughout Tasmania (except for grasslands; Stoddart & Challis 1991). Home ranges for long-tailed mice have been estimated at 0.1 – 0.4 ha (Stoddart & Challis 1991), and average range distances for swamp rats are 60 to 70 m (Norton 1987a), making both species potentially vulnerable to disturbances within forestry coupes that have an average size of 50 ha. Consequently, these two species were ideal for investigating the responses of small rodent responses to varying levels of disturbance.

The aim of this study was to determine how native rodents respond, in the short-term, to three different forestry treatments in old growth wet *Eucalyptus* forests: (1) clearfell,

burn and sow (CBS), (2) unlogged native forests (UNL), and (3) aggregated retention (ARN) (Fig. 2.1). Determining the impacts of aggregated retention on native rodents will help inform forest managers about coupe-level biodiversity values of different logging treatments. However, we also wanted to examine responses of native rodents to three habitat types within ARN coupes compared to CBS and UNL to determine the value of the aggregates as 'lifeboats' for these species. These three habitat types are the harvested matrix (ARN-Harvest, which undergoes a similar logging and burning protocol to CBS), unlogged isolated aggregates within the harvested matrix (ARN-Island), and unlogged edge aggregates connected to the surrounding forest or coupes (ARN-Edge). In addition, we wanted to know how important vegetation cover was in determining rodent abundances. Therefore our main questions were:

1. How do native rodent abundances and sex ratios differ between the three forestry treatments (CBS, UNL, and ARN)?
2. How do native rodent abundances and sex ratios differ between five habitat types (CBS, ARN-Harvest, ARN-Island, ARN-Edge, and UNL)?
3. Within ARN, was there a relationship between island size and the presence of rodents?
4. What is the relationship between native rodent abundance and vegetation cover in production forest landscapes?

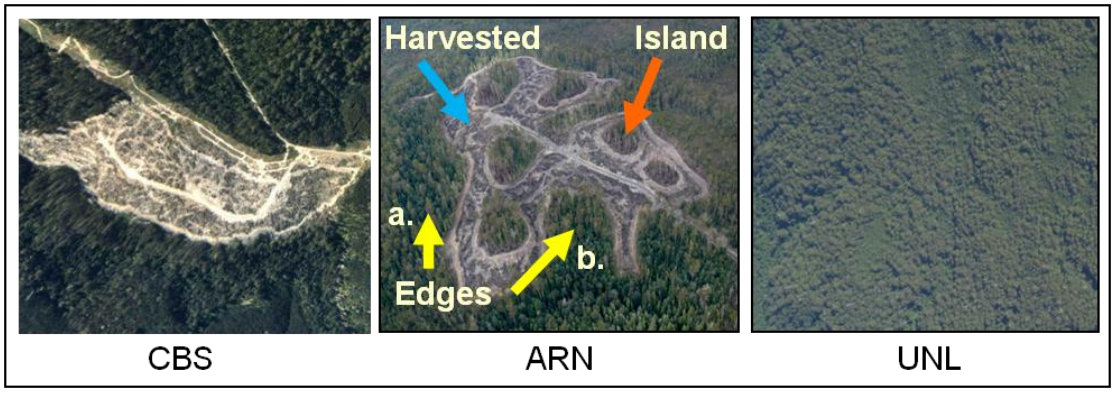


Fig. 2.1 Examples of a clearfell burn and sow coupe (CBS), an aggregated retentioncoupe (ARN) and unlogged native forest (UNL) in wet Eucalyptus forests in Tasmanian State Forest. Within ARN, there are three different habitat types: ARN islands, ARN edges (a. boundary and b. peninsula) and ARN harvested matrix.

We hypothesise that the habitat specialist (swamp rat) would be negatively affected by increased disturbance and a reduction in vegetation cover while the habitat generalist (long-tailed mouse) would be unaffected or positively affected in disturbed habitats and areas with reduced vegetation cover. We expect ARN-Islands to be more disturbed and exposed to edge effects than ARN-Edges, and thus hypothesise a gradient of decreasing disturbance, and its associated effects, from CBS and ARN-Harvest, to ARN-Island, to ARN-Edge and UNL.

2.2 Methods

2.2.1 Study area

Our study was conducted in old growth wet native *Eucalyptus* forests and recently harvested coupes in State Forest in two regions of southern Tasmania, Australia: the Styx (42.81ºS, 146.65E) and Huon (43.11ºS, 146.76ºE) Valleys (Fig. 2.2). We investigated rodent abundances in four replicates (two replicates from each region, all embedded in a forested landscape) of three different forestry treatments: clearfell, burn and sow (CBS), unlogged native forest (UNL) and aggregated retention (ARN). A fourth treatment examining unburnt patches remaining in unlogged forest following wildfire would have been ideal as variable retention aims to retain some of the habitat and biodiversity from the pre-harvest stand, analogous to biological legacies following natural disturbances such as wildfire (Lindenmayer and Franklin, 2002). However, a lack of recent wildfires in our study regions prevented this comparison from being included in the study. Each replicate group (e.g. UNL Site 1, ARN Site 1, CBS Site 1) was initially grouped according to geographic region (Fig. 2), by forest type (pre-harvest for CBS and ARN) and, in the case of CBS and ARN coupes, disturbance history. These coupes were harvested in 2005/06 and underwent a high intensity regeneration burn in March/April 2007 to encourage *Eucalyptus* seedling recruitment followed by aerial sowing of locally collected seeds. Each replicate group was sampled within a four week period during each trapping period to reduce temporal variation between treatments.

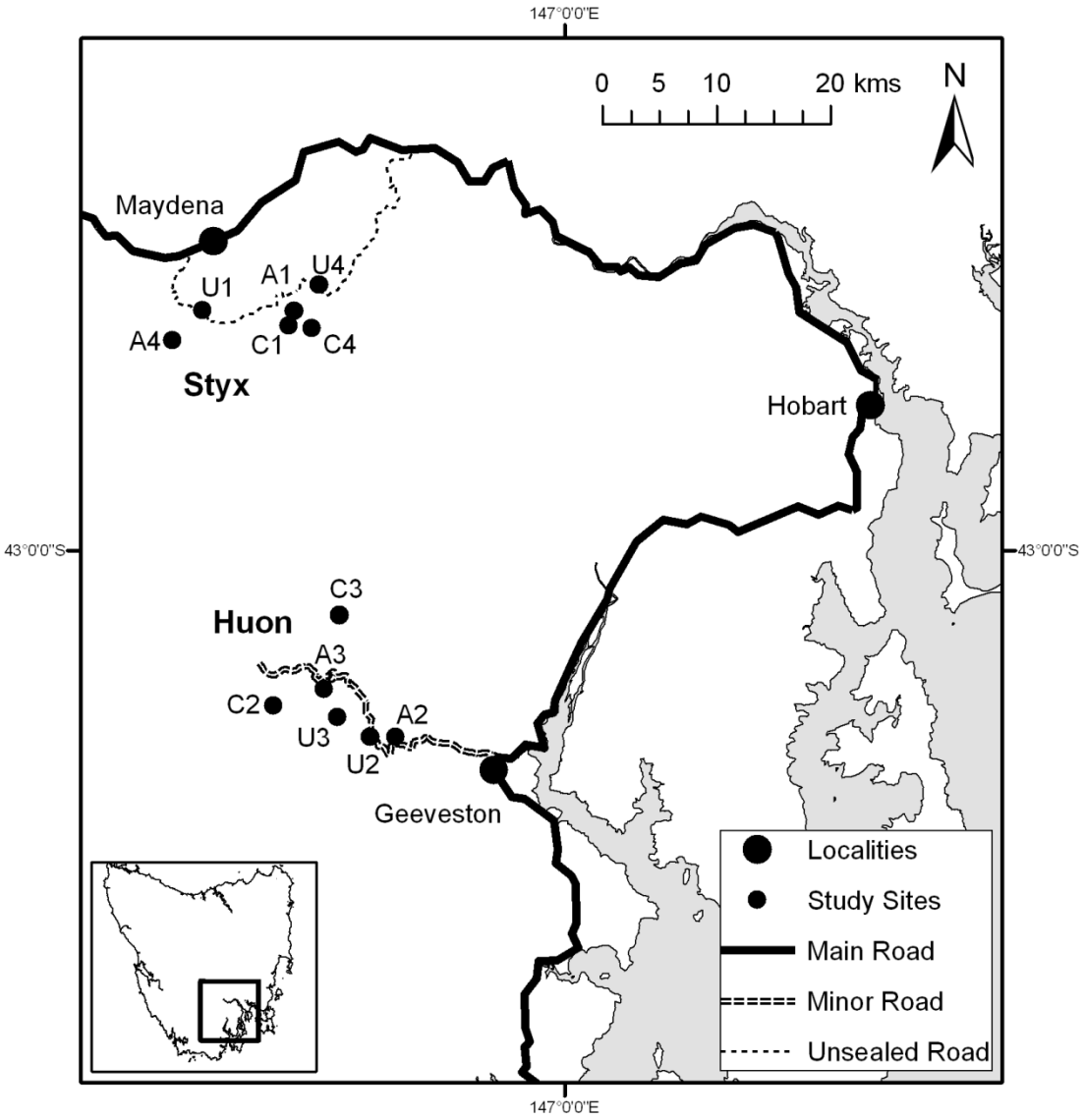


Fig. 2.2 Location of study sites in southern Tasmania, Australia. There are four replicates of each forestry treatment, grouped geographically. Replicates 1 and 4 are in the Styx Valley, south of Maydena, and replicates 2 and 3 are in the Huon Valley, west of Geeveston. Each replicate contains one unlogged native forest site (U), one aggregated retention coupe (A) and one clearfell, burn and sow coupe (C). The first letter denotes the treatment, while the number indicates the replicate.

Our CBS sites were forestry coupes ranging in size from 12 to 74.5 ha. CBS harvesting retains some mature forest structural components such as coarse woody debris but no standing trees. Three UNL sites were in reserves and one site was an unlogged coupe. The areas sampled ranged in size from 12 to 30 ha. All UNL sites had undergone minor selective harvesting in the past and one had been part of an area subject to

wildfire in the 1930s. All UNL sites retained old growth forest elements, including mature trees, and had been left relatively undisturbed for more than 70 years. In ARN coupes (29.8 to 48.5 ha), patches of forest (28-49 % of coupe area) were retained as either edge aggregates connected to the surrounding forest or as island aggregates isolated in the harvested matrix (Fig. 2.1). Edge aggregates were usually incorporated into the coupe boundary although some jutted into the harvested matrix as 'peninsulas'. Multiple islands of 0.6 to 2.6 ha were typically retained, except in one coupe where only one large island of 3.3 ha was retained.

The forested areas (UNL, ARN-Edge and ARN-Island) were old growth *Eucalyptus* forests dominated by *E. regnans, E. delegatensis* and *E. obliqua* with the rainforest species *Nothofagus cunninghamii* and *Atherosperma moschatum* dominating the upper understorey. Common species in the lower understorey included *Dicksonia antarctica, Anopterus glandulosus, Anodopetalum biglandulosum* and *Eucryphia lucida*. In the harvested areas (CBS and ARN-Harvest), the groundcover was often dominated by *Eucalyptus* seedlings and colonising species such as *Pomaderis apetala, Senecio minimus* and *Pteridium esculentum* with *Eucalyptus* species and *Acacia dealbata* becoming more dominant two to three years post-burn.

2.2.2 Target species and trapping protocol

While our study was primarily focused on native rodents, we also documented all small to medium-sized mammals (< 10 kg) that were trapped in the first trapping period of the study (Table 2.1). During the first trapping season (spring/summer 2008-09, 1 year post-burn), two different types of live-traps were used: Elliott traps (33 × 10 × 9 cm, Elliott Scientific Company, Upwey, Victoria) and collapsible Mascot wire traps (30 × 30 × 60 cm, Mascot Wire Works Pty Ltd, Homebush West, New South Wales). In the second and third trapping periods (2009 and 2010, 2 and 3 years post-burn), only Elliot traps were used to better target native rodents (although Mascot traps were also effective in capturing native rodents, Elliott traps were more practical). These latter trapping trips were conducted over autumn and winter to target native rodents during the post-breeding period to reduce captures of females with dependent young.

Table 2.1 Total number of individuals per species captured over three trapping periods from 2008 to 2010[a]

Common name	Scientific name	Taxonomic group	Trapping period 1 Spring/summer 2008/09 (72 traps per site)	Trapping period 2 Autumn/winter 2009 (54 traps per site)	Trapping period 3 Autumn/winter 2010 (54 traps per site)
Swamp rat	*Rattus lutreolus*	Rodent	126	74	52
Long-tailed mouse	*Pseudomys higginsi*	Rodent	86	75	43
House mouse[b]	*Mus musculus*	Rodent	25	42	36
Black rat[b]	*Rattus rattus*	Rodent	5	1	0
Dusky antechinus	*Antechinus swainsonii*	Marsupial	5	5	5
Brushtail possum	*Trichosurus vulpecula*	Marsupial	51	n/a	n/a
Eastern Quoll	*Dasyurus viverrinus*	Marsupial	6	n/a	n/a
Tasmanian pademelon	*Thylogale billardierii*	Marsupial	4	n/a	n/a
Tasmanian Devil	*Sarcophilus harrisii*	Marsupial	1	n/a	n/a

[a] Numbers have not been adjusted for number of traps set or trap availability. Mascot traps (suitable for medium-sized mammals) were used in trapping period 1 (36 per site) while Elliot traps (suitable for small mammals) were used in all three trapping periods (36 in trapping period 1; 54 in trapping periods 2 and 3).

[b]Non-native species

In each site (n = 12) we set up nine plots of eight trap stations (n = 72 traps per site). All plots were randomly allocated within the sites, but at least 50 m apart. Within each plot we set up two parallel transects 10 m apart with four traps spaced at 10 m intervals along each transect. In CBS and UNL, the nine plots were randomly allocated across the site. In ARN, we allocated three plots randomly within each of the three habitat types created during harvesting: edge aggregates, island aggregates and harvested matrix (Fig. 1.1). One ARN coupe had only one large island (3.3 ha) so the three plots were all located within this island. Areas near coupe and island edges were not excluded when randomly allocating plots, since we wanted to encompass the full range of habitats within production forest coupes. Average distances from plots to coupe edges (i.e. contiguous forest) were 84 m (± 48 m S.D.) in CBS, 43 m (± 22 m S.D.) in ARN-Harvest and 102 m (± 35 m S.D.) in ARN-Island. Trap stations were, on average, 34 m (± 13 m SD) from the edge within ARN-Island patches and 32 m (± 7 m S.D.) in ARN-Edge patches. In unlogged sites, plots were either located off unpaved roads (two sites) or narrow (1-2 m), unused walking tracks, with trap stations ranging from approximately 20 to 80 m from the edge in all sites.

During the first trapping season, Mascot traps were placed along one transect while Elliott traps were placed along the other. During the second and third trapping period, we reduced the number of traps to 54 (Elliott traps only) per site to ensure all traps could be checked and managed within an appropriate time frame for animal ethics purposes. All nine plots in each site were used and within each plot, six out of the eight trap stations were randomly chosen to be used. In all three trapping periods, each trap was set for three nights, resulting in 2,692 trap nights in trapping period 1 and 1,944 trap nights in trapping periods 2 and 3. Each trap was rebaited and re-set each morning. Bait consisted of a piece of apple and a bait ball made of peanut butter and oats with either vegemite or imitation vanilla essence for additional scent. To provide protection from wind and rain, Mascot traps were covered with hessian and Elliott traps were two-thirds covered with a ziplock plastic bag. Nesting material was available in all traps.

Each animal captured was identified to species and transferred to a hessian or calico bag for handling. All individuals were weighed and sexed. During the first two trapping periods, PIT-tags (passive integrated transponders; AllFlex, Australia and

Provet, Australia) were used to mark larger mammals and native rodents (using similar methods to Lebl & Ruf 2010) for identification of recaptures within and between trapping periods. In the third trapping period, native rodents were marked by individual ear-clipping patterns (tissue was collected for a related study). House mice were not marked and each capture was considered a new individual. All other individuals were temporarily marked (hair-clipping) for identification within a trapping period. After handling, all animals were released at the site of capture.

2.2.3 Habitat assessment

Habitat surveys were carried out at each trap station once per trapping period (n = 20 surveys per plot). All surveys recorded the vegetation cover within a one metre radius of each trap station. The percentage cover was estimated for canopy cover (> 25 m), understorey cover (1 m – 25 m), groundcover (< 1 m) and total vegetation cover (all strata) using the Braun-Blanquet Scale (Braun-Blanquet 1932).

2.2.4 Statistical analyses

2.2.4.1 Abundance data

Each individual rodent was recorded as 'new' the first time they were captured during a trapping period and only new individuals were included in the analysis. Adequate numbers of the non-native house mouse (*Mus musculus*) permitted analysis as a comparison between native and non-native species. Abundance data needed adjustments for (a) differing trap effort between trapping periods (72 traps per site in trapping period 1 and 54 traps per site in trapping periods 2 and 3) and between habitat types (24 or 18 traps per habitat in ARN, 72 or 54 traps in CBS and UNL), (b) trap availability for house mice (Elliot traps only during trapping period 1), and (c) for site-level comparisons (habitat patch area size within ARN sites). While trap numbers within ARN coupes were equal between the three habitat types (edge aggregates, island aggregates and harvested matrix), the proportion of each habitat area (ha) was not equal. Hence, abundance at the forestry treatment level was adjusted to take this into account for comparisons at the treatment level. The abundance data used in analyses was number of new animals per 54 traps.

To investigate the abundance per species between the three forestry treatments (CBS, UNL and ARN) we fitted mixed models using PROC MIXED in SAS (SAS Institute

Inc. 2008) with forestry treatment included as a fixed factor, replicate (n = 4) as a random factor and trapping period (n = 3) as a repeated measure. Treatment by trapping period interactions were tested as a fixed effect, and replicate by treatment and replicate by trapping period were used as random effects to calculate error terms to test fixed effects. We also wanted to investigate rodent abundance among different habitat types within ARN and how they compare to CBS and UNL. Therefore, we ran a similar mixed model with five treatments: CBS, ARN-Harvest, ARN-Island, ARN-Edge and UNL. Multiple pair-wise comparisons of significant effects (least-squares means) were made using Tukey-Kramer adjustment. Square-root transformations were needed for all variables to satisfy assumptions of normality. To determine whether rodents were responding simply to the amount of unlogged habitat retained rather than the arrangement of retained habitat with several aggregates within ARN sites, we performed a t-test in Microsoft Excel to compare the average observed abundance in ARN coupes per hectare with an 'expected' ARN abundance per hectare. This was calculated from the weighted average of CBS and UNL coupes within each replicate group (weighted by percentage area retained and harvested in ARN coupes).

The relationship between ARN-Island patch size (ha) and the presence/absence of native rodents was tested using logistic regression (PROC LOGISTIC; SAS Institute Inc. 2008). Within harvested sites (CBS or ARN-Harvest), we also tested whether plot proximity to unlogged forest edges influenced the presence/absence of native rodents. The presence/absence of each species per plot was used as the response variable. There were insufficient numbers of house mice for statistical analysis.

The sex ratio was calculated for each species as the proportion of males in the population. A mixed model was also fitted to the sex ratio data for the native rodents with treatment as a fixed factor and replicate as a random factor. Trapping period was not included in the analysis due to many missing values where no animals were captured and, therefore, no sex ratio calculated. Arcsine square root transformations were performed. We also tested whether the sex ratio of either species, irrespective of treatment, deviated from parity using chi-square analysis in Microsoft Excel.

2.2.4.2 Habitat data

Spearman's Rank Correlation (PROC CORR; SAS Institute Inc. 2008) was used to test correlations between the habitat variables (total vegetation cover, canopy cover, understorey cover and groundcover). Total vegetation cover was highly correlated with understorey cover ($r_s = 0.87$, $P < 0.01$) and was, therefore, removed from further analyses. Mixed models (PROC MIXED; SAS Institute Inc. 2008) were used to test the difference of each vegetation cover type between the five habitat types (CBS, ARN-Harvest, ARN-Island, ARN-Edge, UNL). Habitat type was included as a fixed factor, replicate as a random factor and trapping period as a repeated measure. The habitat type by trapping period interaction was tested as a fixed factor, and replicate by habitat type and replicate by trapping period interactions were fitted as random effects to calculate error terms for the relevant main effects. Canopy cover was tested as an explanatory variable only between the three forested habitat types (ARN-Island, ARN-Edge, UNL) since the harvested areas had no canopy. Multiple pair-wise comparisons of significant effects (least-squares means) were made using Tukey-Kramer adjustment. Arcsine square-root transformations were performed on all habitat data.

Spearman's Rank Correlation was used to investigate the relationship between vegetation cover and rodent abundances. We tested data at the plot level (a group of trap stations within a site) averaged over the three trapping periods. Plot level data were used as this was most representative of rodent home ranges compared to overall site (treatment) or trap station (an individual trap) and consequently gave us more information about habitat requirements. We then tested the relationship between habitat cover and rodent abundances across the five different habitat types and also within habitat types.

2.3 Results

2.3.1 Rodent abundance and sex ratios

Swamp rat abundance was significantly different between the three forestry treatments ($F_{2,6}$ = 40.94, P < 0.001), with abundances highest in UNL (4.0 ± 0.56 S.E. individuals per 54 traps), intermediate in ARN (1.2 ± 0.56 S.E. individuals per 54 traps) and lowest in CBS (0.4 ± 0.56 S.E. individuals per 54 traps). There was a trend for swamp rat abundance to decline with increasing disturbance (Fig. 2.3). Across the five habitat types, swamp rat abundance was significantly greater in the unlogged areas (UNL, ARN-Edge, ARN-Island) than the harvested areas (ARN-Harvest and CBS; ARN-Island was marginally significantly different from both harvested areas: ARN-Harvest, P = 0.048 and CBS, P = 0.052). There were no significant differences in long-tailed mouse abundance for the three forestry treatments ($F_{2,6}$ = 0.02, P = 0.98) or the five habitat types (Table 2.2, Fig. 2.3). There were no significant differences between the observed ARN abundance and the weighted UNL and CBS abundance of swamp rats (P = 0.80) nor long-tailed mice (P = 0.77), indicating that total area of retained forest rather than distribution during early post-harvest regeneration influences native rodent abundance.

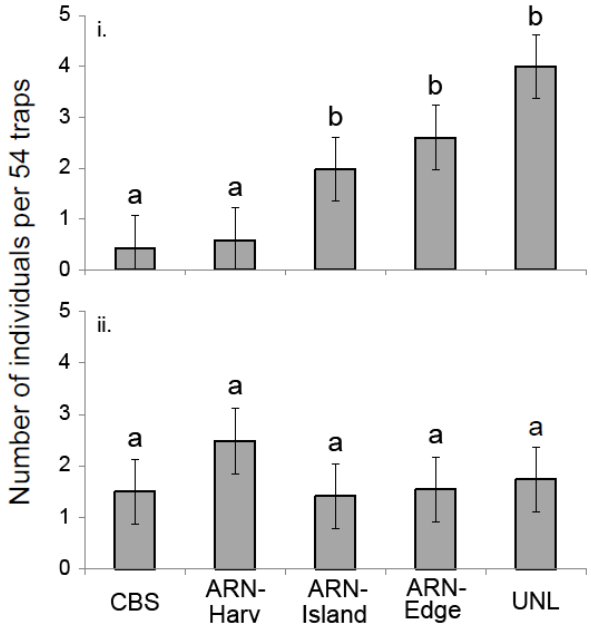


Fig. 2.3 Untransformed least squares mean abundance (± S.E.) of (i) swamp rats and (ii) long-tailed mice per 54 traps in five habitat types within Tasmanian production wet forests: clearfell, burn and sow coupes (CBS), harvested matrices within aggregated retention coupes (ARN-Harv), island aggregates (ARN-Island), edge aggregates (ARN-Edge), and unlogged native forest (UNL). Different letters indicate significant differences between habitat types based on square root transformed data. Standard error based on pooled error term as sample sizes were even across treatments (n = 4).

Table 2.2 *F*- and *P*-values for native rodent abundances and vegetation cover variables surveyed in five habitat types in old growth production forests: clearfell, burn and sow, ARN-Harvest, ARN-Island, ARN-Edge and unlogged forest. Surveys were conducted within a one metre radius of each trap station used throughout the study and re-surveyed during each trapping period.

	Habitat type			Trapping period			Habitat type*Trapping period		
Variable	**d.f.**	***F* value**	***P* value**	**d.f.**	***F* value**	***P* value**	**d.f.**	***F* value**	***P* value**
Swamp rat abundance[a]	4,12	10.78	**<0.001**	2,30	1.63	0.213	8,30	1.98	0.084
Long-tailed mice abundance[a]	4,12	0.22	0.921	2,30	4.81	**0.015**	8,30	1.30	0.280
Canopy cover[b,c] (%)	2,6	0.4	0.678	2,18	4.0	**0.036**	4,18	0.9	0.473
Understorey cover[b] (%)	4,12	134.8	**<0.001**	2,30	10.7	**<0.001**	8,30	5.3	**<0.001**
Groundcover[b] (%)	4,12	1.0	0.432	2,30	19.6	**<0.001**	8,30	2.7	**0.023**

[a]Square-root transformations were performed on rodent abundance data.

[b]Arcsine square-root transformations were performed on all habitat data.

[c]Clearfell, burn and sow and ARN-Harvest were removed from the Canopy model due to a lack of variance as all canopy values were '0'.

Long-tailed mice abundance was significantly higher in trapping periods 1 and 2 (2.0 and 2.3 individuals per 54 traps, respectively) than in trapping period 3 (0.9 individuals per 54 traps) based on the analysis of the five habitat types (Table 2.2), although trapping period was not significant in the analysis of the three forestry treatments ($F_{2,18} = 0.90$, $P = 0.42$). Swamp rat abundance was not significantly different between trapping periods for the three forestry treatments ($F_{2,18} = 1.39$, $P = 0.28$) or the five habitat types (Table 2.2). House mice abundance was not significantly different between forestry treatments ($F_{2,6} = 2.17$, $P = 0.20$), habitat types ($F_{4,12} = 1.97$, $P = 0.16$) nor trapping periods ($F_{2,18} = 0.08$, $P = 0.93$; $F_{2,30} = 0.18$, $P = 0.84$). There were no significant treatment (forestry treatment or habitat type) by trapping period interactions for swamp rats ($F_{4,18} = 1.39$, $P = 0.28$; Table 2.2), long-tailed mice ($F_{4,18} = 1.02$, $P = 0.42$; Table 2) or house mice ($F_{4,18} = 0.23$, $P = 0.92$; $F_{8,30} = 0.25$, $P = 0.98$).

The size of habitat islands in ARN had no effect on the presence/absence of swamp rats (Wald $\chi^2 = 0.48$, $P = 0.49$) or long-tailed mice (Wald $\chi^2 = 0.29$, $P = 0.59$). Within harvested sites, there was no relationship between distance from harvested plots to nearest unlogged edge or aggregate for swamp rats (Wald $\chi^2 = 0.37$, $P = 0.54$) or long-tailed mice (Wald $\chi^2 = 1.34$, $P = 0.25$). The abundance of swamp rats in CBS and ARN-Harvest was equivalent despite the average distance between plots and forest edges being, on average, twice as far in CBS (84 m ± 48 m S.D.) than in ARN (43 m ± 22 m S.D.). A similar result was found for long-tailed mice.

There was no significant difference in swamp rat sex ratios between forestry treatments ($F_{2,4} = 0.35$, $P = 0.72$) or habitat types ($F_{4,8} = 0.91$, $P = 0.50$). Irrespective of forestry treatment or habitat type, the proportion of swamp rat males was 39 % (97 males : 152 females), showing a significant female bias ($\chi_1^2 = 12.15$; $P < 0.001$, n = 249). Sex ratios in the long-tailed mice did not differ significantly from parity; either overall (47 % males, 104 males : 94 females; $\chi_1^2 = 0.51$; $P = 0.48$), or between forestry treatments ($F_{2,4} = 0.01$, $P = 0.99$) or habitat types ($F_{4,8} = 0.31$, $P = 0.86$).

2.3.2 Habitat characteristics

The amount of understorey cover differed significantly between habitat types (Table 2.2). As expected, forested areas had significantly higher understorey cover than harvested areas (Fig. 2.4). ARN-Island had intermediate understorey cover compared

to the harvested areas and the other two forested habitats, most likely due to edge and windthrow effects. Canopy cover decreased over time while understorey cover and groundcover increased over time (Table 2.2). Understorey cover increased with each subsequent trapping period (31.6 %, 34.2 % and 34.7 %; $P < 0.05$), while groundcover increased significantly between trapping period 1 (12.3 %) and trapping period 2 (21.4 %, $P < 0.001$), but not between trapping period 2 and trapping period 3 (22.3 %, $P = 0.78$). There were also significant treatment by trapping period interactions for understorey and groundcover (Table 2.2). These results were driven by increases in regenerating vegetation cover in the harvested areas (CBS and ARN-Harvest) over time as there were no changes to the forested areas.

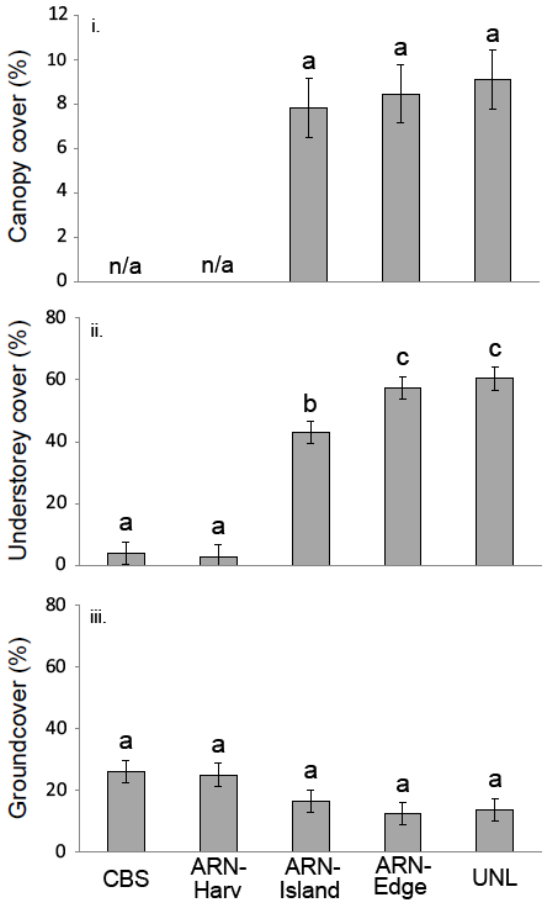


Fig. 2.4 Untransformed least squares mean percentage (± S.E.) of: (i) canopy cover (UNL, ARN-Edge and ARN-Island values only), (ii) understorey cover and (iii) groundcover across five habitat types: clearfell, burn and sow coupes (CBS), harvested matrices within aggregated retention coupes (ARN-Harv), island aggregates (ARN-Island), edge aggregates (ARN-Edge), and unlogged native forest (UNL). Different letters indicate significant differences between habitat types based on arcsine transformed data. Standard error based on pooled error term as sample sizes were even across treatments (n = 4).

2.3.3 Do habitat characteristics influence rodent abundances?

Analysis of plot level data across all habitat types indicated that swamp rat abundance was positively correlated with canopy cover and understorey cover, but not with groundcover (Table 2.3i). Long-tailed mouse abundance showed no relationship with canopy cover or understorey cover, but increased abundance with reduced groundcover.

Table 2.3 Spearman's rank correlations between habitat cover variables and (a) swamp rat and (b) long-tailed mouse abundance using plot level data (6-8 trap stations per plot) averaged over three trapping periods. Correlations presented are (i) across plots in all habitat types (n = 108) and (ii) within each habitat type (n = 36 or 12).

		(a) Swamp rats		(b) Long-tailed mice	
Habitat type	**Cover factor**	**Spearman's R**	***P*-value**	**Spearman's R**	***P*-value**
(i) All habitat types					
	Canopy cover	0.64	**<0.001**	-0.02	0.834
	Understorey cover	0.65	**<0.001**	0.02	0.841
	Groundcover	-0.12	0.229	-0.25	**0.008**
(ii) Results by habitat type					
CBS[a]	Understorey cover	0.45	**0.006**	-0.21	0.218
(n = 36)	Groundcover	0.30	0.079	-0.44	**0.008**
ARN-Harvest[a]	Understorey cover	0.69	**0.013**	-0.35	0.267
(n = 12)	Groundcover	0.54	0.071	-0.17	0.587
ARN-Island	Canopy cover	0.25	0.427	0.42	0.171
(n = 12)	Understorey cover	-0.21	0.511	-0.53	0.074
	Groundcover	0.35	0.253	0.35	0.267
ARN-Edge	Canopy cover	-0.11	0.743	0.00	0.991
(n = 12)	Understorey cover	-0.38	0.217	-0.12	0.702
	Groundcover	0.10	0.768	-0.09	0.782
Unlogged	Canopy cover	0.03	0.848	-0.50	**0.002**
(n = 36)	Understorey cover	-0.05	0.773	0.31	0.065
	Groundcover	0.14	0.414	-0.46	**0.005**

[a]Canopy cover not calculated for cleared areas (ARN-Harvest and CBS) due to all zero values.

The relationships between rodent abundance and cover were not consistent across all habitat types (Table 2.3ii). Swamp rat abundance was not correlated with cover in any strata in the three forested areas (UNL, ARN-Island and ARN-Edge). Within ARN-Harvest and CBS, swamp rat abundances were highest where understorey was high (Supplementary Fig. 1) and showed a similar, although non-significant ($P = 0.071$, 0.079, respectively), trend with groundcover. Long-tailed mouse abundance was not correlated with cover in any strata in the ARN habitat types. In UNL, abundance was high where canopy and groundcover was low. Similarly, in CBS, long-tailed mouse abundance was high where groundcover was low.

2.4 Discussion

The responses of native rodents to the silvicultural practices examined in this study varied between species. The abundance of a habitat specialist, the swamp rat, showed a trend for declining abundance with increasing disturbance while a generalist species, the long-tailed mouse, was found in equal abundance across all forestry treatments and habitat types, as was the non-native house mouse. This is consistent with previous studies that found the abundance of cover-dependent species decreased with increased disturbance while generalist species increased or remained unchanged (Sullivan & Sullivan 2001; Klenner & Sullivan 2009; Lindenmayer *et al.* 2010). In our study, swamp rat abundance was highest in UNL, intermediate in ARN, and lowest in CBS. When ARN was differentiated into three habitat types (ARN-Edge (connected forest patches), ARN-Island (isolated forest patches) and ARN-Harvest (harvested matrix)), we found swamp rat abundance followed a similar pattern of response to relative disturbance. Edges retained the highest abundance, islands intermediate, and harvested matrix the lowest.

In this study, the ARN-Edge patches surveyed were all connected to the larger landscape by unharvested forest retained as streamside reserves, forest reserves or areas unsuitable for harvesting. Continuous forest creates habitat for cover-dependent ground mammals which aids in dispersal (Bennett 1990). However, in production forest landscapes, edge patches may border silvicultural regeneration in adjacent coupes or even roads, which are distinctly different to contiguous forest edges. In such

cases, responses may be more similar to that in habitat islands rather than the connected edges surveyed in the present study. In ARN-Harvest, swamp rat abundance was equivalent to CBS, although plots in ARN were closer in distance to unlogged edges than plots in CBS. Recently harvested forest, therefore, appears to be unsuitable swamp rat habitat, even with edge and island aggregates providing closer proximity to nearby unharvested forest.

The lack of difference between the observed ARN abundance and weighted UNL and CBS abundance of native rodents suggests that, in the early years following harvesting, rodent abundance is related to the amount of unlogged habitat rather than to the arrangement of the habitat. This implies that for a defined level of retention, it may make little difference whether that retention is located within aggregated retention sites, or retained elsewhere in the landscape. Future research will be required to determine whether closer proximity to retained forest with ARN compared to CBS will accelerate re-colonisation of harvested areas and thus result in greater swamp rat abundance in ARN than CBS in the longer-term. In Tasmania's old growth wet *Eucalyptus* forests, the additional retention within ARN sites is not compensated for by additional old growth wet *Eucalyptus* harvest elsewhere (Forestry Tasmania 2009). Mature forest retained in aggregates is therefore additional habitat for swamp rats than would have been retained under a CBS-only regime.

We predicted that vegetation cover would be an important factor in maintaining rodent populations within production forests. Across all plots, regardless of habitat type, there were strong positive correlations between swamp rat abundance and canopy cover and understorey cover. When we looked at relationships with cover within the five habitat types for swamp rats, we found that understorey cover was important predictors for swamp rat abundance in harvested areas (CBS and ARN-Harvest). A study of medium-term impacts (6 years post-harvest) of clearfelling and commercial thinning in wet *Eucalyptus regnans* forest in northeast Tasmania found that swamp rat abundance in the harvested sites was similar to unlogged forest (Flynn *et al.* 2011). They found that understorey cover was not signficantly different between control and harvested sites, reflecting the rapid rate of regeneration following harvesting, enabling recolonisation by swamp rats. In our study, swamp rat abundance was highest in plots with higher percentages of understorey cover, indicating that dense cover at the lower

strata is an important habitat requirement in disturbed areas (Monamy & Fox 2000). This is consistent with the habitat accommodation model by Fox (1982) which predicts recolonisation by a species only when vegetation has reached adequate density, regardless of time since disturbance. Although understorey cover was an important predictor for swamp rat abundance in harvested areas, it was not a good predictor in forested areas (UNL, ARN-Edge, ARN-Island). The forested areas had high percentage cover in the upper strata (canopy and understorey), whereas in harvested areas, cover in the upper strata was either not present or very low. Where understorey cover was present in the harvested areas it consisted of taller seedlings that were at a maximum height of 2.5 metres by trapping period 3. These responses to cover explain the differences in swamp rat abundance between habitat types, where a lack of higher strata cover in the harvested areas increases the importance of dense cover in the lower strata.

Regardless of habitat type, long-tailed mouse abundances were negatively correlated with groundcover. Groundcover was not significantly different between habitat types, perhaps explaining the lack of response of long-tailed mice to harvesting treatments. Within the five habitat types, the trends for correlations of long-tailed mouse abundance with groundcover held for CBS and UNL sites, but there were no habitat correlations within the different ARN habitat types. ARN coupes comprise harvested areas with patches of intact old growth forest. Long-tailed mice are habitat generalists, and thus potentially more mobile than swamp rats and able to use the mosaic of habitat types more successfully (long-tailed mice frequently moved more than 100 m between plots within a trapping period while swamp rats rarely moved between plots; unpublished data).

In our study we did not explicitly test for competition between swamp rats and long-tailed mice, however, we found no indication of competition occurring. Previous work has found that swamp rats are dominant over long-tailed mice in wet *Eucalyptus* forest, with sex of swamp rats and season also playing key roles (Luo *et al.* 1998; Monamy & Fox 1999). Our study found that long-tailed mice were widespread across all habitat types, including densely forested areas with high swamp rat abundance, where we would expect lower long-tailed mouse abundance if competition was occurring. We also found no differences in sex ratio between habitat types for either

species, which may have indicated competition for resources (Monamy & Fox 1999). In our study, swamp rat females were dominant irrespective of habitat type, unlike Monamy (1995b) who found no deviation from parity. Competition may not have been detected in our study due to a lack of sufficient statistical power or because there is no competition in these areas. The long-tailed mice in our study were heavier (mean adult weight of 81.1g ± 9.1g) than the 60-65 g animals captured by Monamy (1995c), although swamp rat size remained similar (mean adult weight of 108.8 ± 17.2g, compared to 95-124 g; Monamy 1995a). As the size difference between the species is lower in these sites, the competitive ability of long-tailed mice to coexist in the 'better quality' habitat may be higher.

Species persistence can be affected by patch size, where larger patches often retain higher species richness and abundance compared to smaller islands (Schieck & Hobson 2000; Michalski & Peres 2007; Matveinen-Huju *et al.* 2009). Therefore, we predicted that larger islands would support larger populations than smaller islands. Although our islands ranged widely in size (0.5 ha to 3.3 ha), we found no relationship between island size and the presence of swamp rats or long-tailed mice. This was not unexpected with long-tailed mice since they appeared to move relatively freely between island, edge and harvested areas within ARN coupes, for example, finding an individual in an island one night and then in the adjacent harvested matrix within the same trapping period (unpublished data). By contrast, swamp rats appeared to be isolated within islands (no recaptures were found outside an island; unpublished data), hence we expected to find more individuals within larger islands. However, another recent study also found that the abundance of cover-dependent small mammals was not affected by island size (0.5 to 1.5 ha; Lindenmayer *et al.* 2010). They hypothesised that the configuration of smaller islands may provide enough connectivity to support larger populations. However, this doesn't appear likely in our system as we rarely captured swamp rats in the harvested habitats, and no individual swamp rats were found to have moved between islands or between islands and edges. Our study may also have lacked the power to detect island size influence due to low capture rates (trap success of 6 % for swamp rats and 4 % long-tailed mice), although this capture rate is not uncommon for small mammal studies in Tasmania (Norton 1987b; Stoddart & Challis 1993; Monamy 1995b,c). Although it is possible that we did not trap all individuals occupying an island, our results indicate the potential for the loss of populations in

island aggregates due to natural mortality (maximum age recorded of two years), predation and lack of immigration. Reduced vegetation cover in islands due to edge effects from post-harvest burns (McElwee & Baker 2009) and increased windthrow (H. Stephens, personal observation) may increase predation risk for small ground mammals within the islands. The relatively long distances between islands and contiguous forest (102 ± 35 m) coupled with the lack of dense vegetation in the harvested matrices may be preventing dispersal of swamp rats, and unless immigration occurs, which we saw little evidence of over the two year study, swamp rat populations surviving within islands may be at risk of inbreeding depression (Eldridge *et al.* 1999).

2.4.1 Conclusions and management implications

Our study clearly indicates that ARN is a more favourable system compared to CBS for short-term population persistence of cover-dependent small mammal species at the coupe-scale. We found that the long-tailed mouse, a habitat generalist, is able to inhabit all habitat types including harvested areas (CBS and ARN-Harvest) while the swamp rat, a habitat specialist, is mostly restricted to forested areas (UNL, ARN-Edge and ARN-Island), regardless of the patch size. The retained forest patches in ARN provide potential 'lifeboats' for swamp rats as well as other taxa (Baker & Read 2011), making this silvicultural practice a better option than clearfelling for biodiversity values. Retention of patches of intact forest may also aid recolonisation of the harvested areas by more sensitive species as the forest regenerates, as has been found within the partially harvested dry *Eucalyptus* forests of Tasmania (Cawthen 2007; Webala *et al.* 2010). This may be particularly important for the maintenance of ground-dwelling species in areas where the surrounding matrix lacks suitable habitat. A useful area of future research would be to examine the recolonisation benefits of ARN compared to CBS across a gradient of disturbances, ranging from highly altered landscapes (e.g. cleared agricultural) through to contiguous forested landscapes and examining whether the proximity to retained habitat facilitates recolonisation. Forest managers may now use regeneration (in particular lower strata of vegetation cover such as understorey) as an indicator of the success of habitat recovery for small mammals, as swamp rat abundances show selection for denser habitat within disturbed sites. In the adoption of ARN design, the use of edge aggregates has operational advantages over islands where post-harvest regeneration burns and subsequent eucalypt regeneration are more successful (R Scott, pers. comm.) and less likely to

escape into unharvested habitat (McElwee & Baker 2009). While not significant, there was a trend for higher quality habitat for swamp rats in ARN edges compared to ARN islands. However, the importance of islands as stepping stones for dispersal in the medium to long-term is as yet unknown, and the positive impacts on other taxonomic groups and landscape context should also be considered.

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CHAPTER 3: Physiological effects of forest harvesting on native rodents: responses from a habitat generalist and a habitat specialist

Stephens H.C., Johnstone C.P., Potts B.M., Baker S.C., Wiggins N.L. & O'Reilly-Wapstra J.M. (In prep) Physiological effects of forest harvesting on native rodents: responses from a habitat generalist and a habitat specialist

Collecting blood samples and morphological measurements from a long-tailed mouse (*Pseudomys higginsi*) in unlogged forest in the Styx Valley in 2010. The mouse is restrained in a 'handling tube', which allows rapid and bite-free handling and the animal is easily released.

Abstract

Physiological stress responses are essential for survival, but prolonged or frequent exposure to stressors can be detrimental to the health, reproduction and survival of individuals and populations. Anthropogenic disturbance can introduce potential stressors through the alteration of habitat suitability, which can result in population declines for many species. Measuring species abundance is commonly performed to determine the impact of disturbance, although sub-lethal effects are often neglected. We investigated the stress response and general health of two native rodents in harvested, partially harvested and unlogged native forests using blood (leukocyte profiles, haematocrit) and body condition indices. The swamp rat (*Rattus lutreolous*) is a cover-dependent species and is found in reduced abundance in harvested sites, while the long-tailed mouse (*Pseudomys higginsi*) is a habitat generalist and found in equal abundance in harvested and unlogged sites. Contrary to expectations, swamp rats showed no difference in any stress or health metric between harvested and unlogged sites. These responses may be explained by individuals in harvested treatments mitigating health impacts through their behaviour, or that swamp rats were exposed to stressors in both the harvested and unlogged sites, due to the presence of roads (and canopy gaps) in the latter. The long-tailed mouse showed better general health in unlogged sites relative to harvested sites. These results highlight potential issues which can arise when solely relying on traditional ecological methods such as abundance estimates, and emphasise the importance of using complementary techniques in assessing impacts of habitat disturbance.

3.1 Introduction

Animals are exposed to environmental stressors regardless of the habitat, whether anthropogenically disturbed or undisturbed. Stress responses to a single or short-term (normally < 1 hour) stressor are typically beneficial for an animal's short-term survivorship, as such responses divert physiological and behavioural processes towards immediate survival needs (Romero 2004). However, where stressors are persistent (hours, days, or longer) or occur frequently (i.e. long-term stress), the physiological and behavioural changes that aid short-term survival may instead become detrimental to the health, reproduction and ultimately the survival and fecundity of an individual (Dhabhar & McEwen 1997; McEwen 1998; Santos *et al.* 2000; Epel *et al.* 2004; Charbonnel *et al.* 2008). If stressors affect many individuals, the population as a whole may be at risk. For example, long-term stress may negatively impact the cardiovascular health of an individual and may hinder their ability to mount a fight or flight response (Cyr *et al.* 2009), and can impact future generations through reduced birth rates, and smaller and lighter offspring (Sheriff *et al.* 2009b).

Anthropogenic habitat fragmentation, loss and degradation can have differing impacts on wildlife (Fischer & Lindenmayer 2007). Changes in habitat connectivity, area and suitability can result in population isolation, restricted dispersal (or high mortality whilst dispersing), reduced foraging opportunities, fewer nesting sites, increased predation risk due to removal of habitat cover, and/or increased competition for resources (Saunders *et al.* 1991; Pattanavibool & Edge 1996; Sullivan *et al.* 1999; Fischer & Lindenmayer 2007). Biodiversity and abundance are commonly used as indicators for estimating the impacts of disturbance. However, habitat disturbance may not necessarily result in immediate population reduction or loss, and sub-lethal negative stress effects may result before longer-term population decline occurs (Martínez-Mota *et al.* 2007). One consequence of anthropogenic habitat disturbance may be increased exposure to short- and/or long-term stressors (e.g. an increase in the number of encounters with predators due to loss of habitat cover). Therefore, anthropogenic habitat disturbance could result in physiological, behavioural and reproductive changes that may lead to population decline through a mechanism in part mediated by the negative effects of long-term stress (Wasser *et al.* 1997; Suorsa *et al.* 2004; Johnstone *et al.* 2012a).

The swamp rat (*Rattus lutreolus*, 110 g) and long-tailed mouse (*Pseudomys higginsi*, 80 g) are relatively common small mammals occurring in old growth wet *Eucalyptus* forests in Tasmania (Monamy 1995b,c). The species share similar diets (Driessen 1987) and breeding cycles (Norton 1987; Stoddart & Challis 1991). They differ in that the swamp rat is a cover-dependent species (Fox & Monamy 2007), whereas the long-tailed mouse is considered a habitat generalist (Stoddart & Challis 1991). The costs associated with being a specialist or generalist may affect an individual's ability to respond to changes in their environment (Van Tienderen 1991). The phenotypic plasticity associated with being a habitat generalist results in higher energetic costs (DeWitt *et al.* 1998). Therefore, in stable or optimal conditions, a specialist is likely to outperform in comparison to a generalist (Wilson & Yoshimura 1994). However, when an environment becomes unpredictable, a generalist may be able to outperform in comparison to a specialist (Gilchrist 1995).

While both the swamp rat and long-tailed mouse occur in forest subject to harvesting, there has been little research on the responses of these species to habitat disturbances (but see Fox 1982). In Tasmanian (State-operated) production wet *Eucalyptus* forests, a partial harvest practice called aggregated retention has been introduced as an alternative to the more traditional and widespread practice of clearfell, burn and sow. Clearfelling (also known as clearcutting) typically removes all standing structural features and results in even-aged forest regrowth. Aggregated retention retains patches of unlogged forest within the harvested matrix as isolated patches or connected to the surrounding forest (Fig. 3.1), with the objective of 'lifeboating' populations and ecological processes, in part through retaining some structural complexity and improving landscape connectivity (Franklin *et al.* 1997). In both Northern and Southern hemisphere systems, aggregated retention is more favourable than clearfelling for maintaining biodiversity of taxa including fungi, insects, birds, plants and small mammals (Rosenvald & Lohmus 2008; Baker & Read 2011; Lindenmayer *et al.* 2012). Stephens et al. (2012) investigated the relative abundances of swamp rats and long-tailed mice in clearfell, aggregated retention and unlogged native wet *Eucalyptus* sites, and found that swamp rats occurred at higher abundances where disturbance was lower, whereas long-tailed mice showed no significant differences in abundances across all treatments. These responses (2-3 years post-harvest) suggest that

aggregated retention could provide a better outcome than clearfelling for abundances of cover-dependent small mammals. However, little is known about physiological effects of harvesting practices on small mammals, nor is there a good understanding of the longer-term effects that these forest practices may have on small mammal populations.

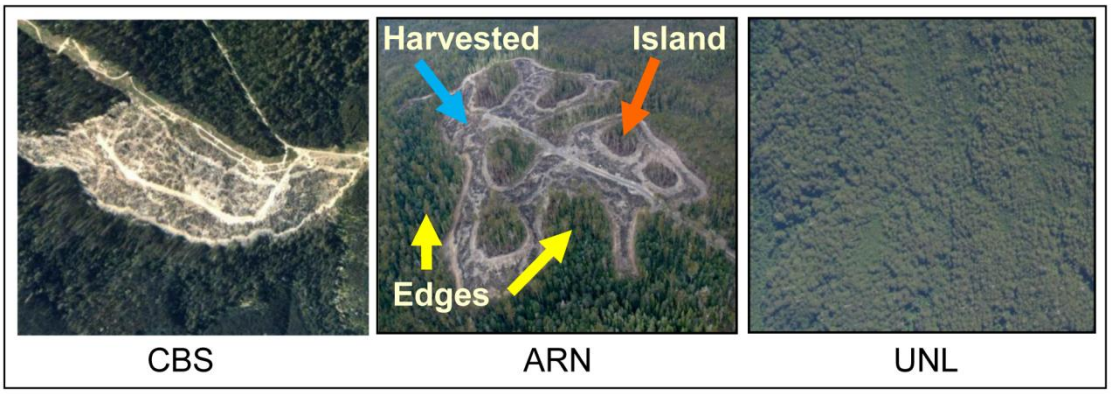

Fig. 3.1 Different forestry practices in wet *Eucalyptus* forests in Tasmanian State Forests. Aerial views of a clearfell burn and sow coupe (CBS), an aggregated retention coupe (ARN) and unlogged native forest (UNL) in wet *Eucalyptus* forests in Tasmanian State Forest. Within ARN, there are three different habitat types: Harvested matrix, Islands (isolated within the harvested matrix), and Edges (connected to the surrounding forest along the coupe boundary).

Here, we used several indices of health status and physiological stress to investigate the impact of forest harvesting on two sympatric, ground-dwelling native rodents, the swamp rat and the long-tailed mouse. As the cover-dependent swamp rat is seldom found in harvested areas and prefers dense vegetation cover (Stephens *et al.* 2012), we predicted that swamp rats could experience higher levels of long-term stress and poorer body condition in harvested sites compared to unlogged sites due to increased exposure to stressors. We hypothesised that the long-tailed mouse, being a habitat generalist, would be more likely (than a habitat specialist) to show similar stress or body condition indices across the treatments.

3.2 Methods

3.2.1 Study sites and trapping protocol

The study was conducted in old growth wet native *Eucalyptus* forests and recently harvested coupes in State Forest in two regions of southern Tasmania, Australia: the Styx (42.81ºS, 146.65ºE) and Huon (43.11ºS, 146.76ºE) Valleys (Fig. 3.2). Blood and morphological data were collected from captured rodents in four replicates (two replicates per region) of three treatments: clearfell, burn and sow (CBS), aggregated retention (ARN) and unlogged native forest (UNL; Fig. 3.1). Over the past few decades, CBS has been the most common harvesting method in Tasmanian wet *Eucalyptus* forests and involves harvesting the standing wood from a site (coupe), burning the remaining debris to encourage germination of *Eucalyptus* seedlings, and sowing locally collected seeds. Clearfell, burn and sow harvesting retains some mature forest structural features such as coarse woody debris, but no standing trees. Aggregated retention is a partial harvest practice that has been used since 2007 in Tasmanian State Forests as an alternative to CBS. Within ARN, three habitat types remain after timber harvesting: the harvested matrix, 'island' aggregates (isolated patches surrounded by the harvested matrix), and 'edge' aggregates (patches of forest connected to the surrounding forest; Fig. 3.1). The harvested matrix undergoes a similar protocol to CBS (harvesting, burning (at a reduced intensity to prevent the likelihood of islands and edges burning) and sowing), while the aggregates are unlogged and relatively unburnt. All UNL study sites retained old growth forest elements including mature trees, and had been left relatively undisturbed by harvesting practices for more than 70 yrs.

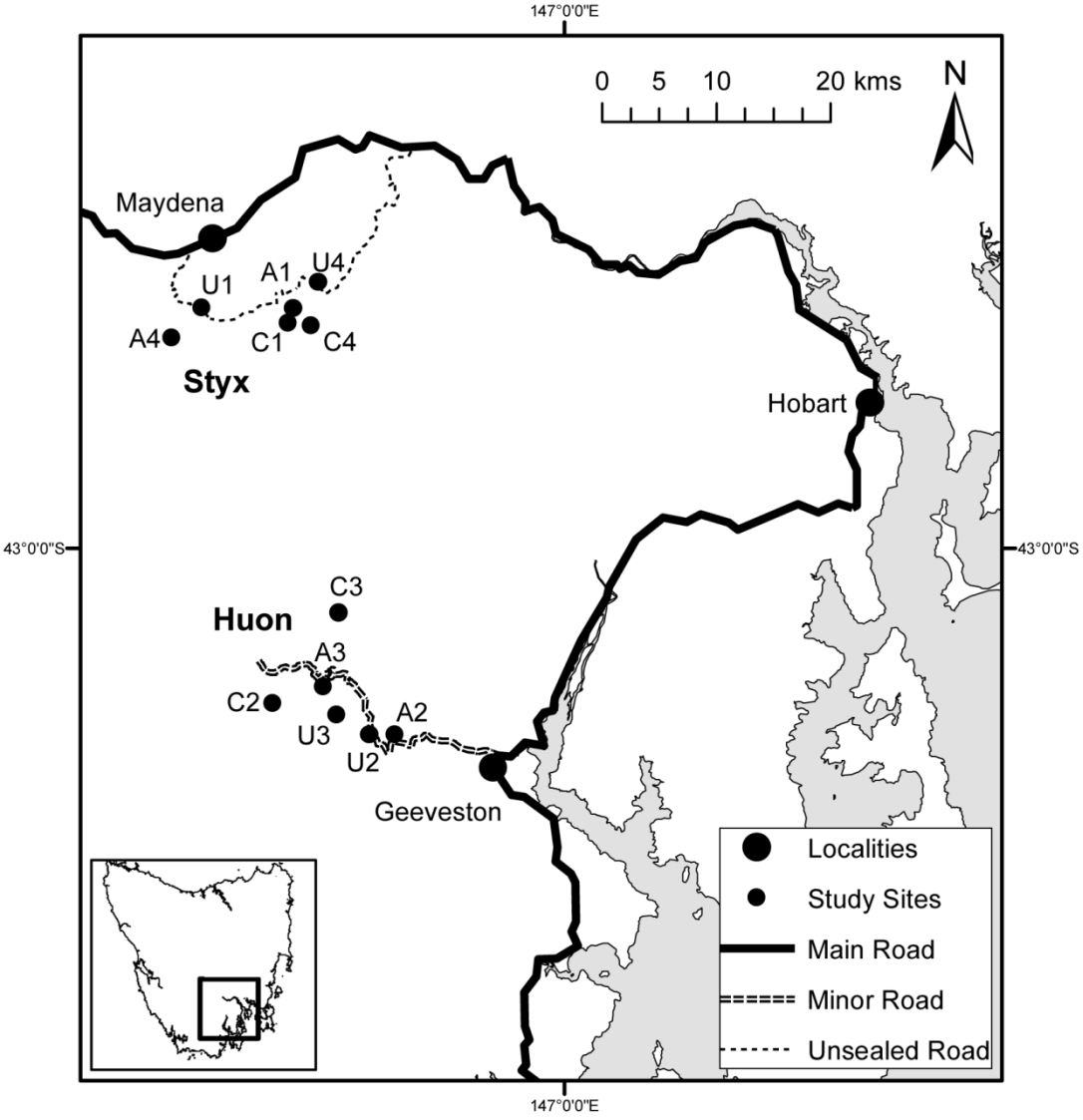

Fig. 3.2 Location of study sites in southern Tasmania, Australia. There are four replicates of each forestry treatment, grouped geographically. Replicates 1 and 4 are in the Styx Valley, south of Maydena, and replicates 2 and 3 are in the Huon Valley, west of Geeveston. Each replicate contains one unlogged native forest site (U), one aggregated retention coupe (A) and one clearfell, burn and sow coupe (C). The first letter denotes the treatment, while the number indicates the replicate.

In each site (n = 12), nine plots of six trap stations were set (n = 54 traps per site). Elliott live traps were used throughout (33 x 10 x 9 cm; Elliott Scientific Company, Upwey, Victoria). Bait consisted of a piece of apple and a bait ball made of peanut butter, rolled oats and vanilla essence. Elliott traps were two-thirds covered with a zip-lock plastic bag to protect them from wind and rain, and nesting material (hessian, non-absorbent fibres) was provided. Within each plot, trap stations were set in a grid, with traps approximately 10 m apart. In CBS and UNL, the nine plots were randomly allocated across the site (at least 50 m apart). In ARN, we allocated three plots randomly within each of the three habitat types (at least 50 m apart): harvested matrix, island aggregate, and edge aggregate. Trapping was conducted in autumn/winter of 2009 (May to July) and 2010 (March to July) to target native rodents during the post-dispersal period and to avoid the effect of breeding season and capturing females with dependent young. Each trap was set for three nights, providing a total of 3,888 trap nights over 2 years. Traps were set each night and checked, cleaned, re-baited and re-set the following morning (on average, all traps were cleared by 4.5 hours after dawn).

3.2.2 Measuring stress responses

Stress response indicators can be obtained through a variety of metrics, but the measurement of circulating stress hormone concentrations, or differential leukocyte profiles are most commonly used (Davis *et al.* 2008; Busch & Hayward 2009; Johnstone *et al.* 2012b). Stress hormone concentrations are produced by activation of the vertebrate stress system, the hypothalamus-pituitary-adrenal axis (HPA-axis). Of these, glucocorticoids, in particular are used to index physiological stress and these can be obtained from blood, urine, faeces, saliva and keratinous tissue (e.g. hair, feathers, scales; Sheriff *et al.* 2011). However, using glucocorticoids can be challenging when collecting data on long-term stress from free-living animals: blood and urine sampling must be completed within a few minutes of exposure to an acute (short-term) stressor such as capture (Fletcher & Boonstra 2006; Lynn & Porter 2008) or handling, depending on the species (Romero & Reed 2005). Baseline hormones in faecal samples do not change as rapidly as in blood or urine samples (within a few hours; Sheriff *et al.* 2009a), but contamination from urine is difficult to prevent, particularly when animals have been held in a trap. Saliva is difficult to collect from free-living animals and analysis using hair, although promising (Meyer & Novak 2012), is a

relatively recent development and it is not clear that application of this method to the study species would be valid.

Differential leukocyte counts offer a method for assessing stress responses in ecological studies that has some advantages over use of stress hormones (Davis *et al.* 2008). Neutrophil to lymphocyte ratio (N:L ratio; in mammals) correlates with an increase in stress hormone levels (Dhabhar *et al.* 1995), although at a slower rate (20 min to several hours, see review by Davis *et al.* 2008). This provides a method for measuring stress responses when immediate blood sampling after a short-term stress such as handling is a concern. Where trapping is a concern, as in this study, the reasonably predictable interaction of short and long-term stress effects on leukocyte profiles still allows for valid interpretation (i.e. attenuation of acute stress responses under conditions of chronic stress). Further to indicating stress hormone levels, leukocyte counts also provide insights into an individual's immune defence system (Jain 1993). For example, increases in monocytes can indicate bacterial infections (Davis *et al.* 2004), while high counts of eosinophils are associated with defence against parasites (Maxwell 1987). Haematocrit (Hct, percentage of red blood cells in whole blood) and body condition indices are useful for inferring information about an animal's overall health status and condition. Haematocrit has a strong relationship with nutritional status and muscle mass in some species (but for a discussion for and against see Fair *et al.* 2007), while body condition estimates calculated from mass-size residuals indicate energy reserves in the form of fat stores and lean dry mass (Schulte-Hostedde *et al.* 2005). Therefore, leukocyte profiles, haematocrit and body condition were used to assess general health in free-living, wild-caught rodent species, the swamp rat and the long-tailed mouse.

3.2.3 Animal handling and blood sampling

All animals were handled and measured by the same researcher (H.C. Stephens) to ensure consistency in the sampling methods and measurements (Blackwell *et al.* 2006). Each individual captured was identified to species and transferred into a calico handling bag for weighing (to the nearest g), then moved to a 'handling tube' made of chicken wire, cable ties and gaffer tape (12-14 cm long × 12-14 cm diameter, depending on animal size). Each animal was visually sexed and checked for an identification marker (passive integrated transponders, PIT-tags, or ear biopsy punches)

to indicate a recapture. Use of handling tubes restrained the animal with minimal physical handling whilst allowing the researcher to take blood samples within 5 - 10 minutes of opening the trap. Ear biopsy sampling, PIT-tag injections and morphological measurements (except full body length) were taken. By using the handling tubes, we reduced handling time and associated handling stress for each animal. Samples were collected on initial capture during each trapping period. If an individual was recaptured within a trapping period, they were weighed and checked for general health, then immediately released at the site of capture.

Blood samples were taken immediately upon transfer of an animal to the handling tube. The handling tube was covered with a towel, and blood samples were taken from one of two lateral tail veins by puncture with a scalpel, with blood collected in heparinised 75 µL capillary tubes (Clark 2003). Approximately 30-50 µL of blood was collected in one to two tubes for determining Hct. An additional 5-10 µL was collected for leukocyte differential smears.

Following blood sampling, nasal-occipital head length was measured using callipers (from the occipitals at the posterior margin of the skull to the tip of the nose, to the nearest 0.1 mm) for use in the body condition indices calculations (Schulte-Hostedde *et al.* 2005). Repeated measurements were taken by the same researcher until the difference between two measurements was < 0.3 mm. Repeated measurements are important for reducing error in morphometric measurements of small mammals (Blackwell *et al.* 2006). Distance from anus to urinary papilla/penis was measured to confirm sex identification (the scrotum can be difficult to distinguish in the non-breeding season, particularly in long-tailed mice). Each animal captured in 2009 was marked for identification using PIT-tags (AllFlex, Australia and Provet, Australia) using adhesive to seal the puncture wound and reduce PIT-tag loss (Lebl & Ruf 2010). In 2010, we marked animals with individual ear-clipping patterns using a 2 mm biopsy punch (tissue was collected for a separate study). After handling, all animals were released at the site of capture.

3.2.4 Leukocyte differential smears

Blood smears were made immediately after blood was taken using the ‘wedge’ method as per Clark (2003). Slides were air dried and stored in a slide box for up to 36 hrs.

Slides were fixed and stained using '*Diff Quik*' (a modified Wright's stain, Lab Aids, Pty Ltd, NSW, Australia) and air dried. Leukocyte differentials were scored manually (by the same researcher to ensure consistency), as per Clark (2003). The monolayer (cells one layer thick) was identified by compound microscope and using 400 × magnification. The first 300 leukocytes were identified as: monocytes, lymphoctyes, total neutrophils, band neutrohils, basophils or eosinophils. An estimate of total white blood cell concentration (WBC) in circulating blood was made using the method in Fudge (1997). This methods estimates total WBC from the leukocytes visible per field of view. The total number of leukocytes was counted in ten consecutive fields of view. The total concentration was calculated as: WBC × 10^9/L = mean (leukocytes per field of view) × 2 (Fudge 1997). The estimated concentration of leukocyte cell types was calculated as: % cell type × estimated total WBC.

3.2.5 Haematocrit

The haematocrit (Hct) samples were processed on site. The capillary tubes were spun in a portable centrifuge (LW Scientific ZIPocrit, Georgia, USA) for 5 min at 11,000 RPM. The total blood volume and packed red blood cell volume were measured with vernier callipers to the nearest 0.1 mm. Haematocrit was calculated as the percentage of packed erythrocyte volume in the total blood volume (Jain 1993).

3.2.6 Body condition

Body condition was calculated as the residuals of a regression of body mass as a function of head length (mass-size residuals; Schulte-Hostedde *et al.* 2005). Ordinary least-squares regressions using PROC REG in SAS (SAS Institute Inc. 2008) were used to generate residuals. Mass-size OLS residuals (the body condition index, BCI) are commonly used in ecological studies to infer metabolic stores in free-living vertebrates, although there is debate about its application in population studies due to changes in body composition with ontogenetic development and/or in sexually dimorphic species (Peig & Green 2010). As our study removed juveniles from analyses and tested for differences between the sexes (below), we consider that the OLS residuals method was appropriate.

3.2.7 Statistical analyses

Juveniles were removed from the analysis as ontogenetic differences were likely to be reflected in blood values (Sindik & Lill 2009) and in the BCI (Peig & Green 2010). Furthermore, the sample sizes for juveniles of both swamp rats (n = 2) and long-tailed mice (n = 1) were too low for separate analysis. Where individuals sampled in 2009 were recaptured in 2010, no sample was included in the analyses from the 2010 trapping period.

Due to low sample sizes for swamp rat blood values from CBS sites (n = 7), we were unable to analyse CBS in isolation. Swamp rat sample sizes from the harvested matrix within ARN were also low (n = 7), therefore, we needed to pool swamp rat samples from each CBS and ARN replicate (including island, edge and harvested matrix samples) to create a 'Harvested' site treatment. To investigate the haematological profile and body condition responses of native rodents among forestry treatments, linear mixed effects models were applied using PROC MIXED in SAS for each leukocyte cell type, total WBC, N:L, Hct and BCI. No transformations were needed for Hct or BCI. For both species, all leukocyte values required log transformations, except for band neutrophils in swamp rats, which were square-root transformed. One outlier was removed from the analysis: a very low Hct of 33 % from a CBS male long-tailed mouse. Forestry treatment (CBS, ARN and UNL for long-tailed mice; Harvested or UNL for swamp rats), and sex and all possible interactions were included as fixed variables, year (2009 or 2010) as a repeated measure, and replicate by treatment and replicate were included as random effects. The random replicate by treatment interaction term was used to test the fixed treatment effect and the residual term used to test other fixed effects. All interaction terms for both species were non-significant ($P < 0.05$) so they were removed from the models to allow interpretation of the main effects (Engqvist 2005). Multiple pairwise comparisons of significant fixed effects (least-squares means) were made using Tukey-Kramer adjustments.

3.3 Results

In 2009, 72 long-tailed mice individuals were sampled (18 CBS, 33 ARN, 25 UNL), and in 2010, 40 individuals were sampled (9 CBS, 5 ARN, 19 UNL). For swamp rats, 74 swamp rat individuals were sampled in 2009 (24 in HARV, 50 in UNL) and 37 swamp rat individuals were sampled in 2010 (14 HARV, 23 UNL). No eosinophils were identified in any sample from either species and basophils were in very low numbers in both species. No statistical analyses were performed for these cell types.

3.3.1 Long-tailed mice

In 2009, long-tailed mice showed significantly higher numbers of total WBCs (1.7 ×; $F_{1,86} = 14.71$; $P < 0.001$), lymphocytes (1.6 ×; $F_{1,86} = 13.08$; $P = 0.001$), neutrophils (1.7 ×; $F_{1,86} = 8.66$; $P = 0.004$), and monocytes (1.8 ×; $F_{1,86} = 7.64$; $P = 0.007$) than in 2010 (Table 2.1, Table 2.2). Haematocrit was significantly higher in CBS (48.01 ± 0.73 %) than in UNL (45.31 ± 0.56 %; $F_{2,7} = 5.06$; $P = 0.044$). Haematocrit was also higher in CBS than in ARN (45.78 ± 0.66 %), but not significantly so ($P = 0.107$). N:L ratio and band neutrophils were not significantly different among treatments, or between the years or sexes (Table 2.2). There was a trend for a treatment effect on body condition ($F_{2,7} = 4.41$; $P = 0.058$), with the highest body condition values in UNL (2.21 ± 1.18) compared to CBS (-1.98 ± 1.48) and ARN (-2.39 ± 1.41). Body condition was not significantly different between year ($F_{1,97} = 0.97$; $P = 0.326$) or sex ($F_{1,97} = 0.01$; $P = 0.931$).

3.3.2 Swamp rats

There were no significant differences between treatments, between years or between sexes for any leukocyte value, haematocrit or body condition for swamp rats (Table 2.1, Table 2.2).

Table 3.1 Haematological variables and body condition in free-living native rodents. Means, standard errors (SE) and samples sizes (n) of leukocytes, neutrophil to lymphocyte ratio (N:L), haematocrit and body condition for the long-tailed mouse (*Pseudomys higginsi*) and swamp rat (*Rattus lutreolus*). Values are differentiated by the main factors of treatment, year and sex for each species. CBS, clearfell, burn and sow; ARN, aggregated retention, UNL, unlogged native forest; HARV, pooled harvested treatments of CBS and ARN.

		Leukocytes (x 10^9 cells.L^{-1})																							
		Total WBC			Lymphocytes			Neutrophils (total)			Band neutrophils			Monocytes			N:L ratio			Haematocrit (%)			Body condition		
Species	Factors	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE
Long-tailed mice	CBS	3.84	±	0.44	2.50	±	0.30	1.13	±	0.17	0.13	±	0.03	0.20	±	0.03	0.46	±	0.08	48.01	±	0.73	-1.98	±	1.48	CBS	3.84	±	0.44	2.50	±	0.30	1.13
	ARN	4.55	±	0.45	3.01	±	0.31	1.29	±	0.18	0.19	±	0.03	0.20	±	0.03	0.48	±	0.08	45.78	±	0.66	-2.39	±	1.41	ARN	4.55	±	0.45	3.01	±	0.31	1.29
	UNL	3.75	±	0.34	2.45	±	0.24	1.09	±	0.14	0.15	±	0.03	0.18	±	0.03	0.48	±	0.07	45.31	±	0.56	2.21	±	1.18	UNL	3.75	±	0.34	2.45	±	0.24	1.09
	2009	5.04	±	0.40	3.29	±	0.28	1.47	±	0.16	0.17	±	0.03	0.25	±	0.03	0.50	±	0.07	46.40	±	0.49	0.02	±	1.04	2009	5.04	±	0.40	3.29	±	0.28	1.47
	2010	3.06	±	0.29	2.02	±	0.19	0.87	±	0.11	0.14	±	0.03	0.14	±	0.02	0.45	±	0.07	46.34	±	0.63	-1.47	±	1.25	2010	3.06	±	0.29	2.02	±	0.19	0.87
	Female	3.90	±	0.34	2.48	±	0.23	1.20	±	0.14	0.17	±	0.03	0.19	±	0.02	0.53	±	0.07	46.19	±	0.55	-0.78	±	1.16	Female	3.90	±	0.34	2.48	±	0.23	1.20
	Male	4.20	±	0.32	2.83	±	0.22	1.14	±	0.13	0.15	±	0.03	0.20	±	0.02	0.42	±	0.07	46.55	±	0.53	-0.66	±	1.07	Male	4.20	±	0.32	2.83	±	0.22	1.14
Swamp rats	HARV	4.50	±	0.40	3.25	±	0.30	1.03	±	0.14	0.17	±	0.02	0.23	±	0.03	0.31	±	0.03	44.86	±	0.63	0.97	±	1.80	HARV	4.50	±	0.40	3.25	±	0.30	1.03
	UNL	4.59	±	0.29	3.35	±	0.22	0.99	±	0.11	0.12	±	0.01	0.25	±	0.02	0.32	±	0.03	44.71	±	0.49	-0.46	±	1.32	UNL	4.59	±	0.29	3.35	±	0.22	0.99
	2009	5.08	±	0.38	3.66	±	0.28	1.17	±	0.12	0.16	±	0.02	0.25	±	0.03	0.33	±	0.03	45.13	±	0.53	-0.39	±	1.41	2009	5.08	±	0.38	3.66	±	0.28	1.17
	2010	4.02	±	0.30	2.93	±	0.23	0.85	±	0.10	0.14	±	0.02	0.23	±	0.03	0.30	±	0.03	44.44	±	0.59	0.89	±	1.68	2010	4.02	±	0.30	2.93	±	0.23	0.85
	Female	4.48	±	0.31	3.21	±	0.23	1.02	±	0.10	0.15	±	0.02	0.24	±	0.02	0.32	±	0.03	44.52	±	0.51	0.97	±	1.37	Female	4.48	±	0.31	3.21	±	0.23	1.02
	Male	4.62	±	0.38	3.38	±	0.28	1.01	±	0.12	0.15	±	0.02	0.23	±	0.03	0.31	±	0.03	45.05	±	0.62	-0.46	±	1.73	Male	4.62	±	0.38	3.38	±	0.28	1.01

Table 3.2 Results of the linear mixed effects models for the main effects of treatment, year and sex for swamp rats and long-tailed mice. Results in bold are significant (*P* < 0.05). There were three treatments for long-tailed mice: clearfell, burn and sow (CBS), aggregated retention (ARN), and unlogged native forest (UNL). For swamp rats, the two harvested treatments (CBS, ARN) were combined for swamp rats due to low sample sizes, resulting in two treatments: Harvested and UNL.

		Treatment			Year			Sex		
Species	**Factors**	**d.f.**	***F* value**	***P* value**	**d.f.**	***F* value**	***P* value**	**d.f.**	***F* value**	***P* value**
Long-tailed mice	Total WBC	2,7	0.64	0.555	1,86	14.71	**<0.001**	1,86	1.04	0.311
	Lymphocytes	2,7	0.75	0.506	1,86	13.08	**0.001**	1,86	2.00	0.161
	Total neutrophils	2,7	0.47	0.642	1,86	8.66	**0.004**	1,86	0.00	0.974
	Band neutrophils	2,7	1.60	0.268	1,86	0.02	0.875	1,86	0.02	0.876
	Monocytes	2,7	0.17	0.847	1,86	7.64	**0.007**	1,86	0.70	0.406
	N:L	2,7	0.25	0.785	1,89	0.03	0.855	1,89	2.87	0.094
	Haematocrit	2,7	5.06	**0.044**	1,83	0.01	0.934	1,83	0.29	0.593
	Body condition	2,7	4.41	***0.058***	1,97	0.97	0.326	1,97	0.01	0.931
Swamp rats	Total WBC	1,6	0.28	0.618	1,88	2.91	0.092	1,88	0.13	0.722
	Lymphocytes	1,6	0.46	0.524	1,88	2.82	0.097	1,88	0.33	0.565
	Total neutrophils	1,6	0.02	0.893	1,88	2.88	0.093	1,88	0.06	0.806
	Band neutrophils	1,6	3.41	0.114	1,88	0.29	0.592	1,88	0.21	0.647
	Monocytes	1,6	0.00	0.995	1,88	0.07	0.800	1,88	0.38	0.537
	N:L	1,6	0.32	0.594	1,91	0.22	0.642	1,91	0.02	0.891
	Haematocrit	1,6	0.04	0.853	1,80	0.78	0.380	1,80	0.45	0.505
	Body condition	1,6	0.43	0.535	1,98	0.37	0.546	1,98	0.45	0.505

3.4 Discussion

3.4.1 Long-tailed mouse stress responses and general health

3.4.1.1 Effect of habitat treatment

The long-tailed mouse is considered a habitat generalist, (Stoddart & Challis 1991; Stephens *et al.* 2012); therefore we did not anticipate that there would be differences among habitat treatments in the condition and physiological stress metrics examined. However, although leukocyte values showed no differences, the metrics for general health (Hct and BCI) did differ between treatments for long-tailed mice. Haematocrit was significantly higher in CBS sites than UNL, while BCI was highest in UNL. The BCI is used here as a correlate of metabolic reserves (both as fat and muscle), and higher values indicate greater reserves than expected for a given skeletal measurement (Schulte-Hostedde *et al.* 2001). This suggests that despite our predictions of a habitat generalist showing no response to disturbance, which was supported by a recent abundance study (Stephens *et al.* 2012), long-tailed mice in undisturbed sites were in better body condition than those in CBS or ARN sites.

Interpreting Hct is more difficult, as both high and low values can be indicative of diseased or stressed states (Fair *et al.* 2007). For example, high Hct values can indicate good aerobic capacity, but could also indicate dehydration, short-term stress or recent physical exertion (elevated heart rates force plasma out of blood and increase Hct), whereas low values could indicate non-regenerative anaemia (Fair *et al.* 2007). This means that Hct ideally needs to be interpreted within a known framework of 'normal' ranges, but this range is not known for our study species. Native mammals in anthropogenically disturbed habitats do sometimes have better condition than conspecifics in less disturbed habitats (Diaz *et al.* 1999; Johnstone *et al.* 2010), but such a response is unusual and the trend for higher BCI in UNL sites would suggest this is probably not occurring here. In contrast to the finding for swamp rats, long-tailed mice showed a health status response following anthropogenic habitat degradation, despite showing no difference in abundance between habitat types in a recent study conducted in the same sites (Stephens *et al.* 2012). This demonstrates the risk of relying only on population distribution data to make inferences about habitat quality and species response to habitat change.

One possible explanation for this observation is potential competition for habitat between the species, with swamp rats occupying the better quality habitat within the unlogged patches. Although abundance data did not indicate competition as long-tailed mice were co-existing with swamp rats in our unlogged sites (Stephens *et al.* 2012), Luo et al. (1998) found swamp rats were dominant over long-tailed mice in an area of wet *Eucalyptus* forest that had been partially burnt by wildfire. This may suggest that competition is only prevalent in areas in which high quality habitat is scarce or degraded, such as in harvested sites. If this is indeed occurring, the subordinate long-tailed mouse may become displaced by swamp rats and shift its habitat use to incorporate lower quality areas within the harvested sites (Abramsky *et al.* 1990).

3.4.1.2 Effect of year, capture stress and interactions between long- and short-term stress

In 2009, the WBC, lymphocyte, neutrophil and monocyte concentrations were higher than in 2010 for long-tailed mice. However, all values were lower than expected for free-living rodents based on values obtained for nominally non-stressed closely related species (mean values of 4.9 – 20.9 × 10^9/L; Monamy 1995a; Weber *et al.* 2002; Ahlers *et al.* 2011), while a study of three wild-caught rodent species showing signs of capture stress were in a similar range to our values (1.6 – 7.7 × 10^9/L; Barker & Boonstra 2005). Therefore, while capture stress was not specifically examined, results of the current study indicate that long-tailed mice (and swamp rats) were suffering from capture stress at the time of sampling.

Despite a likely capture stress effect on the measured leukocyte values, inferences about long-term (environmental) stress can still be drawn from the results by considering the interactions of long- and short-term stress responses, although such conclusions must necessarily be viewed with caution. In rodents, short-term stress (e.g. trapping) temporarily reduces circulating WBC, and concurrently increases N:L ratio and stress hormone concentrations (Dhabhar & McEwen 1997). However, when stressors are prolonged or frequent (e.g. environmental stressors), individuals are less able to mount a stress response to a short-term stressor, and the response becomes attenuated (Dhabhar & McEwen 1997). Therefore, given that it appears that trapping induced a substantial stress response in the current study for both study species, we postulate that individuals experiencing greater long-term stressors (e.g. increased

predator threat due to reduced habitat cover), should show a more attenuated short-term stress response (i.e. to capture), and thus, more physiologically stressed individuals should have a higher WBC, higher lymphocyte concentrations, lower N:L ratios and possibly lower neutrophil concentrations than less stressed individuals. Considering this interpretation, the results we obtained may indicate that long-tailed mice were experiencing greater long-term stress in 2009 than 2010, regardless of habitat treatment. Long-tailed mice abundance was higher in 2009 than in 2010 (Stephens *et al.* 2012) and the differences in abundance and stress results may reflect increased daily stress levels through competition for nesting and food resources and/or a cyclical variation in these populations. Although cyclic population fluctuations have not been previously reported for these species, they are evident in many other small mammal species (Stenseth 1999), most notably in snowshoe hares (Krebs *et al.* 1986). However, the absence of any clear N:L ratio or BCI responses to year makes this interpretation necessarily tentative.

3.4.2 Swamp rat stress responses and general health

Swamp rats are a cover-dependent species (Fox & Monamy 2007), and are found in lower abundances in areas post-disturbance (Fox 1982; Stephens *et al.* 2012). Due to this habitat specialisation, we hypothesised that the harvesting-related disturbance in our sites would result in a local environment that swamp rats would experience as more stressful than in unlogged forest. However, swamp rats showed no differences in leukocyte stress indices, Hct or BCI between harvested and unlogged sites. The lower abundances in harvested sites and lack of apparent effects on stress and condition are intriguing and unexpected, and may be explained by the following theories.

'Edge' effects rather than 'open' effects: The 'Harvested' treatment for swamp rats included all individuals captured in the ARN and CBS sites. However, few individuals were captured in the CBS sites (n = 7) and the majority of swamp rat individuals captured in ARN were from the unlogged areas (islands and edges, n = 24) rather than the harvested matrix (n = 7). Therefore, the majority of samples were from individuals experiencing 'life on the edge', rather than in the harvested patches. The negative impacts of edges have been widely reported in the literature (Andren & Angelstam 1988; Laurance 1991; Mills 1995), although the importance of retaining threshold levels of primary habitat has been shown (Pardini 2004). In the context of this study,

the forested edges appear to be providing sufficient cover for swamp rats to persist in disturbed habitats (Stephens *et al.* 2012). Furthermore, where individuals were captured in the harvested areas of ARN or CBS, they were typically in areas of dense groundcover vegetation (Stephens *et al.* 2012). Thus, the behaviour of swamp rat individuals may be mitigating the impacts of disturbance by reducing their exposure to disturbance-related stressors (e.g. by utilising areas of dense cover, visibility to predators in a more open environment is reduced).

Cryptic degradation: Another possibility is that the swamp rats showed a similar stress response to anthropogenically degraded and undisturbed sites, not because the harvested sites provided a non-stressful habitat, but because the undisturbed control sites were cryptically degraded and swamp rats may have been experiencing stress in those sites as a result. When devising the experiment, we did not fully anticipate the effects that spur roads in unlogged sites may potentially have. In a concurrent study, Stephens *et al*. (2013) investigated the genetic impacts of fragmentation on swamp rats within production forest landscapes. One surprising finding was that narrow, unpaved, seldom used roads (by humans/traffic) were a dispersal barrier for swamp rats. Perhaps this type of fragmentation, although not resulting in large-scale habitat loss, could be experienced as a stressor by swamp rats. It is evident that species responses to roads differ dramatically. Some species in close proximity to roads have shown increased stress hormones (Wasser *et al.* 1997; Newcomb Homan *et al.* 2003; Crino *et al.* 2011), while others show no detectable stress responses and/or potentially beneficial physiological effects (Strasser & Heath 2011; Morgan *et al.* 2012). Consequently, while plausible, it is uncertain at this stage if the effects of roads acted as stressors to swamp rats.

3.5 Conclusion

Contrary to our original hypothesis, the long-tailed mouse, a habitat generalist, showed better condition in the less disturbed site compared with the more disturbed sites. The implication of this finding is that even relatively generalist and ‘resilient’ common native species can be negatively affected by anthropogenic habitat degradation, albeit not at a level that is obvious from population distribution data alone. While significant

differences in swamp rat relative abundances between anthropogenically degraded and undisturbed sites have been reported (Stephens *et al.* 2012), we found no apparent differences in indicators of stress or condition in this cover-dependent species in this study. We present two possible explanations for this observation: 1) The majority of individuals trapped in the harvested treatments were utilising the unlogged portion of these areas, and potentially minimising the impacts of loss of cover in these areas; or 2) populations may have been experiencing elevated physiological stress in both the harvested and relatively undisturbed sites, potentially due to fragmentation of the unlogged forest by minor roads. The results of this study highlight the risks to ecologists and land managers alike, of drawing assumptions from ecological (abundance) measurements in isolation. Our results therefore illustrate the important role of physiological studies in complementing broader population-based studies with ecological monitoring and assessment goals.

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CHAPTER 4:Habitat fragmentation in forests affects relatedness and spatial genetic structure of a native rodent, *Rattus lutreolus*

Stephens H.C., Schmuki C., Burridge C.P. & O'Reilly-Wapstra J.M. (2013) Habitat fragmentation in forests affects relatedness and spatial genetic structure of a native rodent, *Rattus lutreolus*. *Austral Ecology* **doi: 10.1111/aec.12001**

Clockwise from top left: A juvenile swamp rat captured in unlogged forest; three aggregated retention coupes showing: islands and an edge (far right), an edge peninsula with a fire-break, and regrowth three years post-havest; and two unlogged sites with narrow, unpaved roads.

Abstract

Habitat fragmentation can have a range of negative demographic and genetic impacts on disturbed populations. Dispersal barriers can be created, reducing gene flow and increasing population differentiation and inbreeding in isolated habitat remnants. Aggregated retention is a form of forestry that retains patches of forests as isolated island or connected edge patches, with the aim of 'lifeboating' species and processes, retaining structural features and improving connectivity. Swamp rats (*Rattus lutreolus*) are a cover-dependent species that are sensitive to habitat removal. We examined the effects of aggregated retention forestry and forestry roads in native wet *Eucalyptus* forests on swamp rat gene flow and population genetic structure. We characterised neighbourhood size in unlogged forest to provide a natural state for comparison, and examined population structure at a range of spatial scales, which provided context for our findings. Tests of pairwise relatedness indicated significant differentiation between island and edge populations in aggregated retention sites, and across roads in unlogged sites. Spatial autocorrelation suggested a neighbourhood size of 42–55 m and revealed male-biased dispersal. We found no genetic isolation by geographic distance at larger (> 2.3 km) scales and populations were all significantly differentiated. Our results suggest that removal of mature forest creates barriers for swamp rat dispersal. In particular, roads may have long-term impacts, while harvesting of native forests is likely to create only short-term dispersal barriers at the local scale, depending on the rate of regeneration.

4.1 Introduction

The modification and loss of native habitat due to anthropogenic practices such as forestry are recognised as major threats to populations, species and ecological processes worldwide (WCMC 1992). Fragmentation of forest can reduce the quantity and quality of habitat for forest dependent species, disrupt natural processes, and impede animal movement between suitable habitat (Saunders *et al.* 1991; Zanette *et al.* 2000; Siitonen 2001; Lancaster *et al.* 2011). Impeded movement of individuals and their genes can have a range of demographic and genetic impacts, including increased genetic differentiation between populations, reduced genetic variation within populations, and altered within-fragment population structure (Frankham *et al.* 2002; Stow & Sunnucks 2004a,b). These impacts are more likely to be experienced when retained habitat fragments are smaller and more isolated, and, if dispersal and recolonisation of patches remain impeded, population or species extinction may result (Frankham *et al.* 2002; Bradshaw & Marquet 2003).

Current forest harvest practices such as clearfelling and burning of residue changes mature, connected and structurally complex landscapes into patchwork landscapes with large areas of exposed, often inhospitable land that may be difficult to traverse, particularly by species that have limited dispersal capabilities or obligately inhabit mature intact forest (Şekercioğlu *et al.* 2002; Brouat *et al.* 2003; Henle *et al.* 2004; Schmuki *et al.* 2006; Bentley 2008). An alternative harvesting practice to clearfelling is retention forestry (also termed variable retention, green-tree retention), which was developed with the aims of retaining structural complexity at the local scale, providing 'lifeboats' for species, and providing connectivity within production forest landscapes (Franklin *et al.* 1997; Gustafsson *et al.* 2012). While there is a general consensus that variable retention harvesting is beneficial for species richness and abundance compared to clearfelling, levels of success vary among species and taxa (Rosenvald & Lohmus 2008). Aggregated retention (ARN) is a form of retention forestry that retains patches of unlogged forest alongside the harvested edge (bounded by unlogged forest) and/or as 'islands' (isolated within the harvested matrix). The objectives of ARN are to increase connectivity within the landscape by reducing distances between forested patches, and to retain structural complexity during subsequent regrowth. Aggregated retention has been adopted in many systems worldwide (see reviews by Rosenvald &

Lohmus 2008; Gustafsson *et al.* 2012). However there have been few studies on the impact of ARN on ground mammals (Sullivan & Sullivan 2001; Klenner & Sullivan 2003; Gitzen *et al.* 2007; Sullivan *et al.* 2008), particularly in the Southern Hemisphere systems (Lindenmayer *et al.* 2010; Stephens *et al.* 2012), and to our knowledge there have been no published studies on the genetic implications of this practice.

The swamp rat (*Rattus lutreolus* Thomas 1882) is a small (~110 g), mostly nocturnal rodent with a diet predominantly consisting of leaf and stem material, but also fungi, insects and seeds (Watts & Braithwaite 1978; Driessen 1987; Norton 1987a). Breeding occurs over spring–summer (September to March), with females raising one or more litters of three to six young (Green 1967), and longevity is 1–2 years, with a typical generation time of one year. Swamp rats are a widespread, relatively common species across Tasmania (Norton 1987a), but are restricted to habitats with dense cover (Fox & Monamy 2007), and are rarely found in cleared areas (Norton 1987b; Monamy 1995). Despite being a common species, there have been few population studies and little is known of their dispersal capabilities or population structure. Swamp rats have been previously documented in ARN unlogged areas (islands and edges), but very rarely in the harvested matrix (Stephens *et al.* 2012). Our anecdotal (capture-mark-recapure, CMR) evidence suggests that swamp rats may rarely move across the harvested matrix (one crossing from 88 recaptures in ARN) or other cleared areas such as roads (six crossings from 96 recaptures in unlogged sites with roads), although these observations may not be repeated across generations, or result in gene flow (i.e. the reproductive success of dispersing individuals).

In this study we examined and compared genetic diversity and population structure of swamp rats in ARN and unlogged sites. We hypothesised that genetic diversity would be reduced within ARN sites relative to unlogged sites and expected that island populations would exhibit higher levels of genetic relatedness compared to populations in contiguous forest. Roads have been shown to pose a barrier for dispersal in many small mammal species, including narrow, unpaved roads or seldom used roads (Barnett *et al.* 1978; Swihart & Slade 1984; Rico *et al.* 2007; McGregor *et al.* 2008), and our own anecdotal evidence suggests that swamp rats are reluctant to cross roads. Therefore, we also hypothesised that roads within unlogged sites would present barriers to dispersal in this species, and hence similarly affect population genetic

variation. To assist in the interpretation of our localised population analyses, we also examined structuring at broader geographic scales, involving spatial comparisons among ARN and unlogged forest replicates.

4.2 Methods

4.2.1 Study site and sampling

Our study was conducted in native old growth wet *Eucalyptus* forests and recently harvested sites in State Forest in two regions of southern Tasmania, Australia: the Styx (42.81ºS, 146.65E) and Huon (43.11ºS, 146.76ºE) Valleys (Fig. 4.1). The current molecular study contributes to a larger investigation of the impact of different forestry practices on the abundance of two sympatric native rodents that occupy different habitat niches, swamp rats (*Rattus lutreolus*) and long-tailed mice (*Pseudomys higginsi*). Detailed background on the treatments, study sites and trapping protocol are provided in Stephens *et al.* (2012). We focussed our genetic study on swamp rats as they appeared largely restricted to unlogged habitat while long-tailed mice were equally abundant in unlogged and harvested areas.

In this genetic study we collected data from four replicates of two different forestry treatments: aggregated retention sites (ARN, Fig. 4.2a) and unlogged native forest sites (UNL, Fig. 4.2b). Within ARN, trapping was conducted in three habitat types: the harvested matrix (ARN-Harvest), 'island' aggregates (isolated patches surrounded by the harvested matrix; ARN-Island) or 'edge' aggregates (patches of forest connected to the surrounding forest; ARN-Edge). Aggregated retention sites were harvested in 2005/06, with regeneration burning occurring in 2007. Multiple island aggregates of 0.6–2.6 ha were typically retained, except in one site where only one large island aggregate of 3.3 ha was retained. The distance between ARN islands and forested edges are typically 80–150 m (Scott *et al.* 2011). All UNL retained old growth forest elements, including mature trees, and had been left relatively undisturbed from harvesting practices for more than 70 years. Three UNL had narrow unpaved roads (typically <10 m edge to edge) bisecting them. The fourth UNL site was in contiguous forest. In each site, 54 traps were set for three nights in a configuration of nine plots with six traps each. In UNL, the nine plots were randomly allocated across the site. In

ARN, three plots were set in each of the three habitat types: ARN-Harvest, ARN-Island and ARN-Edge. Each site was trapped for three nights in the post-dispersal winter period from May to July 2009 (3–4 years post-harvest) and again in winter 2010 (April to July; 3888 total trap nights), with additional trapping in ARN (1152 trap nights) in November/December 2009 (at the start of the breeding season) to increase sample sizes. Additional trapping was conducted in one UNL site, UNL-H1, in October 2010 (714 trap nights).

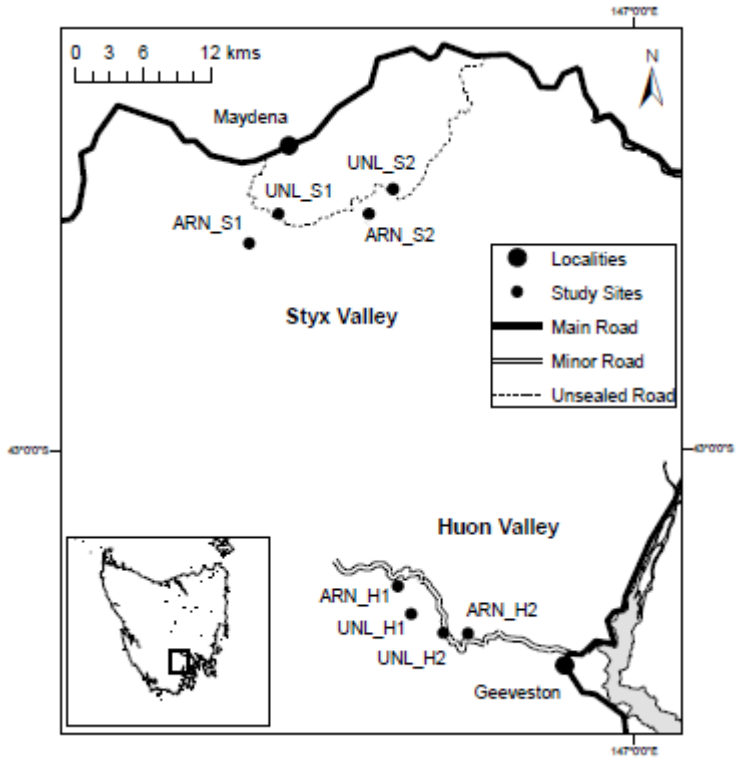

Fig. 4.1 Location of study sites in the Huon and Styx Valleys in southern Tasmania. There are four replicates of each treatment, two in each region. The site codes correspond to the treatment (aggregated retention, ARN_; unlogged native forest, UNL_), region (Huon, H; Styx, S) and replicate within that treatment and region (1 or 2).

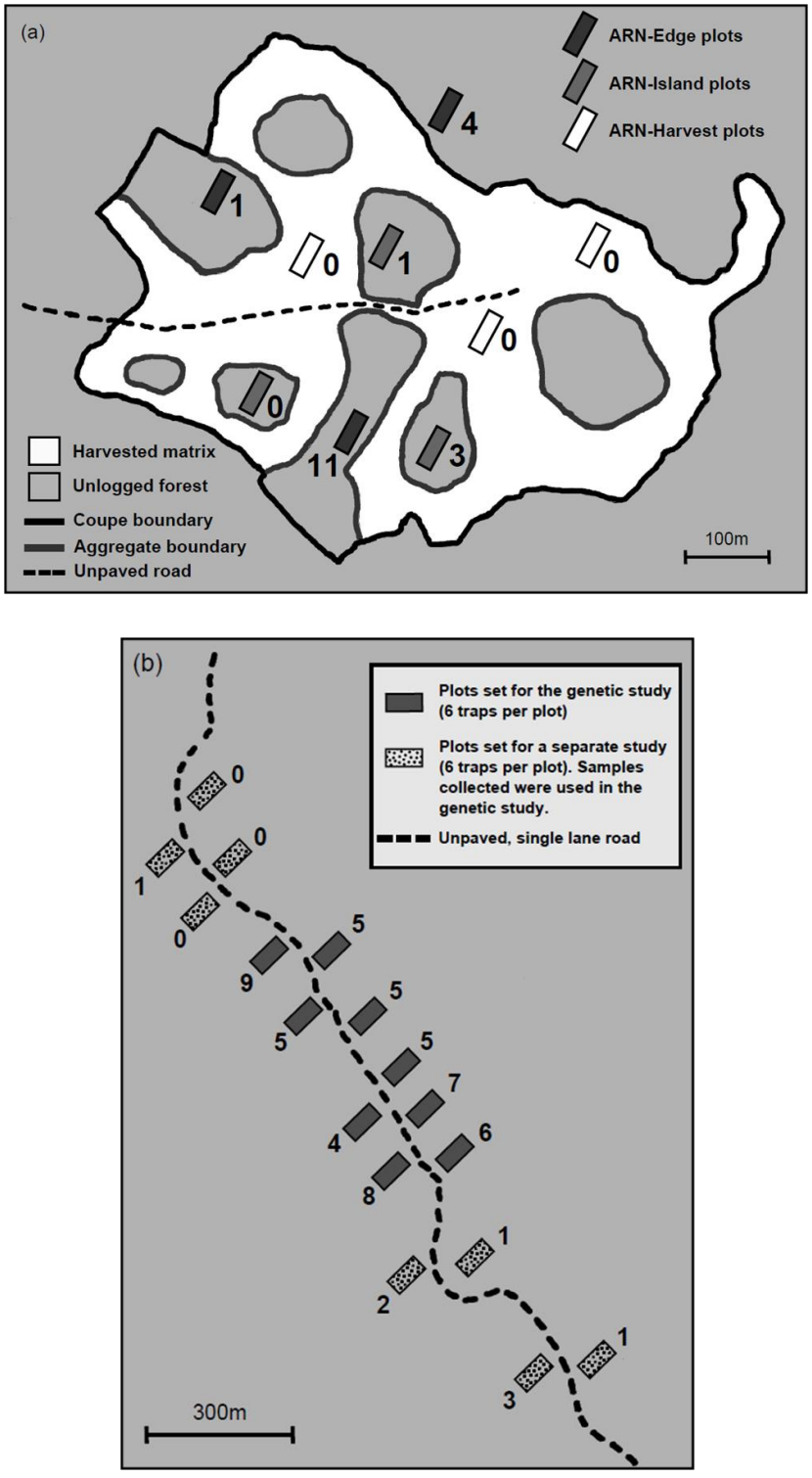

Fig. 4.2 Examples of the trapping design used in (a) aggregated retention (ARN) and (b) unlogged (UNL) sites. Each rectangle represents a trapping plot of six trap stations. The numbers next to each plot represent the number of individuals captured in that plot. Typically, nine plots were used per site. In ARN (e.g. ARN-S1), three plots were set in each of the three habitat types, as depicted by the different shaded boxes: Edges (dark), Islands (medium) and Harvested matrix (white). In this UNL site, UNL-H1, nine plots were set for the genetic study (dark boxes) and eight addition plots (dotted boxes) were set for a separate study, but samples were collected and used in this study.

4.2.2 DNA Extraction

An ear tissue sample was collected from each newly encountered swamp rat (n = 181) using a 2 mm biopsy punch. Samples were stored at room temperature in 100 % ethanol. DNA was extracted from the tissue samples using GenCatch™ Genomic DNA Extraction Kits following the tissue protocol (Epoch Biolabs Inc. 2002).

4.2.3 Genetic marker selection

To date, microsatellite markers had not been developed for swamp rats. Therefore, we tested 17 microsatellite markers that had been developed or tested on other *Rattus* species (Table 4.1). Thirteen loci originated from *R. fuscipes greyii* and had undergone testing for cross-species amplification on one *R. lutreolus* individual (Hinten *et al.* 2007). The remaining four loci originated from consensus *Rattus* sequences (Serikawa *et al.* 1992) and were previously tested on *R. fuscipes* (Hewitson 1997; Lindenmayer & Peakall 2000). We tested for cross-species amplification and polymorphism of all 17 loci on 12 swamp rats. Readily scorable markers which exhibited polymorphism were then genotyped for all individuals.

Table 4.1 Locus characteristics for swamp rats, *Rattus lutreolus*, in southern Tasmanian wet *Eucalyptus* forests. 17 loci from other *Rattus* species were tested for cross-species amplification and polymorphism. The size range (bp), number of alleles, probability of deviation from Hardy-Weinberg Equilibrium (HWE, Bonferroni adjusted, values shown for the lowest site *P*-value), and expected (H_E) and observed heterozygosity (H_O) are shown for the 11 successfully amplified and scored loci. *indicates a significant deviation from HWE, attributable to one site, UNL-H1.

Locus	Source species	Primer 5' end of reverse primer appended to read GTTT[¥]	Primer conc (µM)	Multiplex group	Size range (bp)	No. of alleles	HWE	H_E	H_O
FGA	*Rattus*[‡]	F: CGTGTGGAAATACTTACAAGCA R: CTGCAGACTGATTTGCTCATAA	0.025	4B	95-129	14	<.001*	0.453	0.456
PLANH	*Rattus*[‡]	F: GGGATCTTGCCAAGGTGA R: CGGCTTCTGAATGTATTGGA	0.050	4B	134-142	5	0.053	0.601	0.579
RfgCT2B	*R.f. greyii*[§]	F: CCTTTGGCTCCTGCACCCCA R: GTGCCAGGGAGCGTGGGCT	0.100	4B	307-312	6	<.001*	0.430	0.326
RfgCTGT1B	*R.f. greyii*[§]	F: AGGGGATCTAGGGCCTTCTGCA R: TCCACGACATGATGCTCTGTTACAA	0.200	2A	360-408	19	0.508	0.566	0.610
RfgD1	*R.f. greyii*[§]	F: ATGATGGTGAGGGCCACGC R: TTGAAACCAACTTCGAGGCAGA	0.050	2A	129-171	16	0.115	0.818	0.883
RfgG3	*R.f. greyii*[§]	F: TGCTCCTTTCCCTGGGCGA R: TCTTTGTGCGGCCCTTTCAT	0.050	2A	203-253	28	0.019	0.853	0.864
RfgL3	*R.f. greyii*[§]	F: GGCAATGCCTACACTCGTGCTTT R: TCCCAAGCCTGTGGCGAT	0.050	3B	205-237	12	0.022	0.645	0.688
RfgL5	*R.f. greyii*[§]	F: TGCCCTCTTCTGGCCATGTT R: TGTTTCCCTCTGTGTATTAAGGGCT	0.050	3B	116-132	7	0.048	0.716	0.697
RfgM8	*R.f. greyii*[§]	F: CAAGAAAATTGGGTGTGGGAGG R: GCATCTTGCTATGGTGGTACACAG	0.050	4B	263-299	7	0.580	0.539	0.624
RfgO3	*R.f. greyii*[§]	F: GCAGGCACTGCATTGCACG R: ATCCCCCACCCATCACAGG	0.050	3B	383-443	34	0.002*****	0.866	0.828
RfgO6	*R.f. greyii*[§]	F: TGTGCTGAAAATTCTTTTTTGAGTTT R: GCTTTCTGGGTGGCCTGCTT	0.050	3B	301-309	5	0.379	0.121	0.129
CPB †	*Rattus*[‡]	F: GGTGCTAGTAGACAATAAGATAGAT R: TTCATGAGTTTTCACTGTTTGC	0.300	(3B)	-	-	-	-	-
CRYG †	*Rattus*[‡]	F: CCCAGAAATATGTATTTTTACAAGC R: GCCAGAGCTATGTAGAGAGACC	0.050	(3B)	-	-	-	-	-
RfgC3 †	*R.f. greyii*[§]	F: GTTCAGTAGCTGTGTGGGGCCA R: CAGCTGCCAAAAGTGCCCC	0.050	(2A)	-	-	-	-	-
RfgCTG1H †	*R.f. greyii*[§]	F: GGCTCCAAGCACCACCGGG R: AGCTCAGCAGTATGCCCTTGGGA	0.050	(1)	-	-	-	-	-
RfgG4 †	*R.f. greyii*[§]	F: CCATGTATCCCTGGCTGGCC R: CTTCGACATGCAAGGCACCAA	0.050	(1)	-	-	-	-	-
RfgW6 †	*R.f. greyii*[§]	F: GCGCCTGACGAGGAGTCTCTT R: CAAGACCATGTCTTCAAAAAAGTAGCA	0.050	(4)	-	-	-	-	-

†Loci did not amplify reliably and were not used in further analyses. ‡Serikawa et al. (1992), Lindenmayer et al. (2000). §Hinten et al. (2007). [¥]Brownstein et al. (1996).

4.2.4 Microsatellite PCR and scoring

The forward primer of each locus was labelled with a fluorescent dye using 6-FAM, VIC, NED or PET. The 5' end of reverse primers were modified to read 'GTTT' following Brownstein *et al*. (1996). Multiplexes of 4–6 loci per reaction (Table 4.1) were amplified using Qiagen Multiplex PCR Kits. PCR amplifications were carried out in 10 µL reactions containing DNA template (3.4-49.6 ng/µL), 0.05 µM primer mix (Table 4.1), and 1x QIAGEN Mulitplex PCR Master Mix (containing 3mM $MgCl_2$). The loci were amplified using a modified version of the thermal cycling protocol recommended by QIAGEN; an initial activation step of 15 min at 95ºC was followed by a three-step cycle (repeated 35 times) of denaturation (94ºC for 30 s), annealing (57ºC for 90 s) and extension (72ºC for 60 s). The last step was a final extension of 60ºC for 30 min. Fragment analysis was performed by the Australian Genome Research Facility on an AB3730, using LIZ500 size standard. Scoring was performed using Genemapper ver. 3.7 (Applied Biosystems).

4.2.5 Hardy-Weinberg Equilibrium and Genotypic Disequilibrium

To ensure the suitability of loci for population studies of swamp rats, we tested each site population for deviations from Hardy-Weinberg Equilibrium and Genotypic Disequilibrium in GENEPOP (web ver. 4.1.10; Raymond & Rousset 1995) and calculated expected and observed heterozygosities in GenAlex 6.41 (Peakall & Smouse 2006). Multiple comparisons used sequential Bonferroni corrections to determine statistical significance, with an α of 0.05.

4.2.6 Genetic diversity and explanatory variables

For each site, the following genetic diversity variables were calculated: the fixation index, F_{IS}, representing the correlation of alleles within an individual relative to the subpopulation within which it occurs (FSTAT 2.9.3; Goudet 1995); allelic richness (AR; FSTAT 2.9.3); genotypic diversity (GD; GenoDive 1.1, Meirmans & Van Tienderen 2004); observed (H_O) and expected (H_E) heterozygosity (GenAlex 6.41); and average relatedness (R) amongst all individuals within the site (GenAlex 6.41; PopTools 3.2,Hood 2010; Table 4.2). To investigate the influence of treatment (ARN vs. UNL) and region (Huon vs. Styx) on genetic diversity, we ran generalized linear models with the response variables F_{IS}, AR, R, and GD using PROC GLM in SAS (SAS Institute Inc. 2008).

Table 4.2 Genetic diversity estimates for *Rattus lutreolus* in unlogged forest (UNL) and aggregated retention (ARN) sites in two regions of Tasmanian State Forest: the Huon (H) and Styx (S) Valleys (see Figure 1 for map locations). The number of individuals (n), fixation index (F_{IS}), allelic richness (AR), relatedness (R), genotypic diversity (GD), and expected (H_E) and observed (H_O) heterozygosity are shown for each site population. * indicates a significant within-site effect.

Site type	Region	Site code	n	F_{IS}	AR	R	GD	H_E	H_O
ARN	Huon	ARN-H1	25	0.017	5.12	0.186	0.929	0.626	0.647
ARN	Huon	ARN-H2	14	-0.013	5.71	0.087	0.960	0.560	0.571
ARN	Styx	ARN-S1	20	0.021	5.45	0.118	0.900	0.601	0.618
ARN	Styx	ARN-S2	10	-0.002	4.75	0.121	0.950	0.573	0.591
UNL	Huon	UNL-H1	62	0.071 *	5.55	0.063	0.984	0.654	0.613
UNL	Huon	UNL-H2	14	0.051	5.19	0.111	0.929	0.593	0.584
UNL	Styx	UNL-S1	13	0.010	4.71	0.115	0.923	0.591	0.608
UNL	Styx	UNL-S2	21	-0.012	4.09	0.129	0.952	0.608	0.630

4.2.7 Genetic structure

To test whether spatial population structuring could be confounded by temporal genetic variation, samples were divided by year of capture. Some individuals were captured in both 2009 and 2010 and were included in both groups. Within each site, the two temporal samples were tested for differentiation using exact tests of genic (allele) frequencies, and by calculating F_{ST} in GENEPOP 4.1.10.

To investigate spatial genetic structure and neighbourhood size of swamp rats in continuous (UNL) habitat, spatial autocorrelation analyses were completed in GenAlex 6.41 using 999 permutations and trap station location data. Separate analyses of males and females were also conducted for site UNL-H1 (n=62) but not UNL-S2 (n=21), owing to sample size. Mantel tests in GENEPOP 4.0.10 were used to test for genetic isolation by geographic distance among sites, based on the logarithm of geographic distance and $F_{ST}/(1-F_{ST})$ (Rousset 1997).

To investigate the potential of cleared areas (harvested matrix and roads) as barriers to dispersal, we tested whether pairwise relatedness differed between individuals (1) occupying different habitat types within ARN and (2) separated by roads in three UNL

sites, using the Queller and Goodnight coefficient (Queller & Goodnight 1989) in GenAlex 6.41. In each ARN site, pairwise relatedness was calculated based on comparisons among individuals within, but not between, each ARN island and each ARN edge plot (a spatially distinct group of traps, as described earlier), and within UNL sites we calculated the pairwise relatedness for individuals within subpopulations ('same' side of road) and between subpopulations ('different' side of road). The relatedness values from each site were tested within each site, and also pooled over sites for each treatment (i.e. ARN or UNL), with averages tested in PopTools 3.2. Average and resample functions were used to generate real and randomized mean relatedness values, respectively, and the Monte Carlo function calculated 1000 randomized relatedness differences and the number of randomized relatedness differences greater than the real relatedness difference.

At larger spatial scales, genetic differentiation between all pairs of site populations (ARN and UNL) was tested using exact tests of genic (allelic) frequencies in GENEPOP 4.1.10, with Fisher's method used to combine *P*-values across loci. Population structuring was also quantified via the calculation of F_{ST} and G''_{ST} for all sites and within Huon and Styx regions separately using GenoDive 2.0b22. STRUCTURE 2.3.3 (Pritchard *et al.* 2000) was used to test for the presence of population structuring without requiring the *a priori* assignment of individuals to populations. This program assigns individuals to a number of populations (K) probabilistically using a Bayesian Markov chain Monte Carlo (MCMC) algorithm. The parameters used were admixed ancestry and correlated allele frequencies with no *a priori* population source assumed, and burn-in and run lengths of 100 000 each. Given that each of the eight sites could represent a distinct population, we ran K = 1 to K = 8 (10 iterations per K) plus three additional K (9, 10, 11), as recommended by Evanno *et al.* (2005), to test for any cryptic structuring. The optimal value of K was estimated using the delta K value based on the second order rate of change in Ln (P(X|K) (Evanno *et al.* 2005), calculated in STRUCTURE HARVESTER (Earl & vonHoldt 2012). We tested for further differentiation within the initial clusters identified as advocated by Evanno *et al.* (2005), using the methods as described above, with a reduction in number of K tested as K = number of collection sites in cluster + 3. Plots were created using mean proportional membership (over 10 runs) to each cluster as

calculated in CLUMPP 1.1.2 (Jakobsson & Rosenberg 2007) and visualised in DISTRUCT 1.1 (Rosenberg 2004).

4.3 Results

Over two trapping seasons, 181 swamp rats were sampled from eight sites. All samples yielded reliable genotypes, with only three individuals missing genotypes, and only at single locus. Genotyping also revealed two samples were likely recaptures of individuals that had lost their PIT-tags from the previous season, as their genotypes were identical and evidence of the initial ear biopsy injury remained. Therefore, we used 179 individuals in this study: 69 from four ARN sites and 110 from four UNL sites (Table 4.2).

4.3.1 Microsatellite characteristics

Eleven of the 17 microsatellite loci showed reliable PCR-amplification, were polymorphic, and produced genotypes usually consistent with Hardy-Weinberg and linkage equilibrium (Table 4.1). While, three loci showed deviation from HWE at one site (UNL-H1), this is probably evidence for the Wahlund effect (i.e. the 'site' actually comprised multiple populations), and hence these loci were retained for analyses. Of the six excluded loci, five either did not PCR amplify reliably or produced problematic co-amplified products, and one locus showed significant heterozygote deficit (RfgC3). All eleven successful microsatellite loci were used in testing genetic diversity and population structure.

4.3.2 Influence of treatment on genetic diversity

There were no significant differences between the Huon and Styx for F_{IS} ($F_{1,6}$ = 1.88, P = 0.220), allelic richness ($F_{1,6}$ = 2.08, P = 0.199), relatedness ($F_{1,6}$ = 0.11, P = 0.748) and genotypic diversity ($F_{1,6}$ = 1.12, P = 0.330). There were no significant differences between UNL and ARN for relatedness ($F_{1,6}$ = 1.42, P = 0.278), allelic richness ($F_{1,6}$ = 0.07, P = 0.801) and genotypic diversity ($F_{1,6}$ = 0.52, P = 0.496). F_{IS} was significantly higher in UNL (0.038 ± 0.011 S.E.) than in ARN (-0.003 ± 0.011 S.E.; $F_{1,6}$ = 6.84, P = 0.040), which is most likely driven by the Wahlund effect seen in UNL-H1 (Table 4.2).

4.3.3 Genetic structure

Exact tests and F_{ST} calculations revealed no temporal population differentiation within sites ($F_{ST} < 0.007$, $P > 0.16$ for all). Therefore, any differentiation within sites is attributable to spatial effects. Spatial autocorrelation analyses from the two UNL sites with largest sample sizes showed that genotypes were more similar over shorter distances and indicated neighbourhood sizes of approximately 40–60 m (Fig. 4.3a,b). At a finer scale, spatial autocorrelation using increasing first-distance-bin r-values (Peakall *et al.* 2003) showed relatedness was significantly higher than expected up to 42 m in UNL-S2 ($r = 0.091$, $P = 0.001$) and up to 55 m in UNL-H1 ($r = 0.034$, $P = 0.001$; Fig. 4.4a,b). In UNL-H1, the analysis was repeated separately for females (n = 36) and males (n = 26); females showed a neighbourhood size of 56 m ($r = 0.072$, $P = 0.001$; Fig. 4.3c, Fig. 4.4c), whereas males showed no significant change in relatedness over distances up to 600 m (the maximum range of comparisons for males; Fig. 4.3d).

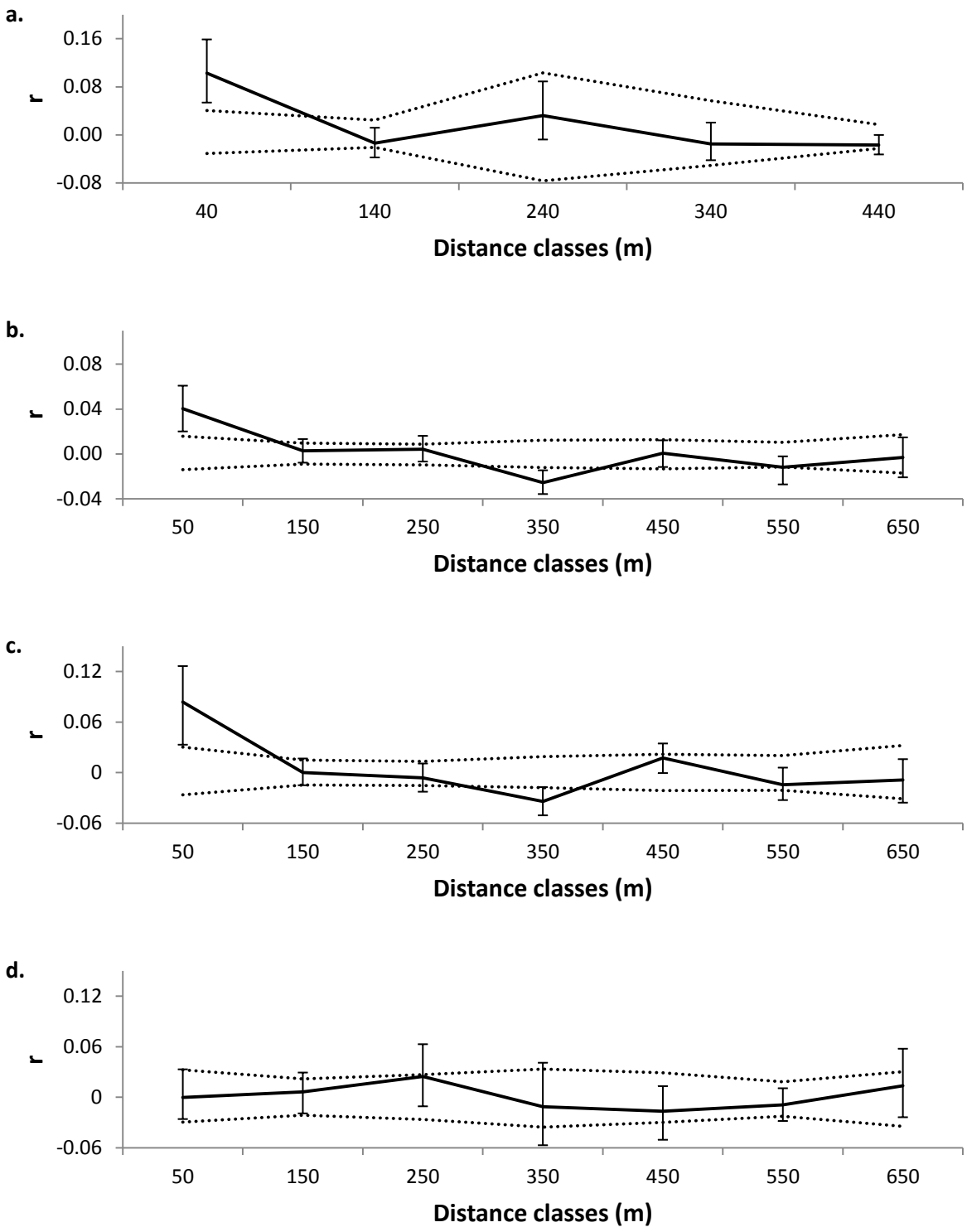

Fig. 4.3 Spatial autocorrelograms for swamp rats in unlogged native forest sites at the site scale in (a) UNL-S2, (b) UNL-H1 for all individuals, (c) UNL-H1 females and (d) UNL-H1 males. When r is above or below the confidence intervals, relatedness is significantly higher or lower than one might expect by chance. Solid lines, autocorrelation coefficient (r, ± SE); broken lines, upper and lower confidence intervals.

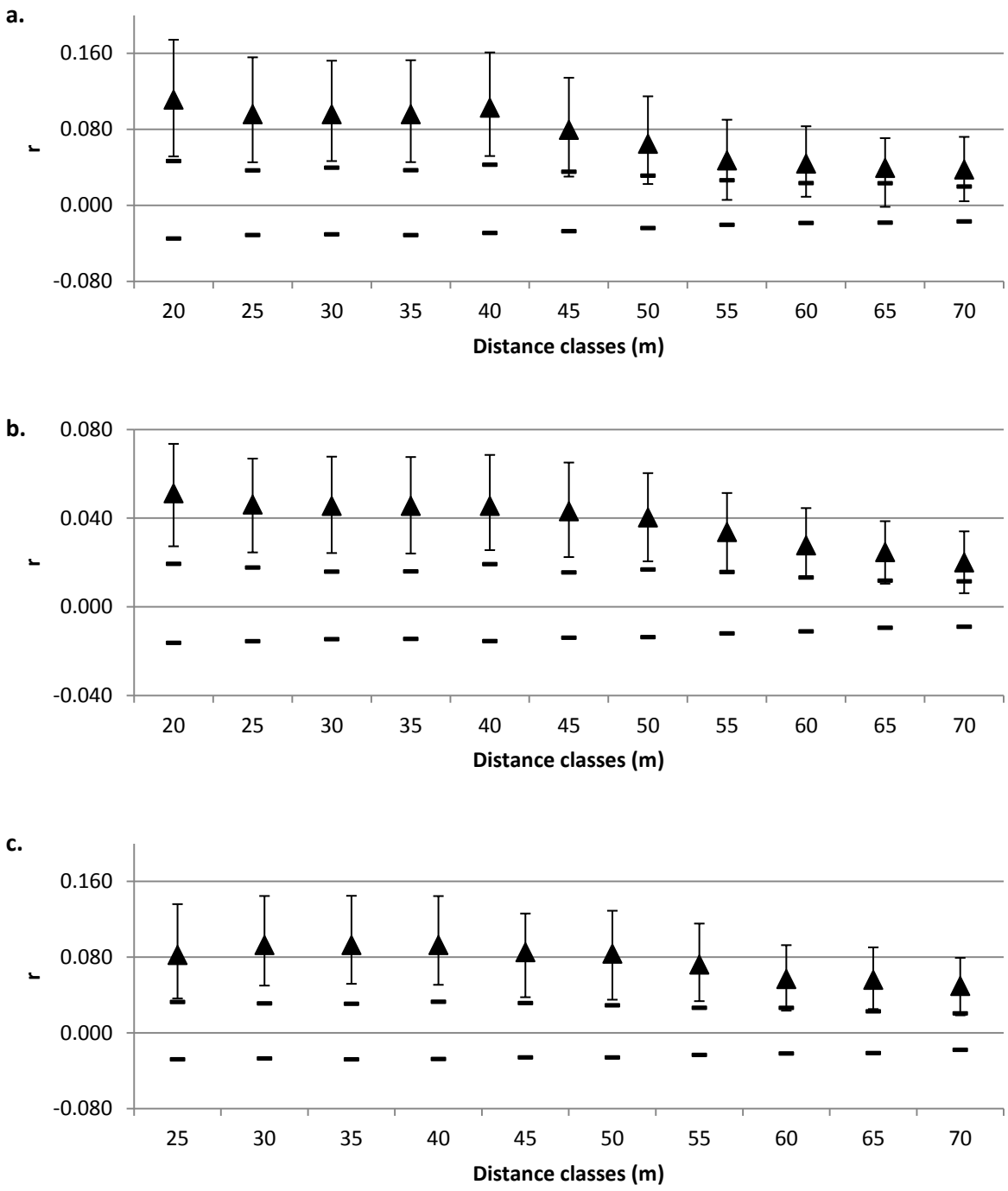

Fig. 4.4 Autocorrelation for increasing first distance classes in unlogged sites, indicating higher relatedness up to (a) 45 m in UNL-S2, (b) 55 m in UNL-H1 for all individuals, and (c) 56 m for UNL-H1 females only. ▲, autocorrelation coefficient (r, ± SE); —, upper and lower confidence intervals.

Overall, individuals were more closely related within ARN-Islands (R = 0.045) than in ARN-Edges (R = 0.038; P < 0.001). When we looked at each site individually, this was confirmed in two sites, ARN-H1 ($P < 0.001$) and ARN-H2 ($P < 0.001$), but not for ARN-S1 ($P > 0.05$) or ARN-S1 ($P > 0.05$). These latter two sites had very low sample sizes for ARN-Islands (n = 3 and n = 2, respectively). Overall, individuals showed significantly higher relatedness with other individuals on their side of the road in UNL sites (R = -0.007) compared to those on the other side (R = -0.035; $P < 0.001$). This was also confirmed during analysis of individual sites ($P < 0.001$ for all sites).

At larger spatial scales, exact tests using allele frequencies showed significant differentiation for all pairwise population comparisons ($\chi^2 > 50$, $P < 0.001$ for all comparisons). Population structuring among all sites was quantified as $F_{ST} = 0.048$ ($P < 0.001$) and $G''_{ST} = 0.145$ (P < 0.001), and were similar for the Huon ($F_{ST} = 0.051$, $P < 0.001$; $G''_{ST} = 0.176$, $P < 0.001$) and Styx ($F_{ST} = 0.031$, $P < 0.001$; $G''_{ST} = 0.108$, $P < 0.001$) regions. There was no evidence of isolation by distance with respect to sites across the entire study range ($P = 0.270$), nor within regions (Styx, $P = 0.136$; Huon, $P = 0.963$) or when separating the sexes (female, $P = 0.306$; male, $P = 0.121$). STRUCTURE analysis did not reveal any cryptic population structuring among individuals within these sites, but also failed to resolve the majority of sites. The optimal number of clusters (K) was two using the delta K method, with UNL-H1 distinguished from the other sites (Fig. 4.5a). When we separated UNL-H1 from the rest of the data and re-ran STRUCTURE analysis on the seven site cluster, the Evanno method returned an optimal K = 2. The two clusters were: (1) the two UNL sites and one ARN site in the Styx region (UNL-S1, UNL-S2, ARN-S1), and (2) the three sites remaining in the Huon region and one ARN Styx site (ARN-S2; Fig. 4.5b).

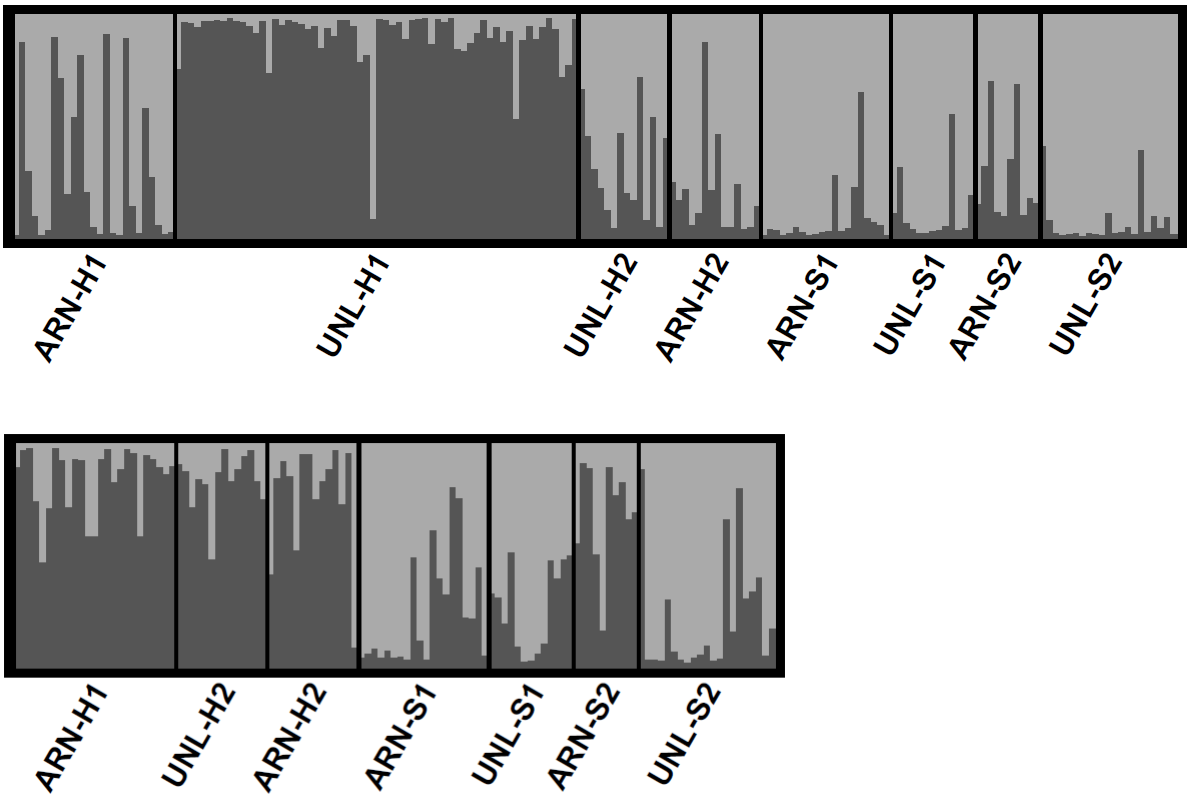

Fig. 4.5 Estimated population genetic structure from STRUCTURE analyses for (a) all individuals from eight sites, assuming clusters K = 2, and (b) individuals from the larger cluster in (a), assuming K = 2. No prior population data was included in the analyses. Each individual is represented by a thin vertical line divided into K colours that represent an individual's membership in K clusters. Thick black lines separate individuals collected from different sites. The order of sites in this graph are based on geographic location and distance (see Fig. 1). From left to right on this graph, Huon sites are ordered from south-east to north-west and Styx sites are ordered from south-west to north-east.

4.4 Discussion

4.4.1 Local fragmentation due to forest harvesting and roads leads to increased relatedness

Comparisons within sites indicated that harvested areas, comprising either regenerating forest or unsealed roads, represented a significant barrier to swamp rat dispersal, as relatedness was significantly higher among individuals that were separated from other individuals by harvested areas or roads. In ARN, higher relatedness in ARN-Islands

compared to ARN-Edges indicated that even within a few generations (three to five in our study) there are genetic impacts of barriers to gene flow. The higher levels of relatedness in the ARN-Islands was likely to represent a higher proportion of close relatives remaining in the forested islands, rather than a product of individuals mating with close kin by choice, as other mammals have shown avoidance of reproduction between close kin in isolated patches (Banks *et al.* 2005). Swamp rats prefer habitats with dense vegetation cover (Fox & Monamy 2007; Stephens *et al.* 2012), and individuals may be unwilling to disperse through the harvested matrix. During our broader study we only witnessed one emigration event across a harvested matrix (between two islands), and the genetic data indicated that gene flow (movement and reproduction, as opposed to just movement) was low in ARN. Not all ARN islands were populated by swamp rats, and previous work has shown no relationship between retained island size and presence or abundance of small mammals (Lindenmayer *et al.* 2010; Stephens *et al.* 2012). This suggests that swamp rats were not recolonising islands despite the provision of suitable habitat within these islands (Stephens *et al.* 2012).

The results of this study are consistent with observations from a closely related species in the southeast of mainland Australia, *Rattus fuscipes*, when it was subjected to experimental population reduction within a fragmented landscape over 24 months (Peakall & Lindenmayer 2006). Most *R. fuscipes* populations within fragments showed some population recovery, but new individuals within remnant habitats were predominantly provided by offspring from residual individuals rather than immigrants, highlighting the negative impact dispersal barriers can present. The importance of continuous habitat connection is supported by other studies of *R. fuscipes*, where movement between habitat patches connected by habitat corridors was observed (Macqueen *et al.* 2008; Holland & Bennett 2011).

While negative impacts of ARN on the population genetics of swamp rats were apparent, it should be considered that ARN practices maintained higher abundance of swamp rats than the previously dominant harvesting practice of clearfelling (Stephens *et al.* 2012). These results have been documented for other forest specialists (Baker *et al.* 2009; Lencinas *et al.* 2009; Pinzon *et al.* 2012), including small mammals in other systems (Klenner & Sullivan 2009; Lindenmayer *et al.* 2010). Sullivan and Sullivan

(2001), for example, examined the effects of different retention systems on small mammals 1–4 years post-harvest. They found that a late successional forest vole species showed higher abundance and recruitment in harvested sites with retained forest patches compared to clearfelled sites, although still at lower numbers than in unlogged forest. Sullivan *et al.* (2008) continued monitoring, and, from 5–8 years post-harvest, abundances declined in partial harvest sites compared to unlogged forest, presumably due to a continued reduction in optimal habitat conditions. However, the generally rapid regeneration of the ARN harvested matrix in wet *Eucalyptus* forests may provide sufficient cover for swamp rats to disperse through or recolonise within a relatively short time frame (Fox 1982; Catling 1986). This suggests that the duration of any negative population genetic effects of ARN forestry will be shorter than in land use practices that remove suitable habitat across larger temporal (e.g. agriculture, roads) or spatial (e.g. clearfelling) scales.

The inability of swamp rats to disperse across cleared forest was perhaps best illustrated by the genetic impact of roads through UNL sites. Individuals on the same side of the road (< 10 m wide) showed significantly higher relatedness than individuals on opposite sides. In addition, the deviations from Hardy-Weinberg equilibrium observed in UNL-H1 may have also reflected a road-mediated Wahlund effect. Large, frequently used roads have been shown to represent barriers to movement for various taxa (Rondinini & Doncaster 2002; Koivula & Vermeulen 2005; Schmuki *et al.* 2006), although narrow and unpaved roads can also impede movement (Oxley *et al.* 1974; Swihart & Slade 1984; Merriam *et al.* 1989). Small mammals have also shown an aversion to the road surface itself, regardless of traffic noise or density (Rico *et al.* 2007; Ford & Fahrig 2008; McGregor *et al.* 2008). At two of our UNL sites, the roads were effectively unused and ended within a few hundred metres of the nearest trap station, such that movement around the end of the road would have only been in the order of 500 m. In addition to the genetic results for swamp rats, there was limited evidence for road crossing from CMR (H.C. Stephens, unpublished data).

Roads represent a significant dispersal barrier, and may be a longer-term and more serious issue for swamp rat gene flow. While the impacts of roads on behaviour, resource accessibility and demography have been documented previously for various taxa (see reviews by Trombulak & Frissell 2000; Balkenhol & Waits 2009), they have

been given lower priority in production forests in favour of studies on the impacts of the harvested areas (Lindenmayer & Franklin 1997; Niemelä 1999; Schmiegelow & Monkkonen 2002; Fisher & Wilkinson 2005). Interestingly, the impact of roads in this study may also, in part, explain the reluctance of swamp rats to move out of ARN islands. The area immediately surrounding islands (and edges of the harvested area) are firebreaks, which are wide tracks (10 m), compacted and cleared to prevent burning of unlogged forest, and to allow vehicle access to the harvested matrix (Scott *et al.* 2012). These firebreaks are analogous to unpaved roads and, due to the soil compaction from heavy vehicle use during harvesting, restrict vegetation regeneration (Hindrum *et al.* 2012). Hence, swamp rats may have been reluctant to disperse across these firebreaks between the islands and the harvested areas, even if the latter is providing sufficient cover (Fox 1982).

In our study, the results suggested that roads may have a longer-term impact than aggregated retention harvesting. The latter practice may even be viewed as a transitional state that retains some structural and vegetation cover. The lack of any structural (e.g. logs), ground or overstorey cover on roads may be a limiting factor for the dispersal of cover-dependent ground mammals, which are at higher risk of predation in open areas and therefore less likely to leave dense cover (Kotler *et al.* 1991) Even on narrow, unpaved and infrequently used roads, impeded gene flow was evident for swamp rats. Despite a relatively small area of habitat loss the effect of fragmentation caused by roads is high and forest managers may need to consider rehabilitation of unused roads as a mitigation measure.

4.4.2 Swamp rats have small neighbourhood size and show significant genetic differentiation at larger spatial scales

The neighbourhood size of swamp rats in unlogged wet forests was estimated at 42-55 m. Using CMR data, Norton (1987) estimated slightly larger home range sizes (55-78 m) for swamp rats living in different habitat types, while Barnett (1978) observed smaller average range of 42 m in plantation forests. These estimates provide us with information on home range size, effectively an area an animal might move within, but they do not reveal successful reproduction and thus a transfer of genes. Our neighbourhood size estimates were based on the multilocus genotypes of surviving individuals across a range of geographic distances in the landscape. These small

neighbourhood sizes may provide an insight into the lack of dispersal seen among islands and edges in ARN sites. The distances between ARN islands and forested edges is typically 80–150 m, to allow safe harvesting practices while still providing influence (e.g. seed dispersal, leaf litter) from the surrounding forest (Scott *et al.* 2011). However, these are farther than the usual distances swamp rats will travel in UNL sites and may explain their reluctance to move between the patches, particularly with the intervening 'hostile' matrix. A small neighbourhood size may also help to explain the lack of differences at the site scale between ARN and UNL for the genetic diversity variables (F_{IS}, AR, R, GD), since these values were calculated from all individuals in a site, ranging from 12 to 49 ha. Alternatively, the lack of difference may have reflected the short time across which populations have been impacted at ARN sites (2-5 generations), and a longer time may be required for impacts on overall genetic variation to become manifested

When we examined males and females separately (in UNL-H1), females showed a neighbourhood size of 55 m while males showed no change in relatedness over the existing range of distances, implying that dispersal is male-biased (Banks & Peakall 2012). This is reflected in our anecdotal evidence that most crossings across cleared land (harvested forest or roads) were by males (six of seven crossings), despite a female-biased sex ratio indicating more females were in residence (97 males: 152 females; Stephens *et al.* 2012). Male-biased dispersal is common in many other mammal species and is often attributed to inbreeding avoidance or preventing resource competition among relatives (Cockburn *et al.* 1985; Paplinska *et al.* 2009; Holland & Bennett 2011). Male-biased dispersal in fragmented landscapes may require individuals to move further distances than they would need to in continuous habitat in order to find suitable mates and habitat (Sumner 2005).

While the spatial autocorrelation analyses did not reveal a limit to neighbourhood size for males, dispersal appears limited at some point, as there was significant genetic differentiation between all sites, some separated by as little as 2.3 km, and there was no evidence for increasing genetic isolation of sites with geographic distance among sites, either across the entire study range, within regions or within sexes. The comparatively lower level of genetic structuring suggested by the STRUCTURE analysis appears consistent with previous simulation studies examining the power of

this approach (Waples & Gaggiotti 2006), as the distinct populations identified seem to reflect their sample sizes. Similarly, Peakall & Lindenmayer (2006) found significant differentiation between *R. fuscipes* populations in forest fragments despite often small geographic distances (< 1 km) separating them. Although our sites were not necessarily located in distinct fragments, the study area is a production forest and as such our sites are part of a landscape mosaic of unlogged forest, regenerating native forest, plantations of native and non-native species, plus small and large, used and disused logging roads. Therefore, it is unsurprising that, combined with our knowledge of small neighbourhood sizes and habitat preference, swamp rat populations were genetically distinct over a relatively small geographic distance.

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CHAPTER 5: Behavioural responses of a native rodent to variation in structural and visual cover in a captive trial

Stephens H.C., Potts B.M., Baker S.C. & O'Reilly-Wapstra, J.M. (In prep) Behavioural responses of a native rodent to variation in structural and visual cover in a captive trial

Swamp rats used in the captive behavioural trial. From top left: a female swamp rat on top of her nest box, another female inside her nest box, a swamp rat using a running wheel, two tubs showing individual housing.

Abstract

Small mammals often use dense habitat cover to minimise predation risk. Swamp rats are a common ground-dwelling mammal in south-eastern Australia, and are known to prefer dense habitat cover. However, the relative importance of different types of cover has not been investigated. This may be particularly important in fragmented landscapes where open areas appear to restrict dispersal. We investigated swamp rat preferences for different ground-level (structure) and overhead (visual) cover densities in both dark and light conditions in a series of behavioural captive trials. There were few cover density effects (both ground-level and overhead) during any of the captive trials. This may in part be explained by animal choice of the experimental arena area being influenced by perceived risk associated with close proximity to a door. However, rats showed a significantly higher preference for the edges (walls) of the experimental arena than the centre area. The solid vertical cover provided by the arena walls may have been analogous to structural features such as coarse woody debris and standing trees in undisturbed forests.

5.1 Introduction

Small mammals inhabiting diverse vegetation types often show a preference for habitat with dense cover (McCay 2000; Fox & Monamy 2007; Tabeni *et al.* 2012). Dense cover provides protection for animals to move between foraging and nesting sites, while minimising detection and capture success by predators (Kotler *et al.* 1991). Overhead cover such as plant foliage conceals animals from aerial predators (Longland & Price 1991), while structural cover such as logs and stems may reduce detection of small mammals by both aerial and ground-based predators and aid in escape by increasing capture difficulty (Jensen *et al.* 2003). Therefore, dense cover is an important habitat feature for many small mammals, particularly when perceived or actual predation risk is high (Kotler *et al.* 1991; Dickman 1992; Lagos *et al.* 1995; Asher *et al.* 2004; Strauss *et al.* 2008).

Species that require habitats with dense cover (e.g. forest-dwelling species) may be disadvantaged when their habitat is altered, particularly when the changes are rapid (Smith & Litvaitis 2000). Anthropogenic practices such as forest harvesting result in an immediate reduction in cover through the loss of canopy as well as understorey vegetation cover and structural complexity such as stems, and in some systems, logs. While the resulting open spaces and edge effects can increase susceptibility of cover-dependent prey species to predation, dispersal across open areas is often necessary to ensure gene flow and population persistence, and is particularly important where patches of preferred habitats are isolated within a 'hostile' matrix (Peakall & Lindenmayer 2006; Quemere *et al.* 2010; Lancaster *et al.* 2011). However, if predation risk is increased within the disturbed area, then it follows that a cover threshold may be required to allow re-colonisation (Fox *et al.* 2003).

The swamp rat (*Rattus lutreolus*, Gray 1841) is a small (~110 g) ground-dwelling, cover-dependent native rodent common to many vegetation types throughout south-eastern Australia, including a subspecies, *R.l. velutinus* (Thomas 1882), that has a widespread distribution throughout Tasmania (Breed & Ford 2007). Numerous studies have shown that swamp rats are dependent on dense vegetation cover, regardless of the habitat type (Norton 1987; Moro 1991; Kearney *et al.* 2007). In coastal heath, Fox *et al.* (2003) found that experimentally removing 60 - 70 % of vegetation cover resulted in a

significant decrease in swamp rat abundance, most likely due to behavioural avoidance of open areas. In Tasmanian wet *Eucalyptus* forests, swamp rats are common, but preferentially utilise more densely vegetated habitat (Monamy 1995). In a study of short-term impacts of different forestry practices on native rodent abundance, Stephens *et al*. (2012, Chapter 2) found that swamp rats were less abundant with increasing disturbance. Partially harvested (aggregated retention) sites with retained patches of unlogged forest in the harvested matrix had higher abundances of swamp rats in comparison to fully harvested (clearfelled) sites, but lower than unlogged native forest sites. While swamp rats persisted in aggregated retention sites, they were reluctant to utilise the harvested matrix, with few individuals captured there (Stephens *et al.* 2012, Chapter 2), and little evidence of dispersal among habitat islands and the forested edges (Stephens *et al.* 2013, Chapter 4). The few swamp rats found in the harvested matrix were in areas of dense understorey and ground vegetation cover (Stephens *et al.* 2012, Chapter 2). Further evidence for the avoidance of open areas is the reluctance of swamp rats to traverse unpaved, narrow (< 10 m) and seldom used roads where canopy gaps are present and ground-level structural cover is absent (Stephens *et al.* 2013, Chapter 4).

The relationship between dense lower strata vegetation cover and swamp rat presence has been shown in different habitat types, particularly after vegetation-removing disturbance (Fox *et al.* 2003; Stephens *et al.* 2012, Chapter 2). Fox & Monamy (2007) hypothesised that tactile ground-level cover may be important for swamp rats, although the role of different cover characteristics have largely been unexplored (but see Braithwaite *et al.* 1978), and their function in re-colonisation of disturbed areas are unclear. We conducted captive preference trials with wild-caught swamp rats to investigate their use of two different types of cover: (1) ground-level tactile (structural) cover, and (2) overhead foliar (visual) cover. While the importance of ground-level structural cover for swamp rats has been hypothesised (Fox & Monamy 2007), it has received little attention in the literature. A structural cover trial aimed to provide both a tactile and visual presence at the ground level, thus emulating stems, roots and fine woody debris found in wet *Eucalyptus* forests. From field habitat assessments, low strata vegetation in disturbed habitats has been shown to correlate with swamp rat utilisation and recolonisation (Monamy & Fox 2000; Stephens *et al.* 2012, Chapter 2), although use of visual cover alone has not been investigated. Therefore, a visual cover

trial emulated the overhead, visual protection that plant foliage provides in forests. Overhead cover can provide concealment from predators, but this can also work in the reverse, with prey species unable to detect predators (Ebensperger & Hurtado 2005).

Swamp rats are primarily nocturnal or crepuscular, but it is not uncommon for them to move above ground during the day (Monamy 1995). Therefore, a secondary objective of this study was to investigate whether the use of cover by swamp rats differed between dark and light conditions. Consequently, both the structural and visual cover trials were conducted in simulated (a) dark and (b) light conditions. In the structural cover trial, we predicted that swamp rats would prefer medium or high density structural cover. From our field studies and previous work (Norton 1987; Fox *et al.* 2003), we hypothesised that, for visual cover, swamp rats would prefer high to medium cover over low to no cover. As swamp rats, and many other small mammal species, are typically more active in darker conditions when predation risk is lower (Kotler *et al.* 1991; Orrock *et al.* 2004; Bengsen *et al.* 2010; Hinkelman *et al.* 2012), we predicted that swamp rats would spend more time moving in dark compared to light conditions.

5.2 Methods

5.2.1 Trapping and husbandry

Swamp rats were trapped in wet *Eucalyptus* forest in the Arve Loop Forest Reserve in the Huon Valley, southern Tasmania (43º 8'S, 146º45'E). Up to thirteen plots of six Elliott traps (33 × 10 × 9 cm; Elliott Scientific Company, Upwey, Victoria) were set in an area of approximately 30 ha. Traps were checked and re-set each morning. Bait consisted of a peanut butter, oats and vanilla essence ball and a piece of apple. To provide protection from the wind and rain, traps were placed under sheltered areas (e.g. logs, shrubs) and partly covered with plastic bags. Non-absorbent nesting material (coconut fibre) was placed in all traps. Upon capture, swamp rats were given an additional piece of apple and transported to the small mammal facilities in the School of Zoology, University of Tasmania, Hobart. In total, 49 swamp rats were collected and used in the study: 30 females and 19 males.

Upon arrival in captivity, swamp rats were weighed to the nearest gram and marked for identification using an individual ear-clipping pattern using a 2 mm ear biopsy (tissue was collected for a separate study, Stephens *et al.* 2013, Chapter 4). Swamp rats were housed in individual plastic tubs (30 × 90 × 30 cm) with a wire mesh lid and paper pellet substrate. Five rooms each held ten swamp rats. Each tub contained a wooden nesting box (16 × 15 × 22 cm), shredded paper for nest construction, and a running wheel for exercise and enrichment. Water and dried food were available *ad libitum*. Dried food consisted of a mix of seeds, nuts, pulses, dried fruit and dry cat food. Fresh fruit and vegetables were supplied every two days. Light was kept at a constant 12:12 hours light/dark photoperiod, and temperature was maintained at a relatively constant 16ºC (± 4ºC). To minimise disturbance to the rats while in captivity, human interaction with rats was restricted to feeding every two days and cleaning of cages once every four weeks. Each rat was weighed during cleaning and at the start of each trial as a check of general health.

5.2.2 Behavioural trials

5.2.2.1 Cover density treatments

To emulate structural cover, small wooden rods (dowels; 1.2 cm diameter, 10 cm length) were secured in a flat wooden board (60 × 60 × 1 cm) at three densities: high, medium and low. The fourth treatment (no cover) was a board with no rods. The distance between the high density rods was 4 cm, which is the approximate width of runways used in some natural habitats (Green 1967), and the width at which an average-sized swamp rat would be able to move between the rods comfortably, but with a constant contact with the rods. The medium density rods were spaced at 8.5 cm apart, to allow easy passage between the rods, but at a distance where the body would not necessarily come into contact with the rods, but whiskers would have a constant tactile sense of the rods. The low density rods were spaced at 12 cm apart to allow easy access through the rods without necessarily touching them.

In the visual cover trial, overhead patches of cover were used to emulate different vegetation cover densities at the height of one metre. Solid dark cloth patches were used to provide cover over the experimental arena at different densities: high (60 %), medium (40 %), low (20 %), and no (0 %) cover.

5.2.2.2 Running the trials

Nine individuals (six females and three males) were used in a preliminary study to determine the optimal time for running the trials, and to test the practicality of the treatments and monitoring systems. After the preliminary trials, the nine individuals were released at their site of capture (± 3 m). The remaining 40 swamp rats were used once in each of the four trials: structural cover in dark conditions, structural cover in light conditions, visual cover in dark conditions, and visual cover in light conditions. Therefore, each of the 40 rats was run four times. On completion of the trials, these 40 rats were also returned to the site of their capture.

Logistical constraints ruled out the possibility of running a complete factorial design, thus two discrete experiments were designed to test two different types of cover: structural and visual in both dark (lower risk, 50W red light) and light (higher risk, 100W white light) conditions. In both structural and visual experiments, light and dark trials were run simultaneously over two 72-hour periods to reduce time in captivity. The structural cover trials were run from 14 to 16 and 19 to 21 November 2010 and the visual cover trials from 24 to 26 November and 30 November to 02 December 2010. Individuals were randomly assigned to two groups of equal numbers, with Group 1 experiencing dark in the first period and light in the second, and vice versa for Group 2. For example, a rat in Group 1 would be run during the night (dark) in the first 72-hour period, and in the second 72-hour period (three to five days later) would be run during the daytime (light). The groupings (between experiments) and order (within trials) were randomised each time, but were adjusted to allow at least three days (but typically five) between trials.

Trials were conducted in a 120 × 120 × 60 cm wooden arena, in a separate room to the housing rooms. The experimental room had no windows and was at a similar temperature to the housing rooms. A single light bulb was fixed above the centre of the experimental arena, with a red 50 W bulb used for dark trials and a white 100 W bulb used for light trials. In each trial, the arena was divided into four quarters representing four different densities of cover: high, medium, low, and no cover (see below). The arena and cover densities were designed in a way such that the individual was able to move freely between the treatments via the edges or the middle of the treatments (Fig. 5.1). The four treatments (across the structural and visual trials) were easily removed

and rotated between the four quarters within the arena. To account for the position of treatments within the arena, one of 24 possible configurations was randomly allocated to each swamp rat individual during each trial.

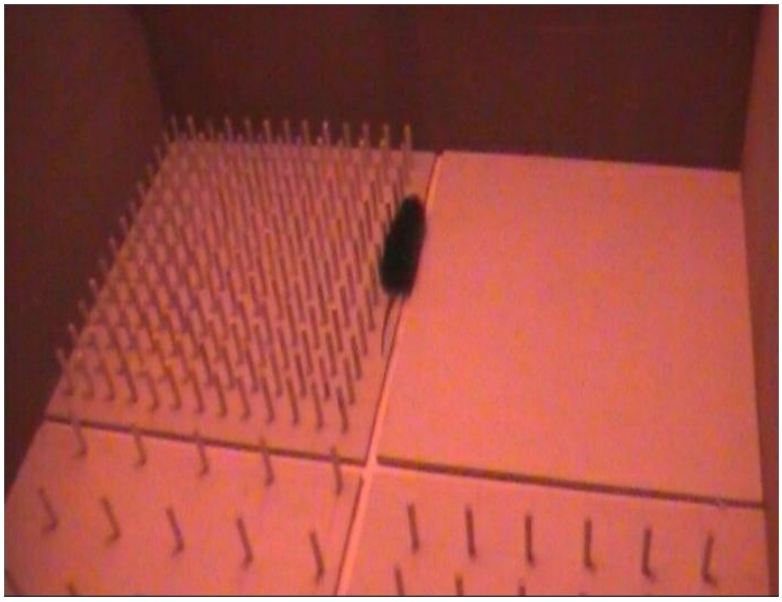

Fig. 5.1 Arena layout for the structural cover + dark conditions (red light) trial. The four density treatments are made from floating boards, allowing the configurations to be easily changed for each individual rat. The random allocation of different configurations to each individual was designed to minimise position effects. This photo shows an average-sized (120 g) female swamp rat in a configuration of (clockwise from top left): high density cover, no cover, medium density cover, and low density cover.

To maintain consistency, the same researcher (H. Stephens) undertook all rodent handling. During the trials, each individual was placed in the centre of the arena and the researcher left both the room and the adjoining room since the preliminary trial had determined that swamp rats were aware of human presence in the adjoining room. Therefore, two video cameras recorded the trials, which were scored at a later date.

5.2.3 Assessment of behavioural responses

In order to quantify preferred treatments (habitats), the time spent moving (recorded as either running, walking, reaching, grooming) or time spent stationary was recorded for each treatment for a total of 20 minutes. Furthermore, the time spent in each treatment was differentiated into edges (touching the walls of the arena) or centre (not touching

the walls) as the 'protection' of the walls were likely to influence the swamp rats' use of the arena (Fig. 5.2).

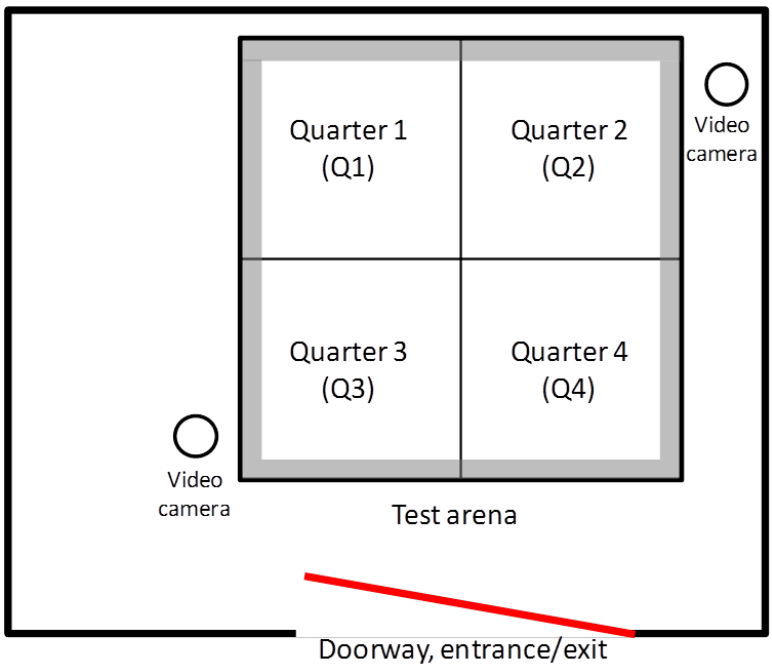

Fig. 5.2 A representation of the test arena and surrounding area. The test arena was separated into four quarters, each with different cover densities, dependent on the random configuration allocated to each individual for each trial. The light fixture was directly over the centre of the arena to prevent any shadows cast from the arena walls. Quarters 1 and 2 were considered 'far' from the door, while quarters 3 and 4 were 'near' the door. The grey shaded area along the inside edge of the arena wall indicates the 'edge' area against the wall, while the white area was scored as the centre.

5.2.4 Statistical analysis

A total of 102 videos were available for scoring and analysis (technical issues resulted in a loss of 58 of the 160 videos originally recorded). These videos were not evenly distributed between the trials and resulted in a reduction of multiple recordings for individuals (i.e. not all rats were scored for each of the four trials; 18 rats were scored in both structural cover trials while four were scored in both visual cover trials). Consequently, each trial was analysed separately: (1) structural cover in dark conditions, (2) structural cover in light conditions, (3) visual cover in dark conditions, and (4) visual cover in light conditions.

Preferences for each of the four treatments in each trial were determined by assessing the time spent moving and the time spent stationary in two time periods: the first 10 minutes and the last 10 minutes. The preferred treatment (greatest time spent in that treatment) for each of the four dependent variables for each individual was scored as '1' and all other treatments for that individual were scored as '0'. If a rat was either stationary or moving for the entire time of any time period (first 10 min, last 10 min), then the other activity would receive a 'null' preference. For example, if a rat did not move for the first 10 minutes, then all scores for moving would be '0' and no preference could be scored. Chi-squared tests using PROC FREQ in SAS (SAS Institute Inc. 2008) were used to test the preference of different cover densities. If a significant effect was detected ($P < 0.05$), pairwise chi-squared tests were undertaken, with expected relative frequencies of 0.50, and a Bonferroni correction applied to account for multiple comparisons, with an adjusted alpha of $P = 0.0083$.

The preferred position within the arena regardless of treatment was also of interest, due to the observation during data collation that the half of the arena furthest from the door (Q1 and Q2; Fig. 5.2) appeared to be used more frequently than the half nearest the door. Therefore, chi-squared tests were used to test the preference of position in the arena in relation to proximity to the door, the 'door' effect, with expected frequencies of 0.50 for each half of the arena. Another possible effect was that of the arena walls. During preliminary observation of the trial recordings, the potentially preferential use of the arena edges (i.e. moving along the wall, Fig. 5.2) in comparison to the centre area was noted. The edge area comprised approximately 20 % of the entire arena (and the centre area 80 %). However, the associated expected frequencies of preferences based on 0.20 for the edge and 0.80 for the centre were too few (< 5) for chi-squared testing. Therefore, more conservative chi-squared tests were run with expected frequencies derived from a proportion of 0.50 for each variable to test for the preferences for the 'wall' effect.

A MANOVA (PROC GLM) using time data (time spent in each treatment in seconds) was run in SAS to test whether there were differences in the rats' use of the arena in dark and light conditions. The model used either cover density (no cover, low, medium, high), the door effect (near, far) or wall effect (edge, centre) as the dependent variables and dark/light conditions as the independent variable for each of the two different

cover trials. The two different time periods (first 10 min, last 10 min) and activities (moving, stationary) were analysed separately. Where the MANOVA model resulted in significant effects using Wilk's Lamda, a *post hoc* univariate analysis was performed. The *post hoc* analysis tested the difference between light and dark conditions for each dependent variable (e.g. low density visual cover dark vs. low density visual cover light).

5.3 Results

5.3.1 Cover density effects

5.3.1.1 Structural cover

Only one significant ($\alpha = 0.05$) preference for cover density was revealed during the dark conditions trial, this was during the second half of the trial (last 10 min) for stationary rats ($\chi^2_3 = 8.15$, $P = 0.043$; Table 1a). Surprisingly, *post hoc* analysis showed a significant preference after Bonferroni adjustment ($\alpha = 0.0083$) for the no cover '0' treatment when compared to the high density cover treatment ($\chi^2_1 = 8.33$, $P = 0.004$; Fig. 3a). In light conditions, there was no evidence for structural cover density preferences in any activity or time period ($\chi^2_3 < 4.3$, $P > 0.05$; Table 1a).

Table 5.1 Treatment preferences of swamp rats in a captive study testing different habitat cover types in dark and light conditions. Four separate trials were conducted: (1) structural cover in dark conditions, (2) structural cover in light conditions, (3) visual cover in dark conditions, and (4) visual cover in light conditions. Three different treatments were tested in each trial: (a) cover density (at four levels), (b) the door effect (proximity to the door), and (c) the wall effect (position within the arena). Shown are the sample size (n), chi-squared value, degrees of freedom (df) and probability for tests of treatment differences based on preferences in each experimental trial (*P*-value).

	(1) Structural + Dark				(2) Structural + Light				(3) Visual + Dark[1]				(4) Visual + Light			
	n	Chi-Sq	df	*P*-value	n	Chi-Sq	df	*P*-value	n	Chi-Sq	df	*P*-value	n	Chi-Sq	df	*P*-value
a. Cover density: high, medium, low and no cover																
First 10 minutes																
Moving	25	7.16	3	0.067	27	3.67	3	0.300	19	9.42	3	**0.024**	21	7.38	3	0.061
Stationary	28	6.00	3	0.112	30	0.67	3	0.881	17	1.12	3	0.773	24	1.00	3	0.801
Last 10 minutes																
Moving	26	1.39	3	0.709	28	4.29	3	0.232	19	0.58	3	0.901	23	5.35	3	0.148
Stationary	26	8.15	3	**0.043**	30	3.60	3	0.308	18	4.67	3	0.198	23	6.04	3	0.110
b. The Door effect: far vs. near																
First 10 minutes																
Moving	25	0.04	1	0.842	27	8.33	1	**0.004**	19	0.05	1	0.819	21	0.05	1	0.827
Stationary	28	7.00	1	**0.008**	30	1.20	1	0.273	17	2.88	1	0.090	24	0.67	1	0.414
Last 10 minutes																
Moving	26	0.65	1	0.433	28	9.14	1	**0.003**	19	1.32	1	0.251	23	0.39	1	0.532
Stationary	26	0.15	1	0.695	30	2.13	1	0.144	18	2.00	1	0.157	23	0.04	1	0.835
c. The Wall effect: edge vs. middle																
First 10 minutes																
Moving	25	6.76	1	**0.009**	27	16.33	1	**<0.001**	19	8.90	1	**0.003**	21	8.05	1	**0.005**
Stationary	28	9.14	1	**0.003**	30	13.33	1	**<0.001**	17	13.24	1	**<0.001**	24	16.67	1	**<0.001**
Last 10 minutes																
Moving	26	2.46	1	0.117	28	9.14	1	**0.003**	19	2.58	1	0.108	23	15.70	1	**<0.001**
Stationary	26	3.86	1	**0.049**	30	22.53	1	**<0.001**	18	8.00	1	**0.005**	23	19.17	1	**<0.001**

[1]It should be noted that the visual cover trial in dark conditions had a maximum sample size of 20, with lower samples when differentiated into moving and stationary animals in each 10 min half, as some individuals scored null preferences (e.g. they didn't move, therefore there was no 'moving' preference score).

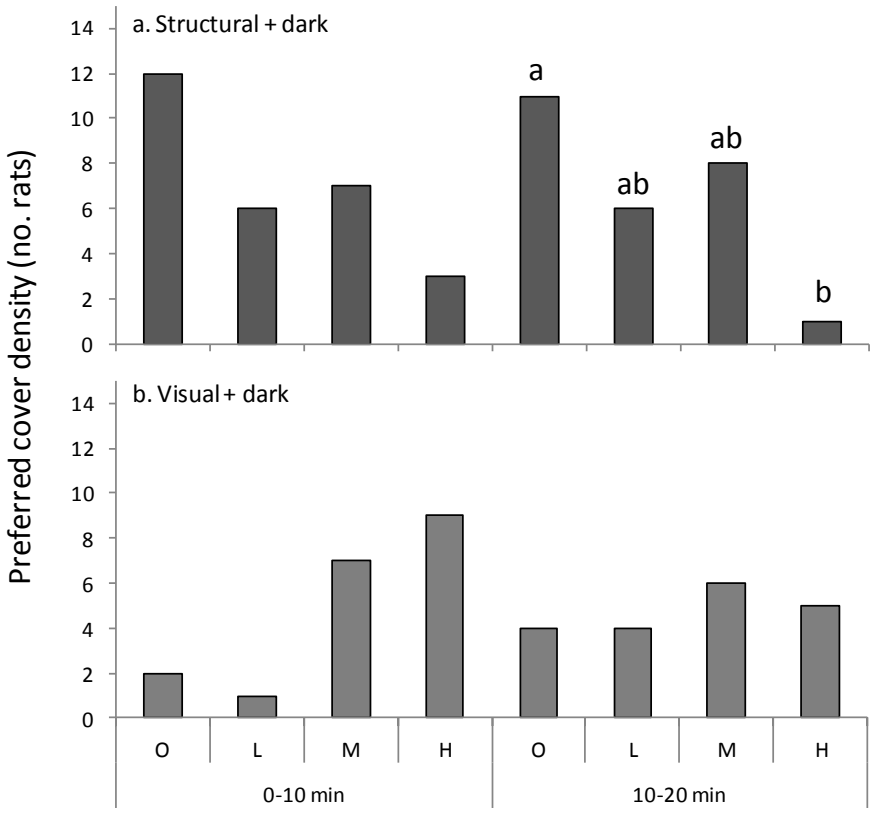

Fig. 5.3 The preferred cover density in the first 10 minutes and last 10 minutes for (a) stationary rats in the structural cover + dark conditions trial, and (b) moving rats in the visual cover + dark conditions trial. The letters (a, ab, b) directly above the columns denote significant differences between the cover density treatments of no cover (O), low cover (L), medium cover (M), and high cover (H).

5.3.1.2 Visual cover trials

In the dark conditions, there was a significant overall treatment effect for moving rats in the first 10 minutes ($\chi^2_3 = 9.42$, $P = 0.024$; Table 5.1a). While pairwise comparisons did not meet the Bonferroni adjusted significance level ($\alpha = 0.0083$), there was a trend for preferences for high density cover compared to low (90 %, $\chi^2_1 = 6.40$, $P = 0.011$; Fig. 5.3b) and no cover (82 %, $\chi^2_1 = 4.45$, $P = 0.035$). In light conditions, there was no evidence for visual cover density preferences in any activity or time period ($\chi^2_3 < 7.4$, $P > 0.05$).

5.3.2 The Door Effect

The door effect was evident in the first 10 minutes of the structural cover trial in dark conditions, with the far half of the arena away from the door preferred over the near half for stationary rats ($\chi^2_1 = 7.00$, $P = 0.008$; Table 5.1b*;* Fig. 5.4a), however this did not continue into the latter half of the trial ($\chi^2_1 = 0.15$, $P = 0.690$). Swamp rats in the structural cover trial with light conditions showed a preference for the far half of the arena when moving in the first 10 minutes ($\chi^2_1 = 8.33$, $P = 0.004$; Fig. 5.4b) and the last 10 minutes ($\chi^2_1 = 9.14$, $P = 0.003$). The visual cover trials detected no significant preferences for any time period or activity (*Table 1b*).

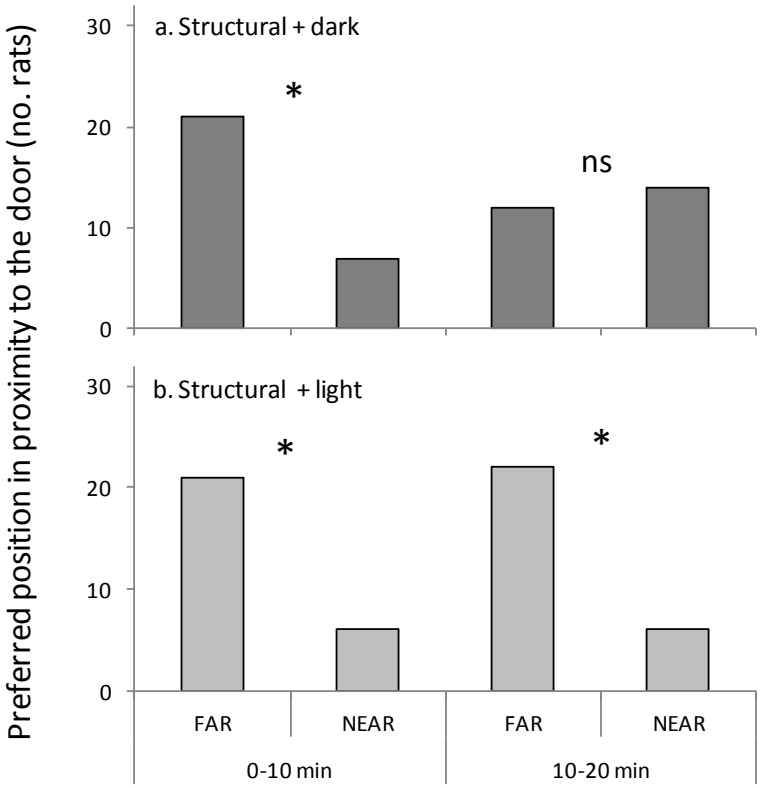

Fig. 5.4 The preferred position of swamp rats within the arena that was far or near to the door from which the researcher entered and exited. The two trials shown here are (a) structural cover + dark conditions for stationary rats, and (b) structural cover + light conditions for moving rats. * denotes a significant difference between preferences for far and near areas within either the first 10 minutes of the trial (0-10 min) or the last 10 minutes of the trial (10-20 min). 'ns', no significant difference between far and near areas.

5.3.3 The Wall Effect

Although the area covered by the edge area was less than 20 % of the total area, the preference for edges was significantly higher than for non-edge (centre) areas in most time and activity categories across all four trials (Fig. 5.5; Table 5.1c). While not all tests were significant (moving 10-20 min for dark conditions in the structural cover [$\chi^2_1 = 2.46$, $P = 0.117$] and visual cover [$\chi^2_1 = 2.58$, $P = 0.108$] trials), the trend for edge preferences was apparent in all categories (Fig. 5.5).

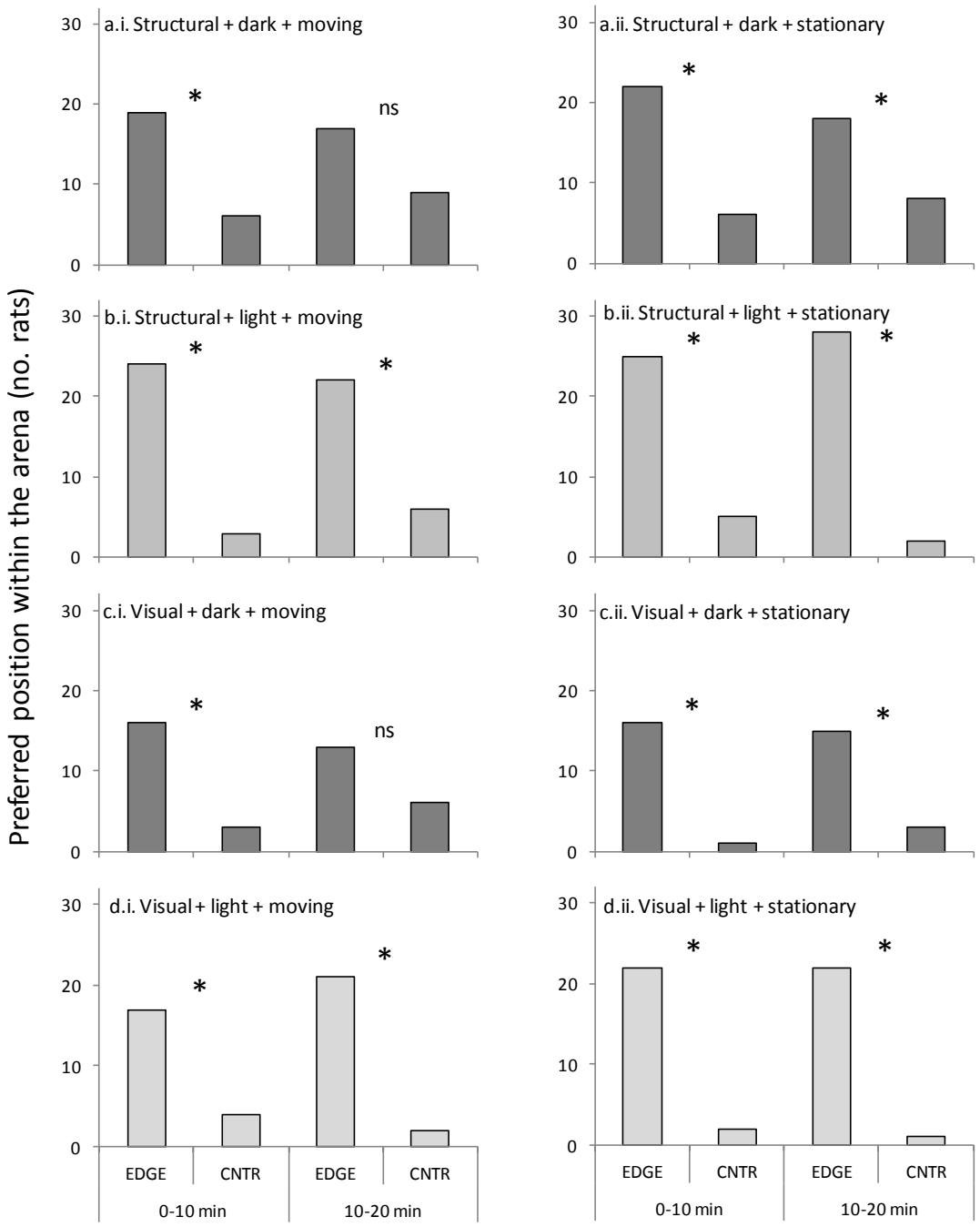

Fig. 5.5 Preferences of swamp rats within the arena for the edge areas (EDGE; i.e. close to the walls) or the centre area (CNTR) for (i) moving rats and (ii) stationary rats for the four different trials: (a) structural cover + dark conditions, (b) structural cover + light conditions, (c) visual cover + dark conditions, and (d) visual cover + light conditions. * denotes a significant difference between preferences for edge and centre areas within either the first 10 minutes of the trial (0-10 min) or the last 10 minutes of the trial (10-20 min). 'ns', no significant difference between edge and centre areas.

5.3.4 Preferences in dark and light conditions

5.3.4.1 Structural cover trials

For the structural trials, multivariate analyses only revealed significant differences between light and dark conditions for moving rats in all time periods in relation to proximity to the door (Table 5.2a). Univariate *post hoc* analysis revealed that rats spent more time moving in dark conditions in the near half of the arena compared to light conditions. This was evident for the first 10 minutes ($P = 0.015$; Fig. 5.6) and the last 10 minutes ($P = 0.028$). Although there were no other significant effects for structural cover (Table 5.2a), general trends suggested that rats moved more in dark conditions than in light conditions (results not shown).

Table 5.2 MANOVA tests of the difference between light and dark conditions in different cover trials. Results are shown for (a) the structural cover trials and (b) the visual cover trials using time spent (seconds) in the different treatments of cover density (high, medium, low or no), door effect (near or far), or wall effect (edge or centre) as the dependent variables. The table shows the *F*-value, degrees of freedom (d.f.) and *P*-value obtained using Wilk's Lamda for each model.

	Cover density			**Door effect**			**Wall effect**		
	F-value	d.f.	*P*-value	*F*-value	d.f.	*P*-value	*F*-value	d.f.	*P*-value
(a) Structural cover trials									
First 10 minutes									
Moving	1.12	4,53	0.355	4.97	2,55	**0.010**	1.92	2,55	0.156
Stationary	1.31	4,53	0.277	2.09	2,55	0.133	1.97	2,55	0.149
Last 10 minutes									
Moving	2.23	4,53	0.078	4.69	2,55	**0.013**	1.97	2,55	0.149
Stationary	1.37	4,53	0.257	0.72	2,55	0.491	0.93	2,55	0.399
(b) Visual cover trials									
First 10 minutes									
Moving	5.15	4,39	**0.002**	3.50	2,41	**0.040**	3.29	2,41	**0.047**
Stationary	1.40	4,39	0.253	3.27	2,41	***0.048***	3.58	2,41	***0.037***
Last 10 minutes									
Moving	2.48	4,39	0.060	0.59	2,41	0.560	4.89	2,41	**0.013**
Stationary	1.84	4,39	0.140	0.59	2,41	0.561	0.91	2,41	0.412

P-values in bold indicate significant differences between light and dark conditions.

P-values in bold italics indicate where univariate *post hoc* analysis revealed no significant differences between light and dark conditions for a specific dependent variable.

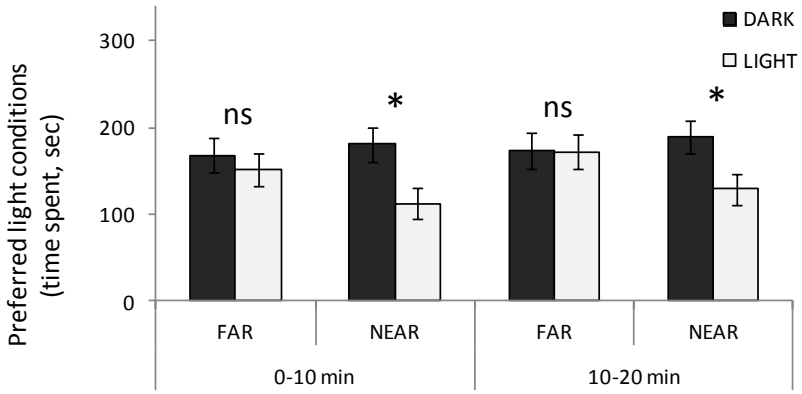

Fig. 5.6 The preferred light conditions of moving swamp rats in the structural cover trials in proximity to the door (far half of the arena, near half of the arena) from which the researcher entered and exited. * denotes a significant difference between dark and light conditions within each half of the arena (far, near) and each half of the trial (first 10 min, last 10 min). 'ns', no significant difference between dark and light conditions.

5.3.4.2 Visual cover trials

Multivariate analyses for the visual cover trials also showed that rats moved more in dark conditions in comparison to light conditions, although not in all treatments or time periods (Table 2.1b). Rats moved more in dark conditions in medium (M) and high (H) cover densities for the first 10 minutes of the trial (M; $P = 0.003$; H, 2.0 ×; $P = 0.006$; Fig. 5.7a). They also spent more time moving in dark conditions in the first 10 minutes in both the far ($P = 0.035$; Fig. 5.7b) and near positions of the arena ($P = 0.011$). In proximity to the wall, rats spent more time moving in dark conditions when in the middle of the arena in the first 10 minutes ($P = 0.012$; Fig. 5.7c) and the last 10 minutes ($P = 0.029$). Rats also spent more time moving in dark conditions in the edge area of the arena, but only in the first 10 minutes ($P = 0.034$). Analyses also showed a significant effect of different light conditions for stationary rats in the first 10 minutes for the wall ($F_{2,41} = 3.58$, $P = 0.037$; Table 5.2b) and door ($F_{2,41} = 3.27$, $P = 0.048$) positions. However, univariate *post hoc* analyses revealed no significant differences between dark and light conditions for the edge, middle, far or near positions.

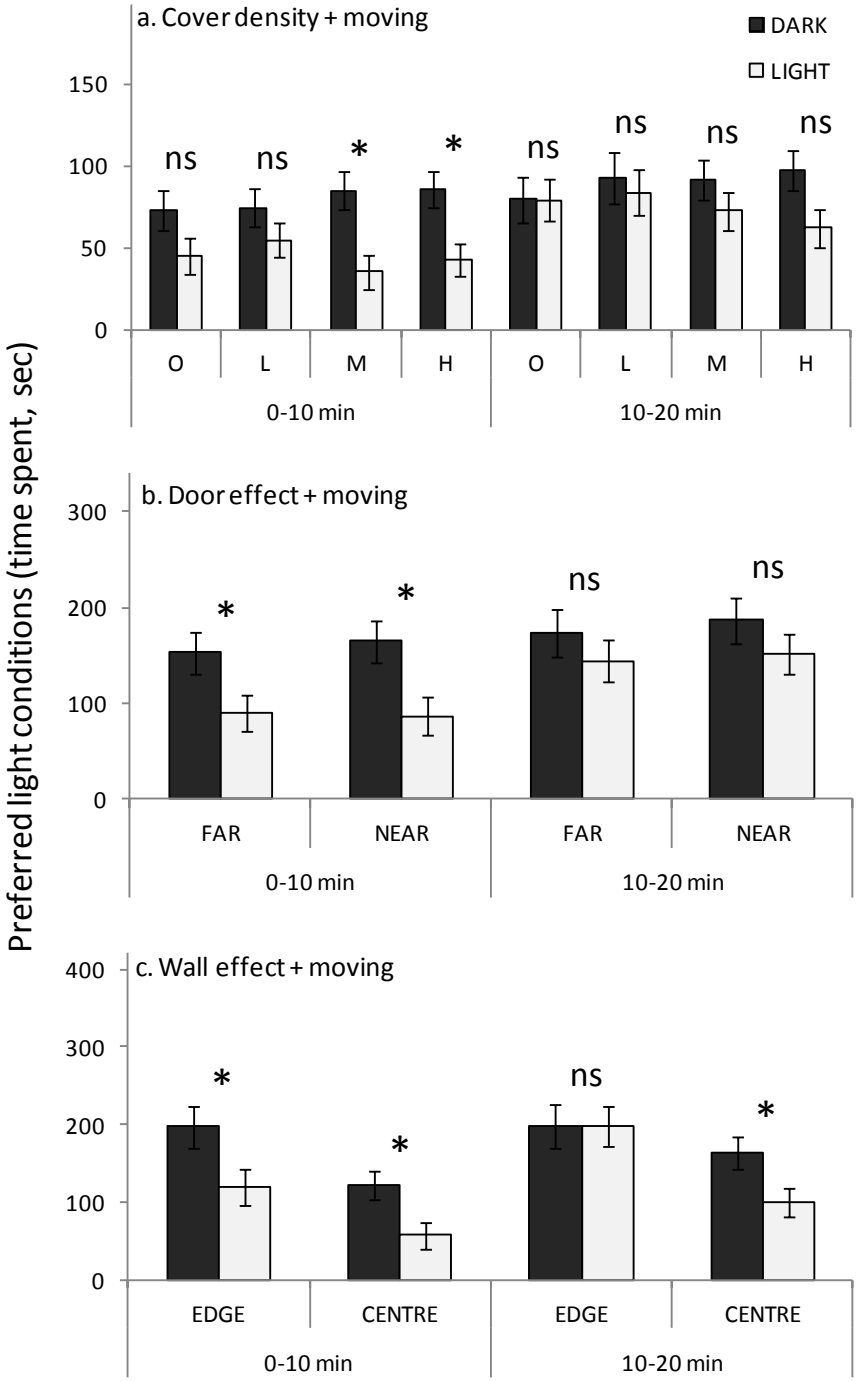

Fig. 5.7 The preferred light conditions of moving swamp rats in the visual cover trials in relation to (a) cover density (O, no cover; L, low; M, medium; H, high), (b) proximity to the door (far from the door, near to the door), (c) proximity to the wall (alongside the wall edge, centre area). * denotes a significant difference between dark and light conditions for each treatment comparison and each half of the trial (first 10 min, last 10 min). 'ns', no significant difference between dark and light conditions.

5.4 Discussion

5.4.1 Cover density treatments have little effect on swamp rat 'habitat' preferences

Contrary to our original hypotheses, there were few preferences for different cover densities in either the structural or visual cover trials in the dark conditions, and no preferences at all within the light conditions. The latter result is particularly surprising, since we had predicted cover to be more important in the light conditions, as lighter conditions are typically 'riskier' for nocturnal or crepuscular small mammals that are typically active at darker times (Kotler *et al.* 1991). A recent study reported a population of swamp rats in northern New South Wales showed distinctly diurnal activity patterns (Meek *et al.* 2012), which may have explained the results we obtained. However, in Tasmania, recent state-wide small mammal camera trapping surveys have shown predominantly crepuscular or nocturnal activity patterns by swamp rats (T. Hollings, pers. comm.), indicating that the Tasmanian subspecies, *R.l. velutinus*, is unlikely to be diurnal.

Many small mammal species avoid open areas in more illuminated conditions as concealment from predators is reduced (Longland & Price 1991; Dickman 1992; Orrock *et al.* 2004; Bengsen *et al.* 2010; Hinkelman *et al.* 2012). Therefore, we had expected to see a difference in the use of the treatments between dark and light conditions, but there were no differences for the structural cover. In contrast to the structural trials, the visual cover trial showed that swamp rats moved more in the first 10 minutes in dark conditions compared to light conditions. Movements such as running, extending (reaching) and grooming are considered exploratory behaviours (McEvoy *et al.* 2008), while brief pauses in locomotion are used to improve anti-predator vigilance (McAdam & Kramer 1998; Vásquez *et al.* 2002). Animals that move more are potentially at higher risk of predation (Norrdahl & Korpimaki 1998), therefore we would expect more movement from swamp rats when risks are lowest (i.e. in the dark, with dense cover). This was evident in medium and high visual cover density treatments (in the first 10 minutes), indicating that dense visual cover is still an important habitat feature, even in dark conditions. Overall, however, the limited effect of cover density in the trials may have been overridden by the protection provided by the arena walls and the perceived risk posed by the researcher (the door effect).

5.4.2 Evidence that large structural features offer important habitat cover

One of the clearest results from this study was that the protection provided by the arena walls ('edge') was important to swamp rats, despite offering no direct overhead cover. In every trial, and almost every time period, preference for the arena edges were significantly higher than for the centre area. The solid, physical protection offered by the walls of the arena edges may be analogous to coarse woody debris (CWD; fallen logs) and vertical cover (dead standing trees, living trees) found in mature forests. Where dense ground-level cover or runways are sparse or absent (e.g. in wet *Eucalyptus* forests, pers obs; rainforests, Green 1967), other types of protection during movement are needed to minimise exposure to predators. Many studies have shown a strong relationship between CWD and small mammal abundance and persistence in disturbed habitats (Barnum *et al.* 1992; Tallmon & Mills 1994; Loeb 1999; Greenberg 2002; Fauteux *et al.* 2012). Larger structural features such as CWD allow small animals to move between foraging areas and nesting sites with cover and protection which may be of higher quality than the available ground-level structure (e.g. fine woody debris, small stems, tree roots) or visual cover (e.g. overhead plant foliage). Interestingly, the only non-significant wall effects were observed for moving rats in the last 10 minutes in dark conditions of both the structural and visual cover trials. The latter half of the dark condition trials were likely to be the times when rats felt least threatened due to short-term habituation to the arena and because detection by potential predators that predominantly use visual cues is reduced in the dark (Kotler *et al.* 1991).

In a production forestry landscape, regenerating harvested areas retain some large structural elements such as CWD (albeit burnt in some systems such as wet *Eucalyptus* forests), which may provide cover for small mammals (Fauteux *et al.* 2012). In Tasmanian wet *Eucalyptus* production forests, the areas immediately surrounding the harvested matrix (and in aggregated retention sites, the areas surrounding the forested patches) are relatively bare. These areas are wide tracks (on average 10.6 m; Scott *et al.* 2012) used as fire breaks and are typically composed of mineral-earth compaction, which negatively affect eucalypt and understorey seedling regeneration (Neyland *et al.* 2009; Hindrum *et al.* 2012). Along with the reduced vegetation cover, there is often little structural complexity remaining on these tracks, as they have typically been used as roads during harvesting, as firebreaks during regeneration burning, and often also as

trails for motorised quad bikes for post-harvest access, and are thus kept clear of larger debris. These conditions are comparable to unpaved roads, which have been shown to pose a long-term impediment to swamp rat dispersal (Stephens *et al.* 2013, Chapter 4). Therefore, regeneration and structural complexity within harvested areas may provide sufficient cover for swamp rats earlier than anticipated, but the fire breaks surrounding forested patches and along the edge boundaries may pose a road-like barrier. These potential effects may need to be considered in future research on harvesting impacts on small cover-dependent mammals. Mitigation measures may be as simple as providing a few structural features along the tracks to allow movement across the tracks. However, in some areas, narrow openings will be required for other stand management activities.

5.4.3 Perceived threats increase vigilance, but habituation may have diminished the effect

The minimal cover density effects may also be explained by swamp rat behaviour in relation to other perceived threats. There appeared to be a trend for swamp rats avoiding the half of the arena nearest to the door (Fig. 5.2). These effects were significant in the structural cover trials, with the far half of the arena preferred in the first 10 minutes of the dark trial for stationary rats and throughout the whole light trial for moving rats. These results appear at first glance to be contrasting, but may be explained by different strategies employed in response to managing different threats. Korpimaki *et al*. (1996) found that vole behaviour changed in response to different predator hunting strategies. When avian predators, kestrels, were present, vegetation cover was preferred as it provides visual concealment but when ground predators, weasels, were present, voles preferred areas of no cover as weasels hunt by ambushing prey. However, when both kestrels and weasels were present, voles preferred vegetation cover indicating that avian predators were a bigger threat. In our study, the different light conditions may have altered the perception of the threat posed by the researcher (entering and exiting the door area), thus modifying swamp rat behaviour. In the dark conditions, stationary swamp rats showed a preference for the far area only in the first 10 minutes. In these dark (lower risk) conditions, small mammals are more likely to exhibit exploratory behaviours (Bowers & Dooley 1993), particularly when threats are reduced (Norrdahl & Korpimaki 1998). Therefore, it may be hypothesised that after the first few minutes of the trial, swamp rats became habituated to the arena

and in the dark (lower risk) conditions, and the need to avoid the area near the door diminished. In light conditions, small mammals are more vulnerable to predation, and behavioural modifications may be needed to minimise risk (e.g. reduced foraging, Kotler *et al.* 1991). In habitats that lack overhead cover, small mammals are vulnerable to aerial predators, which predominantly hunt using visual cues. Therefore, in the trial with no overhead cover and in light conditions, moving swamp rats preferred the far area where the perceived risk was presumably lower, and this vigilant behaviour was evident throughout the entire trial.

The door effect was not as strong during the overhead visual cover trials, with a significant preference only seen for far areas by stationary rats in dark conditions. Due to the loss of video data (from a technical failure) before scoring was completed, most of the data for the visual trials were from rats that had been in the arena three times before (40 out of 44 samples). Habituation to the arena may have altered their perception of risk, and the door (and the researcher behind it) may not have been as threatening as during the earlier trials.

5.4.4 Future research

While we were unable to detect clear and consistent treatment (cover density) differences the outcomes of this research have suggested the importance of large vertical structural features for the small native rodent, the swamp rat. There are a number of possible explanations for the lack of cover density effect, but the most likely are (1) the protection offered by the arena walls appeared to be of higher quality to the swamp rats than that offered by the cover treatments and/or (2) the perceived threat of the researcher. The wall effect is in itself an important finding, but it does not reveal how swamp rats behave when large objects such as coarse woody debris are absent. The perceived threat of the researcher resulted in preferences for areas further away from the threat, thus overwhelming the preference for different cover densities. For future captive studies of swamp rat habitat preferences, we recommend the following modifications to the test arena, format of the trials and analyses to better ensure testing of the planned treatments. The swamp rats' use of edges as a type of protection could be reduced by using different materials for the arena walls. For example, the transparency of perspex walls may reduce protective qualities, particularly in light (high risk) conditions. Alternatively, in studies with sufficient sample sizes, the edge

areas could be removed from analyses to allow investigation of use of middle areas only. To mitigate the effect of the perceived predator (i.e. the researcher), placement of the study animal could be in a covered box on a rotating apparatus (to disorient the animal) with remote release of the animal once the researcher had left the room. Therefore, the animal would be naïve to the location of the researcher.

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CHAPTER 6: General Discussion

In my thesis, I assessed the success of an alternative harvesting practice, aggregated retention, for two native ground-dwelling rodents, the cover-dependent swamp rat (*Rattus lutreolus*) and the habitat generalist long-tailed mouse (*Pseudomys higginsi*). I adopted a multi-disciplinary approach to investigate the impacts of aggregated retention on native rodents using traditional ecological methods (capture-mark-recapture, demographics), physiology (stress responses and general health), genetics (population differentiation), and behaviour (habitat preferences). By applying these different techniques, I was able to detect responses that may have been overlooked had I used only one approach. My research has shown how small mammals respond to different disturbances within their environment, and as a result, I am able to advocate practices that will support ecologically sustainable forestry management.

My general discussion is divided into three sections. The first section synthesises the key findings from this thesis for the ecology and impact of anthropogenic disturbances on swamp rats and long-tailed mice and describes future research priorities. The second section assesses the success of aggregated retention (ARN) in fulfilling its three main objectives: lifeboating, structural enrichment, and landscape connectivity. The final section discusses limitations of this study.

6.1 Impacts of habitat modification on native rodents

6.1.1 Swamp rats, a cover-dependent species, show lower abundance and restricted dispersal due to the removal of suitable habitat

While swamp rats occupy many different habitat types throughout south-eastern Australia, including Tasmania, they are known to prefer habitat that provides dense cover (Fox & Monamy 2007). Few studies have examined their responses to disturbance, although those that have indicate that they generally avoid disturbed areas (Fox 1982; Monamy & Fox 2000). Swamp rats have a generalist and mostly herbivorous diet, and the Tasmanian subspecies feed predominantly on monocots (grasses and sedges, Driessen 1987). In early regenerating forests, monocots are abundant and food is unlikely to be a limiting factor for use of the harvested areas. Therefore, vegetation cover is the most likely driver of habitat use. I hypothesised that

swamp rats, in comparison to unlogged native forests, would be in lower abundance in clearfelled (CBS) sites, and intermediate in ARN sites, where patches of forest are retained. These predictions were confirmed with my initial study of rodent abundances and associations with vegetation cover (Stephens *et al.* 2012, Chapter 2). Swamp rat abundances were highest in unlogged, lowest in CBS, and intermediate in ARN sites. There was also a trend for decreasing abundance with increasing disturbance of habitats within aggregated retention sites. There was no strong relationship with vegetation cover in forested areas, but a strong positive relationship with lower strata vegetation in harvested areas. This suggests that utilisation of the harvested areas will only occur once vegetation density has reached a certain threshold, and follows the habitat accommodation model proposed by Fox (1982). The reluctance to recolonise unsuitable habitat may also explain the lack of physiological and health responses of swamp rats in disturbed sites (Chapter 3). If individuals trapped in the harvested areas were transients from the forested edges or islands, rather than residents within the harvested areas, then they may be experiencing short-term stress, but not necessarily the long-term stress which was being assessed.

Swamp rat abundances in both CBS and ARN harvested areas were low (Stephens *et al.* 2012, Chapter 2), and I observed during my initial trapping survey that swamp rats were reluctant to move out of ARN islands, and somewhat surprisingly, across narrow, unpaved and seldom used roads in unlogged areas. I instigated a population genetic study (Stephens *et al.* 2013, Chapter 4) which revealed swamp rats were more related in islands compared to edges, confirming that the harvested matrix was a dispersal barrier, at least over the short-term. Previous studies have indicated that swamp rats have relatively small home ranges of 42-78 m (Barnett *et al.* 1978; Norton 1987). In my study (Stephens *et al.* 2013, Chapter 4), this was confirmed using spatial autocorrelation analysis which revealed a neighbourhood size (breeding range) of only 42-55 m, and also showed male-biased dispersal. Therefore, the distances between ARN islands and coupe edges (in my study, 60-160 m) and among ARN islands (80-120 m) within the harvested landscape may have explained the reluctance to move between these areas. However, analyses within unlogged sites also confirmed a reluctance of swamp rats to move across narrow (< 10 m), unpaved, and seldom-used roads, with higher relatedness among the ‘same side of road’ populations (Stephens *et*

al. 2013, Chapter 4). It therefore appeared that it was not only distance that played a role in limiting dispersal, but the type of cover (or lack of cover) that was provided.

Swamp rats have long been linked to a dependence on habitat that provides dense cover (Fox & Monamy 2007); however, few studies have attempted to disentangle the importance of different types of cover (but see Braithwaite & Gullan 1978). Overhead vegetation may provide protection from aerial predators by reducing visual detection (Kotler *et al.* 1991), but at the same time may impede the visual detection of predators by prey (Ebensperger & Hurtado 2005). Structural ground-level cover such as fine woody debris and runways through small stems and above-ground roots may assist in evasion from predators (Jensen *et al.* 2003). Although my captive behavioural study was unable to detect preferences for different cover densities (Chapter 5), I detected a strong preference for solid, vertical, structural features in the test arena. The dependence on analogous structures in natural habitats, e.g. coarse woody debris (CWD), has been shown for many small mammal species (McCay 2000; Greenberg 2002), particularly in disturbed areas where other vertical structural features have been removed (Fauteux *et al.* 2012; Sullivan & Sullivan 2012). The lack of these structural components on roads may explain the reluctance of swamp rats to move across roads or other similar cover-free areas. Therefore, I believe that there are three important questions that need to be addressed in relation to swamp rat movement and dispersal.

The first two questions relate to swamp rats use (or lack thereof) of the harvested matrix. During my project, I treated the harvested matrix as one habitat type; however, with the discovery of roads being a dispersal barrier, there may be at least two: the 'main' harvested area that typically contains CWD and is burnt post-harvest to encourage rapid eucalypt germination, and fire-breaks, which are composed of tracks of compacted soil resulting in restricted regrowth and surround ARN islands and the coupe boundary (e.g. edges). Therefore, if there are distinct habitat types in the harvested matrix, is the main harvested area really hostile for swamp rats? The main harvested area contains components that appear to enable swamp rat movement, i.e. CWD and dense, but patchy, vegetation cover, although I found little evidence of swamp rats utilising these areas. To answer the first question, I would suggest a manipulative study which would measure swamp rat movement and behaviour within the main harvested area, which may also be of particular interest in determining

dispersal distances for males. For example, Bakker & Van Vuren (2004) conducted a translocation experiment with squirrels, moving them from forest into adjacent open areas to measure their gap crossing decisions and use of microhabitat. The second question follows on from the theory of two habitat types within the harvested matrix: is swamp rat dispersal limited by the fire-breaks? In Tasmanian ARN, some CWD remains on the fire-breaks during harvesting, or can be created post-harvest due to windthrow (R. Scott, pers. comm.), although the volume and spatial distribution (e.g. lying across the whole fire-break) has not yet been quantified. If swamp rats are able to utilise CWD for movement in more open areas as other species have been shown to (Zollner & Crane 2003), then we would expect that with sufficient volume and distribution then fire-breaks would not be a dispersal barrier.

This leads me to my third question: roads are presenting a dispersal barrier to swamp rats, but will CWD or similar structural features allow swamp rats to cross the road? Before attempting any mitigation measures for roads (see below), I would recommend experimentally testing the use of CWD or other structural features in fire-breaks and on unused roads, e.g. in reserves. One of the most well-known methods of assessing risk and habitat use in mammal behavioural studies is 'giving up densities' (GUDs, Brown 1988). This method assesses the subject's perception of predation risk by measuring how quickly they will give up foraging in a high risk (e.g. no cover) compared to a low risk (e.g. dense cover) environment (Kotler *et al.* 1991). This could easily be applied in ARN by placing food trays on fire-breaks near CWD (or other structural features) and in areas with no cover, to determine the importance of these features. Additionally, to determine an individual's behaviour in relation to potential dispersal barriers (Bakker & Van Vuren 2004), tracking (e.g. radio, GPS) studies could be employed to survey movements of individuals in ARN sites, unlogged forests with roads, and unlogged forests with no roads. At the same time, the efficacy of mitigation measures for roads and fire-breaks could be assessed.

While these questions remain unanswered, providing effective mitigation prescriptions is not entirely possible. A recent discussion of the road literature recommended that rigorous studies that include before and after comparisons, thus requiring close collaboration between researchers and road planners, are needed to complete successful and applicable research on roads (Lesbarrères & Fahrig 2012). In light of

these considerations, I would suggest trials be conducted that incorporate potential solutions for small mammal dispersal across roads but are also practical for road users, even if road use is infrequent (e.g. for fire-fighting). Culverts, overpasses and underpasses have been successful for some species on larger roads (Ng *et al.* 2004); however, they are impractical and expensive for smaller roads. Mitigation measures are also unlikely on longer roads that are still regularly used. Perhaps for these reasons, I was unable to find any studies on mitigation measures for the impacts of smaller roads, although there have been many studies indicating they are an issue (Barnett *et al.* 1978; Swihart & Slade 1984; Rico *et al.* 2007; van Langevelde *et al.* 2009). Where roads are used infrequently, or not at all (e.g. in reserves), mitigation may be an option. For example, in two of my unlogged sites, population differentiation was evident despite the roads ending less than 500 m from the study sites (Stephens *et al.* 2013, Chapter 4). In cases similar to these, minor mitigation measures may be employed without causing disruption for forestry workers. A potential trial option is to construct tunnels (half-pipes) across roads using a semi-rigid plastic that vehicles could drive over, but would still allow small mammals to pass through. This method is without precedent on larger roads, but nonetheless may be worthwhile trialling in areas that are highly fragmented by road networks and are unlikely to negatively impact forest practices, or in systems where road use has been discontinued (e.g. reserves).

The investigation of larger roads within the forestry landscape was beyond the scope of my project, but considering the impact that smaller roads are having on swamp rat populations (Stephens *et al.* 2013, Chapter 4), this is a key area requiring future research. For example, a genetic study considering populations on either side of a large logging road, with populations straddling a natural barrier (e.g. a river) and in an unimpeded landscape as controls could inform us about the larger-scale implications of forest fragmentation effects on long-term gene flow and population differentiation.

6.1.2 The long-tailed mouse, a habitat generalist, persists in disturbed habitat, but at what cost?

While less is known about the habitat requirements of long-tailed mice in comparison to swamp rats, their ability to inhabit areas with both dense and sparse vegetation cover (Stoddart & Challis 1991) suggests that they are habitat generalists. Therefore, I hypothesised that long-tailed mice would inhabit both forested and harvested areas of

ARN, as well as unlogged sites and clearfelled sites. The investigation of rodent abundances following harvesting confirmed these expectations, with long-tailed mice found to be equally abundant in all forestry treatments and in all habitat types within ARN (Stephens *et al.* 2012, Chapter 2). There were no clear habitat associations in ARN sites, while there was a negative relationship with ground-level (< 1 m high) vegetation in both clearfelled and unlogged sites. Importantly, however, the study of physiological responses to harvesting (Chapter 3) revealed that long-tailed mice in clearfelled sites were in poorer health compared to those in unlogged sites, and to a lesser extent compared to ARN. These results suggest that some other factor was influencing their decision to inhabit sub-optimal habitat.

One possible factor for explaining the presence of long-tailed mice in harvested areas despite poorer condition, is competitive interaction between the two species, which has been previously examined in one southern Tasmanian population (Luo *et al.* 1998; Monamy & Fox 1999). Competition has also been investigated between swamp rats and another *Pseudomys* species, *P. gracilicaudatus*, in a heathland population in New South Wales (Higgs & Fox 1993; Thompson & Fox 1993; Luo & Fox 1995). All these other studies suggested that some degree of microhabitat partitioning was occurring, as swamp rats and *Pseudomys* spp. were occupying different areas within a site although still co-occurring. My initial capture-mark-recapture study also documented the co-occurrence of swamp rats and long-tailed mice in unlogged habitat, but I observed no evidence of competition within these areas, although this was not explicitly tested. That is, there was no evidence of clear partitioning between microhabitats since long-tailed mice and swamp rats were regularly captured in the same trap station on subsequent nights (H. Stephens, unpublished data). My hypothesis for the lack of evidence for competitive habitat partitioning was that the long-tailed mice in our study were much larger (81 ± 9 g SE) than those in other competition studies (e.g. 60–65 g; Luo *et al.* 1998; Monamy & Fox 1999) and were therefore not competitively excluded.

The results from the harvested sites suggest a different story to the unlogged sites. Long-tailed mice are able to persist in harvested areas, but they appear to do so with associated health impacts, while swamp rats mainly inhabit areas of optimal habitat and do not show long-term stress responses or poor health. These results suggest that

long-tailed mice may not colonise harvested (sub-optimal habitat) areas out of choice, but rather out of necessity. Where optimal habitat is not limited (i.e. unlogged areas), the two species are able to co-exist; however, where optimal habitat is limited (on the disturbance borders), swamp rats out-compete long-tailed mice. Therefore, a removal experiment in disturbed and non-disturbed sites may provide greater insights into possible competition between these two species for optimal habitat. For example, if swamp rats are dominant and occupy the optimal habitat to the detriment of long-tailed mice, their removal out of optimal habitat adjacent to disturbed areas (e.g. harvested matrix) would result in an increase in long-tailed mice in the optimal habitat (Higgs & Fox 1993).

While I was able to assess stress responses and health metrics in native rodents during this project by using indirect methods (i.e. blood profiles; Dhabhar & McEwen 1997; Davis *et al.* 2008), this sampling approach is not ideal as I may not have been able to detect more subtle stress responses. In future studies I would recommend trialling alternatives which measures responses using a more direct approach (e.g. measuring stress hormones). One method that could improve investigation of stress responses in swamp rats and long-tailed mice (and was not widely known prior to my study), is the use of hair (or feathers or scales in other wildlife) to obtain longer-term measures of stress hormones (Meyer & Novak 2012). Hair sampling is still in early development, and has only been used in a handful of studies (Koren *et al.* 2008; Martin & Réale 2008; Bennett & Hayssen 2010). However, it has great potential for wildlife studies where obtaining uncontaminated urine and faecal samples are problematic, and immediate sampling upon animals entering traps (to avoid capture stress) is difficult due to large spatial scales of study sites and low capture rates. Although this method is relatively new, the benefits are promising (easy to collect from wild animals in all weather conditions and non-invasive), and may be a solution to current difficulties encountered during wildlife ecophysiological studies (Romero & Reed 2005; Lynn & Porter 2008).

6.2 Assessing the success of aggregated retention for native rodents

The first objective of ARN is to ‘lifeboat’ species and processes post-harvest that may otherwise be lost during harvesting, and to enable them to persist before forest cover is

re-established. Aggregated retention is clearly successful for lifeboating swamp rats, for at least the first few years post-harvest, which supports findings from other partial harvest studies on small mammals (Sullivan & Sullivan 2001; Lindenmayer *et al.* 2010). The retained patches of mature forest were able to maintain individuals and populations despite the lack of use of harvested areas. In contrast, swamp rats rarely used clearfelled sites, suggesting that they avoid these areas, resulting in a decline or loss of local populations in these conditions. Long-tailed mice were found in equal abundance in ARN and clearfelled sites, therefore this objective is potentially redundant for this species.

The second part of Objective 1 aims to retain species until forest cover is re-established. I could not assess this objective directly in the time frame of this thesis (2 to 5 years post-harvest). Sullivan *et al.* (2008) found that up to 8 years post-harvest, the abundance of a cover-dependent vole decreased, despite it persisting up to 3 years post-harvest in an earlier study (Sullivan & Sullivan 2001). This may indicate that small mammals may persist over the short-term, but if conditions do not improve rapidly enough (e.g. resource depletion), then persistence over the longer-term is not possible. However, in my study, lower strata vegetation cover was increasing in the harvested areas over the lifetime of the study (Stephens *et al.* 2012, Chapter 2), and previous work on swamp rats suggests that the species is able to recolonise once a cover threshold is reached (Fox 1982). Therefore, it is likely that the impacts of harvesting would only last for a few generations and that with a larger abundance of swamp rats retained within the coupe (in island and edge aggregates), that recolonisation of the harvested matrix will be faster in comparison to CBS. However, only longer-term monitoring of swamp rat populations in ARN would be able to conclusively confirm their persistence. Long-tailed mice showed a trend for poorer health in CBS sites in comparison to ARN, therefore, longer-term implications for persisting within ARN may be better than persisting within CBS.

The success of lifeboating for swamp rats is strongly associated with the retention of structural features such as standing trees and CWD that provide dense habitat cover (Stephens *et al.* 2012, Chapter 2). Consequently, lifeboating is intrinsically linked to the second ARN objective of structural enrichment. Therefore, unsurprisingly, the

second objective is also achieved successfully for swamp rats, but is not necessarily applicable to long-tailed mice.

To my knowledge, evaluating landscape connectivity, the third objective, in variable retention sites has only been attempted in one study. Chan-McLeod & Moy (2007) used translocation and tracking trials to determine the use of retained tree patches in the harvested matrix by frogs. They found that frogs did not use the islands as stepping stones, that movement was only directed towards large patches or when the distance was small (≤ 20 m). The lack of evaluation of landscape connectivity is a large gap in assessing the success of variable retention, as highlighted in the review by Rosenvald & Lohmus (2008). However, this can be a difficult objective to assess, depending on the scale of movement of the species concerned. The main premise for this objective is enhancing movement of organisms within a managed landscape, i.e. promoting dispersal through the harvested matrix. Considering the neighbourhood size of swamp rats is 45 to 55 m (Stephens *et al.* 2013, Chapter 4) and the maximum recorded distance travelled for a long-tailed mouse in this study was < 200 m (unpublished data), then examining landscape connectivity in sites 12 to 75 ha is an appropriate scale. From the capture-mark-recapture data, long-tailed mice appeared to move easily through the harvested matrix in both CBS and ARN sites. Their movements may have been enhanced by the 'stepping stones' provided by the island aggregates, but I do not have evidence to support this. Swamp rats, while making use of the island aggregate lifeboats, were unwilling to utilise the harvested matrix to disperse over the wider landscape 2-5 years following harvesting. This was observed in the capture-mark-recapture data (Stephens *et al.* 2012, Chapter 2), and later supported by the genetic analyses that revealed increased relatedness within ARN islands (Stephens *et al.* 2013, Chapter 4). Therefore, over the short-term, ARN islands do not provide landscape connectivity for swamp rats, although with sufficient vegetation regrowth and cover within the harvested matrix, this may not continue over the longer-term.

The islands and edge aggregates both provided suitable habitat for swamp rats and long-tailed mice within ARN sites. However, edges were clearly more beneficial than islands for swamp rats in terms of landscape connectivity. Island populations showed higher relatedness compared to edge populations (Stephens *et al.* 2013, Chapter 4), which could increase inbreeding effects or local extinction if immigration does not

occur (Peakall & Lindenmayer 2006). In Tasmanian State wet *Eucalyptus* forests, current practice suggests, where possible, that at least 80 % of aggregate area is retained as edges rather than island aggregates (Baker *et al.* 2009). A configuration that includes edge aggregates only (including peninsulas) or prioritises edge aggregates over islands may be more beneficial for other cover-dependent species in other systems, although benefits to other taxa and operational constraints should also be considered.

6.3 Research limitations

As with all research, there are limitations to the studies described in this thesis. In this study, two important limitations were (1) the lack of pre-disturbance assessments, and (2) the lack of wildfire control sites. The lack of pre-disturbance assessments is a common problem where large-scale (temporal or spatial) ecological questions are being asked, but the time span for data collection in a typical research project is relatively short-term (e.g. 2-3 years). However, the use of sufficient replication for the spatial scale of this project, and the use of unlogged sites as controls should have mitigated the first limitation. Additionally, by using genetic and physiological methodologies, I was able to evaluate effects over a longer-term scale than the duration of the project. The second limitation relates to the theoretical basis for variable retention practices (including aggregated retention). Variable retention was designed as a practice that would, in part, emulate natural disturbances, which leave a mosaic of disturbed and undisturbed patches within the landscape and retain biological legacies within the disturbed patches (Franklin *et al.* 1997). In Australia, wildfire (bushfire) is prevalent throughout *Eucalyptus* forests, and is important for maintaining *Eucalyptus*-dominated systems (i.e. preventing conversion to other forest types such as rainforest). Therefore, using wildfire sites for controls would have tested the theory of emulating natural disturbances. However, there were no natural wildfire sites of comparable forest type and time since disturbance available, and creating these disturbances for the project would have been impractical.

6.4 Concluding comments

This thesis has greatly increased our knowledge not only of the effectiveness of ARN as an alternative to CBS for small mammals, but has also increased our knowledge of the species themselves. I was able to conclude that ARN is a preferable harvesting method to CBS for small ground mammals. By using a multi-disciplinary approach I was able to elucidate more subtle effects of harvesting, which would not have been apparent by abundance data alone. While long-tailed mice appeared to readily utilise the harvested areas in both CBS and ARN (Stephens *et al.* 2012, Chapter 2), the individuals captured there were in poorer health than those in unlogged forest (Chapter 3). Additionally, Chapter 3 marks the first physiological study of long-tailed mice, and will provide guidance for future studies.

This thesis investigated the ARN objective of landscape connectivity for small mammals, which to my knowledge, has not been attempted before. In testing this objective, I also discovered that swamp rats are reluctant to cross narrow, unpaved roads in unlogged forest (Stephens *et al.* 2013, Chapter 4), which is likely to pose a greater problem for dispersal and population connectivity over the long-term. This thesis also included the first population genetic study of swamp rats, therefore it was necessary for me to test several microsatellite markers to find a sufficient and successful number, which will assist any future population genetic work on swamp rats.

One of the recurring themes throughout this thesis was the cover-dependence of swamp rats, which was not unknown before (Fox & Monamy 2007), but which has been greatly expanded from this thesis. I was able to confirm their cover-dependence (Stephens *et al.* 2012, Chapter 2; and perhaps the reason for this in Chapter 3) and their reluctance to cross ‘open’ areas (Stephens *et al.* 2013, Chapter 4), and uncover strong preferences for large structural features (Chapter 5). Knowledge of this behaviour is particularly important in disturbed habitats where ecotones exist (e.g. on the harvested/forested boundaries), resulting in dispersal barriers. This thesis also highlights the strength and benefit in embracing different fields to investigate species’ responses to disturbances, where impacts are not necessarily detected by the use of one approach alone.

6.5 References

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