# Impacts of Habitat Fragmentation on the Vertebrate Fauna of the Tropical Savannas of Northern Australia; with special reference to medium-sized mammals.

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Declaration

I hereby declare that the work herein, now submitted as a thesis for the degree of Doctor of Philosophy of the Charles Darwin University, is the result of my own investigations, and all references to ideas and work of other researchers have been specifically acknowledged. I hereby certify that the work embodied in this thesis has not already been accepted in substance for any degree, and is not currently submitted in candidature for any other degree.

Date:

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ABSTRACT

Across the Northern Territory, the natural vegetation remains extensive with limited modification. This expanse of relatively unmodified landscape provides an opportunity for conservation planning that is potentially unmatched in the world. However, the intactness of this native vegetation is coming under increasing threat. In this study I investigate the effects of habitat loss and fragmentation on the fauna of Australia's tropical savanna woodlands. In particular, I focus on fauna inhabiting the open eucalypt forests of the Darwin and Daly regions of the Northern Territory, that are taking the impact of current development. Although there is a substantial body of information for temperate Australia on the ecological effects of land clearing and fragmentation, I present the first study of how these processes affect the fauna in the tropical eucalypt forests of the Northern Territory and one of few studies conducted in tropical Australia. In contrast to the restoration works elsewhere in Australia, there is the rare opportunity to enact clearing controls informed with the principles of ecological sustainability, thus ensuring long-term maintenance of the Territory's biodiversity.

The first component of the study investigated the abundance of all vertebrate species in a range of fragments of varying size and isolation, including continuous forest and completely modified sites. The data from this survey were used to investigate patterns in vertebrate species composition and richness, and to determine species-specific relationships with a range of fragmentation and environmental variables. There were 75 species of bird, mammal, frog or reptile recorded frequently enough to analyse. Only a small proportion of these (25%) used modified land, but most (69%) did use corridors. There were no species that could confidently be classified as edge specialists, preferring the interface between woodland and modified land. Fourty-two percent of species analysed were statistically less abundant in more fragmented sites. Three variables were found to have a strong positive influence on the animals that occur in a fragment. They were the area of the fragment, the total amount of woodland within 4 km of the fragment, and the extent of corridors linking the fragment to other large woodland tracts.

The second component of the project focused on the effects of habitat fragmentation on the survival and dispersal of medium-sized mammals. Medium mammals were selected as the faunal assemblage to investigate, as their requirements are believed to broadly encompass the needs of the other species. A mark-recapture study of four mammal species (black-footed tree-rat *Mesembriomys gouldii*, northern quoll *Dasyurus hallucatus*, northern brown bandicoot *Isoodon macrourus* and the common brushtail possum *Trichosurus vulpecular*) was conducted for two years, within a selection of fragmented and continuous sites from the initial study. The abundance of all four medium-sized mammals was greatest in the fragmented sites. As land

clearing and habitat fragmentation is only a recent phenomenon in the study area, these fragments may still be undergoing increased population densities and over crowding, especially for the common brushtail possum and northern brown bandicoot. Despite this higher abundance, survival rates were lower in the fragmented sites with relation to the continuous site. Although, in general, these survival rates were not substantially lower than in continuous areas they do highlight the fact that habitat fragmentation is having an effect on the survival of small mammals in this study.

Of these four species, the black-footed tree-rat was radio-tracked in fragmented and continuous habitats to investigate possible differences in movement, activity area and home range. The size of home range estimates for the black-footed tree-rat in the un-fragmented environment suggest that black-footed tree-rats require large areas (67.3 ± 10.4 ha) when compared to other similar sized mammal species of Australia's tropical savannas. Home range and activity area size decreased significantly under fragmented conditions; however, black-footed tree-rat were able to cross relatively large areas of cleared land. Although they require large areas in order to obtain enough resources, it appears they are able to cope with low levels of habitat fragmentation, using many smaller patches to achieve this.

Although abundance of all four medium-sized mammals was greatest in the fragmented sites, abundance varied widely between fragments. As these differences may be attributed to differences in habitat quality, a more intensive study of denning and food resources preferred by black-footed tree-rats was conducted. Black-footed tree-rat populations were limited by the diversity of food resources and the availability of large trees. Fire history influenced the diversity of the fruiting species present at the site. Sites that were long unburnt had a greater fruiting species diversity and hence were able to support a greater population of black-footed tree-rats. Fire regimes were found to have a direct effect on the habitat quality by influencing vegetation structure and composition and in turn affecting mammal populations.

Most habitat fragmentation studies have been conducted in areas where extensive clearing has resulted in an extreme loss of native vegetation. For these areas, the aim is usually to report on the effects that habitat fragmentation and loss has had on the biota of the region and to suggest the best ways to restore and manage the remaining vegetation. In contrast, the main aim here was to determine the requirements of the region's fauna in order to guide the design of future agricultural landscapes. The Northern Territory has a rare opportunity to enact clearing controls, informed with the principles of ecological sustainability, to help ensure the long-term maintenance of the Northern Territory's native flora and fauna. The configuration of habitat

patches capable of maintaining viable wildlife populations can be pre-determined, with guidelines being put into place before vegetation clearance occurs.

CHAPTER 1

General Introduction

Introduction

Across the Northern Territory, the natural vegetation remains extensive with limited modification (Woinarski 2004). This expanse of relatively unmodified landscape provides an opportunity for conservation planning that is potentially unmatched in the world (Woinarski *et al.* 1992). Currently around 40 % of the Northern Territory is gazetted as Aboriginal land and another 45% is leased by the Crown for pastoralism (Woinarski *et al.* 1992; Hosking 2002). National Parks and conservation reserves cover only 4% of the territory, and are considered to be unrepresentative of the ecological variation for the area (Woinarski *et al.* 1992). It is estimated that almost one quarter of vertebrate species do not occur within any conservation reserves (Woinarski 1992). To date, the monsoonal area of the NT has not suffered the loss of species that has plagued the rest of the continent since European settlement (Woinarski and Braithwaite 1990). While no species from this region are known to have become extinct in recent times (Woinarski 1992) there are clear signs of significant biodiversity declines (Braithwaite and Griffiths 1994; Franklin 1999; Woinarski 2000; Woinarski *et al.* 2001b). A large proportion of the fauna from this area is highly mobile, with huge fluctuations in population a characteristic feature of much of the wildlife (Woinarski *et al.* 1992). With these characteristics in mind the current state of formal reserves within the Northern Territory cannot satisfactorily conserve the biodiversity of the area. Thus, the preservation of the fauna requires informed management and protection of natural vegetation outside the formal reserve system (Woinarski 1992; Woinarski *et al.* 1992).

Objectives of this study

The intactness of this extensive native vegetation is coming under increasing threat. Currently less than 0.5% of land within the Northern Territory has been cleared, but the rate of clearing is increasing with proposals for large agricultural developments (Brock 2000). In this study I investigate the effects of habitat loss and fragmentation on the fauna of Australia's tropical savanna woodlands. In particular, I focus on fauna inhabiting the open eucalypt forests of the Darwin and Daly regions of the Northern Territory, that are taking the impact of current development.

Although there is a substantial body of information for temperate Australia on the ecological effects of land clearing and fragmentation, I present the first study of how these processes affect

the fauna in the tropical eucalypt forests of the Northern Territory and one of few studies conducted in tropical Australia. In contrast to the restoration works elsewhere in Australia, there is the rare opportunity to enact clearing controls informed with the principles of ecological sustainability, thus ensuring long-term maintenance of the Territory's biodiversity.

During this study I have sought to address the following question:

What are the landscape requirements needed to maintain important biodiversity values in land primarily under intensive agricultural management?

In order to investigate this question the study was broken into two major components.

Effects of Habitat Fragmentation on Vertebrate Fauna

The first component of the study investigates the abundance of all vertebrate species in a range of fragments of varying size and isolation, including continuous forest and completely modified sites. This combination of sites provided me with baseline data on which species would occur in modified land and those absent from fragments. This component of the study was achieved by conducting a systematic biological survey within the different habitat types. The data from this survey are used to investigate patterns in vertebrate species composition and richness, and to determine species-specific relationships with a range of fragmentation and environmental variables. By carrying out fauna surveys and looking at the species present in habitats of differing size, age and configuration, I was able to determine which species are the first to disappear from fragmented areas. These species or faunal assemblages then become focal or target species which can then act as umbrella species to determine the minimum patch size required to obtain a large species diversity.

Survival and Dispersal of Selected Species

The second component of the project focused on the effects of habitat fragmentation on the survival and dispersal of medium-sized mammals. Medium mammals were selected as the faunal assemblage to investigate, as their requirements are believed to broadly encompass the needs of the other species. A mark-recapture study of four medium mammal species, black-footed tree-rat *Mesembriomys gouldii*, northern quoll *Dasyurus hallucatus*, northern brown bandicoot *Isoodon macrourus* and the common brushtail possum *Trichosurus vulpecular*, was conducted for two years, within a selection of fragmented and continuous sites from the initial study. This assemblage of mammal species includes aboreal and ground-dwelling species that have different diet and resource requirements, are capable of moving reasonable distances and differ in their abundance. As specialised species have been targeted, a landscape designed and

managed to meet their needs will encapsulate the requirements of other species (Lambeck 1997). Of these four species, the black-footed tree-rat was radio-tracked in fragmented and continuous habitats to investigate possible differences in dispersal behaviour.

Thesis Structure

In the remainder of Chapter 1, I review the main aspects of habitat fragmentation, including the conceptual theories behind it and the plethora of empirical studies on the topic, and discuss reasons why this study was required despite the wealth of study already conducted on this topic. In chapter 2, I present an overview of Australia's Tropical Savannas, describing their distribution and setting the environmental context for this study. I provide a brief overview of the vegetation, fauna and land uses that occur in the tropical savannas, with a particular focus on the current state of land clearing in the Northern Territory. Chapter 3 describes a biological survey of the flora and fauna of fragmented Eucalypt open forests near Darwin. The data collected from this initial survey are used to investigate patterns in vertebrate species composition, and richness, and to determine species specific relationships with a range of fragmentation and environmental variables. I identify species that are affeeted by habitat fragmentation and determine which structural and landscape variables relate to the abundance of these species within a fragmented landscape. I examine the species that are capable of using the matrix of modified habitats within the area and those species likely to use corridors. An evaluation of the extent of edge effects on habitat structure and the impacts this may have on the vertebrate fauna are also investigated.

Chapter 4 investigates the second component of the study, describing a two-year mark-recapture survey conducted in a subset of the initial survey sites. I examine the factors that affect survival and recapture of four medium-sized mammals, in fragmented and un-fragmented sites. Program MARK is used to investigate what environmental and/or fragmentation variables are affecting the survival of each species. Utilisation of the inter-patch matrix and effects of habitat fragmentation on movement and home range of the black-footed tree-rat is investigated in Chapter 5. The availability and influence of shelter and food resources on abundance of black-footed tree-rats in fragments is examined in Chapter 6. Finally, Chapter 7 collates the outcomes of previous chapters, providing a synopsis of the effects of habitat fragmentation on the fauna of the open forests of Australia's tropical savannas. This chapter also outlines recommendations for potential management strategies to maximise the conservation value of fragments and proposes recommendations for the design of future agricultural landscapes in the region.

Habitat Fragmentation: A Review of Theory and Research

Habitat fragmentation is a consequence of large-scale clearing of native vegetation for agriculture and development, and is one of the major factors degrading biodiversity on a global scale (Bennett 1990a). As human populations grow, human-dominated transformations of the landscape intensify, with once continuous expanses of native vegetation being converted into fragmented remnants surrounded by a matrix of modified habitats. In most areas around the world, the conservation of wildlife depends largely or entirely on the retention and management of these remnants (Saunders *et al.* 1991).

Fragmentation consists of three main components: loss of original habitat, reduction in the size of remaining patches and increased isolation of patches (Andrén 1994; Burgman and Lindenmayer 1998). Bennett (1990a) indentifies three consequences of habitat loss and fragmentation for biota: changes to the composition and structure of communities; changes to species populations, and changes to ecological processes within fragments. Community and population changes are often associated with:

a reduction in area and increased isolation (MacArthur and Wilson 1967),

connectivity and corridors (Bennett 1990a);

edge effects (Andrén and Angelstam 1988; Laurance and Yensen 1991);

the influence of the surrounding matrix (Suckling 1982; Goosem and Marsh 1997; Laurance 1997; Gascon *et al.* 1999);

time since isolation (Suckling 1982; Soulé *et al.* 1988; Andrén 1994; Bennett 1990a) and;

second order or cascade effects (Malcolm 1997; Laurance 2000).

Understanding how species are affected by fragmentation requires information on how they respond to all components of the landscape, i.e. habitat patches, areas of continuous forest and the intervening matrix (Harris 1988; Laurance 1990; Laurance 1994; Fahrig and Merriam 1994; Gascon *et al.* 1999).

Different Models and Approaches to Habitat Fragmentation

The Fragmentation Model (patch-corridor-matrix)

Research investigating the effects of habitat fragmentation on wildlife initially focused on the concepts applied to oceanic islands within the theory of island biogeography (MacArthur and Wilson 1967). However, the recognition that terrestrial habitat remnants differ from true islands resulted in a shift in research effort towards fragmentation-induced changes in the landscape, such as increased areas of edge habitat and the creation of matrix habitat (Cox 2003). Terrestrial ecosystems can be classified as a mosaic landscape consisting of three types of spatial elements;

patch, corridor and matrix (Forman 1995). Each of these in turn can be characterised by attributes such as area, shape, width and connectivity (Forman 1991, 1995).

Many of the effects of patch size and isolation on species composition and richness were described by the basic processes of island biogeography and species-area relationships. The realisation that large areas of habitat generally contain more species than small areas of the same habitat, with the number of species increasing with increased area lead to the formation of the species-area relationship. This relationship is most commonly represented by the equation;

$$S = cA^z$$

Where S is the number of species, A is area and c and z are fitted constants. This model was used by Preston (1962) to expand his theory of dynamic equilibrium of species exchange between isolates of habitat. This theory was further developed (by MacArthur and Wilson 1967) into the equilibrium theory of island biogeography, with the realisation that islands contained fewer species than areas of similar size on the mainland. In general, the theory states that, in time, an island will reach an equilibrium number of species, which will be determined by a dynamic balance between the rate of colonization (by immigrant species) and extinction (by resident species), where the number of species remains relatively constant while species composition changes over time (Brown and Kodric-Brown 1977). The rate of immigration or colonization is primarily determined by the degree of isolation of the island, with increased immigration on islands close to the source pool, while the rate of extinction is determined by the size of the island, with higher extinction rates on small islands (MacArthur and Wilson 1967).

With similarities between continental habitat fragments and true islands the theory of island biogeography has been applied to fragmented environments. Although the species-area relationship and the equilibrium theory of MacArthur and Wilson (1967) may provide some useful insights, they fail to take into account the complexity of interactions that occur in fragmented environments (Lomolino and Perault 2001). Although habitat 'islands' may undergo similar processes of colonization and extinction, they differ from true islands as the matrix in which they exist may not be completely inhospitable. In fragmented environments the rates of colonization and extinction will be primarily influenced by the ability of species to move through and use the matrix. The matrix of developed land surrounding habitat 'islands' supports a different assemblage of flora and fauna, and has land uses that interact with the biota of the fragments (Saunders et al. 1991). Land uses carried out in the matrix expose habitat patches to various ecological changes such as edge effects that are not experienced on true islands. Realisation of these differences, plus empirical findings that species diversity on many islands is

not at equilibrium and the inability to demonstrate changes in species composition at equilibrium on true islands, has related much of the deterministic mechanics of the equilibrium theory of island biogeography (Brown and Lomolino 2000).

Variegated and Contour Models

The fragmentation model perceives the landscape as a mosaic of habitat patches of varying connectivity, situated within a mosaic of non-habitat (Forman 1995). This simplistic classification of the landscape can lead to the neglect of small patches and habitat features not recognised by humans (Haila 2002). Recognising the limitations of the fragmentation model McIntyre and Barrett (1992) developed the 'variegated' landscape model, providing an alternative way to conceptualize the landscape, recognising gradients in habitat and habitat suitability. McIntyre and Barrett (1992) believed that the variegated landscape was characterised by a gradual change in vegetation cover, which matched the distribution of some fauna, such as woodland birds. McIntyre and Hobbs (1999) examined the relationship further suggesting that there is a temporal element to landscape change, with different states of landscape alteration, classified as intact, variegated, fragmented or relictual. Hence, the most important difference between the fragmentation and variegated models is their ability to deal with spatial continua in habitat quality or vegetation type. The variegated model was developed to explicitly to incorporate gradients.

Both the fragmentation and variegated models are based on biophysical patterns of the landscape deemed relevant by humans and hence can not deal with species-specific differences in response to a landscape. (Fischer *et al*. 2004). The key features of the contour model are that it; (a) allows for species to differ in what constitutes suitable habitat, (b) recognises differences in the spatial grain of species (Fischer *et al*. 2004).

Habitat Loss

Habitat fragmentation is typically not random (Burgman and Lindenmayer 1998). Land clearing usually occurs on a selective basis, with the most productive soils being cleared first (Hobbs and Hopkins 1990; Saunders *et al*. 1991; Hobbs and Saunders 1993; Burgman and Lindenmayer 1998). Remaining habitat patches are more likely to exist on land with low quality soils or are located in areas that are unsuitable for proposed land uses, such as areas of high slope, valleys and gullies. This pattern may lead to significant loss or elimination of some habitat types, while others may remain relatively intact. This results in the remaining vegetation not being a representative sample of the unmodified landscape and therefore not representative of the biota

of the original landscape, with species that were previously abundant and associated with vegetation on productive soils becoming rare or locally extinct (Burgman and Lindenmayer 1998).

The alteration of habitat from human activities changes both the relative and absolute amount of various habitats in the area (loss or gain), and the spatial configuration of those habitats (Wiens 1997). Both habitat loss and fragmentation will have negative effects on the number of species in the landscape. It is believed that the effects of fragmentation on wildlife will initially be a result of loss of habitat, but as the proportion of available habitat in the landscape decreases, the effects of patch size and isolation will start to influence the biota (Andrén 1994). Because fragmentation involves simultaneous loss of habitat, decreased patch size and increased isolation, many fragmentation studies do not distinguish between the effects of habitat fragmentation and habitat loss, making it unclear whether the effects of habitat fragmentation are more important than the effects of habitat loss alone (Fahrig 1997).

There is evidence that species loss from a landscape is slow in the early stages of habitat loss, and increases dramatically above a certain threshold (Andrén 1994; Fahrig 2001, 2002). A worldwide review of habitat fragmentation for birds and mammals by Andrén (1994), found that the effects of fragmentation depended on the amount of habitat that remained in the landscape. With ≥30% habitat retained in the landscape, fragmentation did not appear to cause decreases in species richness (Andrén 1994). However, once the proportion of remaining habitat dropped below 30% increased fragmentation intensified decreases in species richness (Andrén 1994). This suggests that habitat loss is the immediate factor leading to a decrease in species richness when there is ≥30% of habitat retained in the landscape. The most likely reason for the threshold is that it occurs when landscape connectivity begins to break down and movement and dispersal are interrupted, a conclusion supported by simulation modelling (Ims 1995; With and Crist 1995). Using computer simulation, Henein et al. (1998) also found that retention to 30% of original habitat in the landscape was a critical threshold for a modelled species with a high dependence on native vegetation. Thresholds are likely to vary across species and differing landscapes (Andrén 1997).

Empirical studies have shown that the proportion of original habitat within the landscape influencs the likelihood of species occurrence (e.g. van Dorp and Opdam 1987; Askins et al. 1987). Lomolino and Perault (2001) found that species richness and composition of mammals in old-growth forest patches was not significantly correlated with patch area or degree of isolation, but showed a significant positive relationship with the amount of old-growth fragments and the amount of older regeneration in the surrounding landscape. Although the general rule of Andrén

(1994) provides us with a generlised threshold at which many species will be lost from the landscape, thresholds will differ across different taxonomic groups, species and across different landscapes (Andrén 1997). A study by Summerville and Crist (2001) showed that butterflies demonstrated thresholds ranging from 20-60% retained vegetation.

The Crowding Effect and Relaxation

When natural vegetation is removed, species populations go through two distinct phases, with short and long term effects. Initially, loss in the amount of habitat available may lead to increased population densities and over crowding in the habitat patches that remain (Lovejoy et al. 1986; Saunders et al. 1991), known as the 'crowding effect'. As land clearing occurs, species that inhabited the now cleared area are forced into the remaining habitat patches. Bierregaad Jr. et al. 1992) found a dramatic increase in the capture rates of birds in newly isolated habitat patches, however, within 200 days of isolation the number of birds fell to levels lower than those before isolation. This collapse in abundance after the initial crowding is a pattern referred to as 'species relaxation' (Diamond 1972). Inevitably patches will also suffer from reduced species richness. It may take time for populations of animals or plants to adjust to the landscape. The basic problem is that fragmentation may not kill individuals, but instead reduces their reproductive success, to levels that will not replace those dying naturally. Soulé et al. (1988) discovered that the time since a patch was isolated had a negative influence on the survival probabilities of species within the patch. In studies of fragmentation around the world, it has been found that species keep disappearing from fragments more than 70 years after they have become isolated (Sieving and Karr 1997). Brooks et al. (1999) estimated that fragments of approximately 1000 ha in size will have only suffered half the extinctions they are likely to experience within the first 50 years after isolation.

The speed with which species re-adjust is particularly dependent on generation time (Brook et al. 2003), so small rodents and dasyurid marsupials will adjust quickly while longer-lived cockatoos and wallabies may take several decades to adjust. The species most likely to become extinct are those that depend solely on resources within the natural habitat, have large home ranges, or naturally exist at low densities (Saunders et al. 1991).

The phenomenon of 'species relaxation' can have dramatic effects on the design of habitat fragmentation studies and the interpretation of their results. Studies conducted within a few years of clearing events (such as this study) may portray a better picture than is likely to occur in reality. Many species will be doomed to local extinction long before the actual event. Variation in the amount of time required for species relaxation to occur makes it hard to

determine the full effects of fragmentation, with many studies only able to portray a snapshot in time.

Patch Size and Isolation

It is widely accepted that small habitat patches will contain fewer species than large patches, with species richness often being positively correlated with patch size (e.g. Kitchener et al. 1980; Suckling 1982; Bennett 1987; Saunders and de Rebeira 1991). However, there are a number of variables that are often highly correlated with the size of a patch, such as habitat diversity, quality and isolation, which may also exert significant effects on species richness. For small patches, ecosystem dynamics are likely to be dominated by external forces (i.e. edge and matrix effects), while larger patches have bigger core areas that are driven by internal forces and are less affected by changes associated with edge effects (Saunders et al. 1991). Large patches are more likely to contain greater habitat diversity than smaller patches (Saunders et al. 1991). Small fragments are unlikely to support a diverse array of disturbance regimes (e.g. fire) and hence tend to become more homogenous than when they first became isolated. As a result the number of species within a patch will reflect the number of different habitats that are available (Bennett 1990a).

Habitat fragmentation will also result in changes to the composition of wildlife communities (e.g. Ambuel and Temple 1983; Bennett 1987). The idea that small patches generally contain fewer species than large patches can be further refined into nested patterns of distribution. This implies that smaller patches will contain subsets of large patches, provided there is a consistent sequence of species loss because of fragmentation (Patterson and Atmar 1986; Boecklen 1997; Deacon and Mac Nally 1998; Gibb and Hochuli 1999). This is due to differences in species properties, such as body size (Wilcox 1980; Bennett 1990ab; Forman 1995), dispersal ability and area requirements or home range (Forman 1995), the degree of dependence on native vegetation (Saunders et al. 1991), and the original density of the species (Terborgh and Winter 1980), rendering some species more susceptible to fragmentation-induced extinction than others. Mammals often exhibit strong patterns of nestedness within fragmented landscapes because they are relatively immobile and usually occur at low densities (Deacon and Mac Nally 1998). A study by Bennett 1990a of mammal communities at Naringal, Victoria showed a nested pattern for species composition with increasing patch size, with species being added to the community in a relatively ordered sequence. Small patches were found to support introduced species and the most common native species, while uncommon species were only recorded in larger patches (Bennett 1990a). Bennett (1990a) also found that species with greater body size were more vulnerable to habitat fragmentation than smaller species.

Restrictions on population size and Minimum Viable Populations

The size of a patch will influence the possible size of the local population because of limited resources (Foley 1997). However, the number of individuals that can exist in a patch will also depend on the area requirements and social structure of that particular species. Larger patches are likely to contain larger populations of most species, making them less likely to suffer from demographic and environmental fluctuations and natural catastrophes (Soulé 1987). Smaller populations will be more susceptible to these fluctuations and may also suffer from reduced genetic variability, because of genetic drift and inbreeding depression, which in turn will reduce fitness (Soulé and Simberloff 1986; Lande and Barrowclough 1987). Many believe that demographic stochasticity is potentially a more important short-term danger for most small populations than reduced genetic variation (Shaffer 1981).

The concept of a minimum viable population (MVP) (Soulé 1980; Shaffer 1981; Soulé 1987) recognised that in order for a population to persist it needs to retain a large proportion of its original genetic variation for an extended length of time. Models suggest that preventing inbreeding depression in the short-term requires an effective population of approximately 50 individuals, while the minimum effective size of 500 individuals is required for long-term survival (Soulé 1980). However, like all generalisations, the rule of 50/500 is limited in its application for several reasons. Firstly, the rule only considers genetics in isolation from environmental factors (Shaffer 1981). Much larger populations are required to survive environmental stochasticity, such as droughts, floods, fire, changes in weather or disease (Belovsky 1987; Goodman 1987). Distribution and life history parameters that influence genetic variability will also differ between species (Lande and Barrowclough 1987). Thus, the MVP of a species is individualistic and will differ markedly between species.

Metapopulation Dynamics

When a landscape becomes fragmented, species that inhabit the area will exist as a series of populations isolated within patches of habitat by a largely inhospitable matrix. These local or sub- populations together make up the overall regional population. In general, populations that reside in small habitat patches are more susceptible to external disturbances and random variation, making them vulnerable to wide fluctuations in density. Extinction and colonization are likely to become dominant processes, with small sub-populations going extinct more often, and relying on recolonization for survival. However, as long as individuals are able to move between sub-populations, to supplement declining populations with new genes, the regional population should become more stable and persist longer (Simberloff and Cox 1987; Nee and May 1992; Sarre *et al.* 1994; Harrison and Taylor 1997; Bennett 1998). This concept of divided

populations being linked through dispersal is commonly referred to as metapopulation dynamics (Hanski 1991; Hanski and Gilpin 1991; Opdam 1991).

The term 'metapopulation' was introduced by Levins (1969), who defined a metapopulation as a set of local populations that are able to persist through a balance between local extinction and colonization. However, natural populations have a variety of different structures (Harrison and Taylor 1997), leading to Levins' original definition becoming known as a 'classical' or idealised metapopulation. Recently, models have been developed that include spatially structured populations (Hanski and Simberloff 1997; Harrison and Taylor 1997). These models have become useful for describing the spatial configuration of sub-populations for species persisting in fragmented landscapes (Arnold et al. 1993). The 'island-mainland' model (Hanski and Gilpin 1991), is based on a network of habitat patches or islands located within dispersal distance from a large mainland patch or source population (Hanski and Simberloff 1997). In this model the mainland population will never become extinct, however, extinction and recolonization of sub-populations may occur within the surrounding habitat islands (Hanski and Simberloff 1997). The second model is based on a system of isolated sub-populations with each population having a defined likelihood of extinction (Merriam 1991; Opdam 1991). For this model, patch characteristics, such as size and configuration will determine the likelihood of extinction while the structure and composition of the surrounding matrix will influence recolonization (Forman 1995; Bennett 1998). Other models include source-sink metapopulations where some patches will have positive growth rates, and thus a surplus of individuals able to colonize other patches (sources), while other patches will suffer from negative growth rates, requiring immigration from source populations (sinks) (Donovan et al. 1995; Dias 1996; Hanski and Simberloff 1997).

Clearly, metapopulation dynamics shares key underlying elements with the theory of island biogeography (MacArthur and Wilson 1967), with the subdivision of nature into discrete entities, with individuals dispersing among relatively unstable populations (Andrén 1994; Hanski and Simberloff 1997). There is also a distinct difference – the theory of island biogeography deals with communities using species richness, while metapopulation dynamics deals with individual species (Hanski and Simberloff 1997). A shift away from the theory of island biogeography as a dominant paradigm in conservation biology has corresponded with an increased interest in metapopulation dynamics (Merriam 1991; Hanski and Simberloff 1997). Despite this, there have been few studies of metapopulation dynamics that have been applied to fragmented environments, with most metapopulation models remaining untested (Hanski 1997). Although the number of empirical studies is increasing, metapopulation dynamics has been adopted by many without evidence that it truly represents situations occurring in nature (Simberloff et al. 1992).

Corridors and Connectivity

Fragmentation creates patches of habitat that are spatially separated by a modified and often alien environment. Many forest dependent species may be unable to move through this modified environment causing isolated populations. Increasingly, studies in fragmented environments are focusing on elements that improve landscape connectivity.

Much of this attention has centred on habitat corridors, which can be defined as elements of linear habitat that differ from the surrounding vegetation, and connect two or more patches of similar habitat, that were historically connected (Soulé and Gilpin 1991; Hobbs 1992). Corridors are believed to be beneficial in fragmented landscapes by adding to the amount of available habitat (Bennett 1990a; Loney and Hobbs 1991), allowing movement and dispersal between otherwise isolated populations (Bennett 1990a, Saunders et al. 1991), increasing immigration rates (Kitchener et al. 1980; Bennett 1987; Dunning et al. 1995) (otherwise known as the 'rescue effect' – Brown and Kodric-Brown 1977), and helping to maintain ecosystem functions, such as water quality and reduced wind, soil and water erosion (Bennett 1990a; Loney and Hobbs 1991).

Studies have shown a wide variety of species occur in corridors and will use corridors to travel through otherwise unsuitable habitat (Bennett 1990a). Corridors are capable of facilitating a variety of forms of animal movements, which can occur at a range of spatial scales (Bennett 1990a, 1992). Movements through corridors can be daily or regular (e.g. Saunders and Ingram 1987; Arnold et al. 1991; Arnold et al. 1993; Bennett et al. 1994; Goosem and Marsh 1997), dispersal movements between habitat patches or populations (Suckling 1984; Bennett 1990b; Abensberg-Traun 1991; Prevett 1991; Saunders and de Rebeira 1991; Beier 1995; Haas 1995; Machtans et al. 1996; Sutcliffe and Thomas 1996), seasonal (e.g. utilisation of resources that display temporal variation) (Date et al. 1991), or migratory movements and occasionally range expansion (Bennett 1991).

The capability of a corridor to enhance the survival of isolated populations will depend on characteristics of the corridor, such as the width (e.g. Arnold et al. 1987; Saunders and de Rebeira 1991; Saunders et al. 1991; Beier and Noss 1998; Sieving et al. 2000), shape, length (e.g. Beier and Noss 1998 Sieving et al. 2000), appropriate habitat (Soulé and Gilpin 1991) (i.e. vegetation quality, composition and structure e.g. Lindenmayer et al. 1993a; Bennett et al. 1994; Lindenmayer et al. 1994), and intensity of edge effects (Yahner 1988; Angelstam 1992; Bierregaad et al. 1992), as well as the movement capabilities of the species (Forman 1995; Brooker et al. 1999).

Although there is little doubt that habitat connectivity is a necessary element in maintaining fragmented populations, the idea that corridors are both effective and advantageous has not been uncritically accepted (Hobbs 1992; Simberloff *et al.* 1992). Critics of corridors have concentrated their concerns around three main points: insufficient scientific evidence demonstrating the benefits of corridors; there may be negative effects that outweigh any benefits; and corridors may not be the most cost effective option of using limited conservation resources (Bennett 1998). Reported disadvantages include increased immigration rates, which in turn may facilitate the spread of disease (Simberloff and Abele 1982) or introduced pest species (Simberloff *et al.* 1992) and decreased individual fitness due to 'outbreeding depression' (Simberloff and Cox 1987). Corridors may also increase exposure of wildlife to hunters and other predators (Noss 1987), act as a 'sink habitat' where mortality exceeds reproduction (Bennett 1998), and facilitate the spread of abiotic disturbances (e.g. wildfire) (Simberloff and Abele 1982).

Direct evidence supporting the effectiveness of corridors in providing connectivity is limited, with the majority of studies involving small closely spaced patches (Suckling 1984; Bennett 1990a), and focal species with greater movement abilities than the areas and corridors used within the study (Beier and Noss 1998). Nevertheless, Beier and Noss (1998) reviewed evidence and concluded that well-designed studies suggested that corridors are valuable tools for conservation. In general, the relative merits of corridors and their required characteristics (i.e. width) are likely to vary depending on the ecosystem and the species being targeted for conservation (Saunders *et al.* 1991).

Edge Effects

'Edge effect' is a term used to describe a diverse group of interactions that occur at the ecotone between two distinct habitats. Edge effects may occur naturally, where two major habitat types connect (Harris 1988), or as a result of land clearing and habitat fragmentation, where native vegetation adjoins a highly modified environment, such as forest and farmland (Laurance 1991b). Studies have shown a range of physical and biological effects that occur along edge habitats, which in turn can affect wildlife, either directly or indirectly through changes to habitat (Harris 1988; Yahner 1988; Angelstam 1992; Bierregaard Jr. *et al.* 1992). The effects of human-induced edges are summarised below.

Edge effects can be loosely divided into either physical or biotic changes associated with patch edges where forests adjoin cleared lands. Physical or microclimatic changes include increased solar radiation, wind speeds, light levels, temperatures and altered humidity and leaf-litter

moisture levels (Lovejoy *et al.* 1986; Saunders *et al.* 1991; Hobbs 1992; Chen *et al.* 1995; Laurance *et al.* 1998). Edge habitats also take the brunt of human-induced disturbances resulting from activities in adjacent developed land (Bennett 1998). These disturbances may include drift of fertilizers and chemicals, compaction of soil and grazing by domestic stock, control burns and fires, access tracks and recreational disturbance and littering (Bennett 1990a; Bennett 1998).

Changes in the structure and composition of plant communities at the edge of patches arise in response to the altered microclimatic conditions discussed above. Altered wind and water regimes redistribute the fertilizers across the landscape and into remnant vegetation. Increased nutrient levels can alter the growth patterns of the native vegetation and provide increased opportunities for weed invasion (Hobbs and Saunders 1993), which in turn can alter fuel loads and therefore fire regimes (Panetta and Hopkins 1991). The transfer of nutrients to remnant bush has also been identified as a potential factor in the increased level of rural tree dieback, caused by the increased abundance of defoliating insects (Landsberg *et al.* 1990).

Changes in plant communities and habitat structure will lead to altered habitats for animals (Bennett 1998), having important consequences for biological communities (Yahner 1988). The composition of species within edge habitat will be largely determined by the capability of individual species to adapt to edge related changes (Laurance and Bierregaard Jr. 1997). Laurance (1990) found that along tropical rainforest edges in north Queensland, arboreal mammal species such as the coppery brushtail possum, *Trichosurus vulpecula* and the green ringtail possum *Pseudocheirops archeri*, which feed on a number of successional plant species persisted in edge habitat, while the lemuroid ringtail possum *Helibelideus lemuroides*, which feeds on mature-phase rainforest leaves declined. Edge adapted species and introduced species typical of disturbed environments may compete with interior species for food and shelter resources, or completely exclude them from edge habitat altogether (Loyn 1987; Laurance 1994; Goosem 2000). The exploitation of edge habitat by small mammals, *Melomys cervinipes, Rattus leucopus* and *Antechinus flavipes*, has excluded other species along the edges of tropical rainforest in Queensland (Laurance 1994; Goosem 2000). In south-eastern Australia, the noisy miner *Manorina melanocephala*, a bird that favours open woodlands and utilises forest edge habitat, displays territorial aggression towards small insectivorous birds. Small patches in which noisy miners are present have lower bird species richness than sites where they are absent (Loyn 1987). Species residing in edge habitats may also face increased levels of predation and parasitism (Yahner 1988). Studies of predation on birds' nests have shown significantly higher levels of predation at forest edges compared to the patch interiors (Andrén and Angelstam 1988; Yahner and Scott 1988).

The distance that edge effects extend into a patch will ultimately depend on the shape and area of the fragment, with small and thin elongated patches having a higher proportion of edge habitat than large or round patches (Diamond 1975; Saunders *et al.* 1991), and the particular characteristics of the effect itself (Yahner 1988; Laurance 1991b; Chen *et al.* 1992; Bennett 1998). For example, edge widths in Douglas-fir *Pseudotsuga menziesii*, forests range from 16 m to 136 m deep for vegetation variables (Chen *et al.* 1992), and from 30 m to 240 m for microclimatic variables (Chen *et al.* 1995).

Matrix Effects

Although habitat fragmentation implies a loss of the natural habitat, it also means an increase in the area of new habitat (Angelstam 1992; Andrén 1994), often referred to as the matrix. The matrix may often influence the structure and dynamics of communities within patches (Laurance 1990, 1991; Bierregaad *et al.* 1992; Malcolm 1991, 1997; Bierregaard and Stouffer 1997; Tocher *et al.* 1997; Warburton 1997; Laurance and Laurance 1999). Unlike 'true islands' the developed land surrounding habitat 'islands' is not completely inhospitable, and will support a different flora and fauna community (Saunders *et al.* 1991). For example, 8-25% of all frog, bird, small mammal and ant species recorded in the Biological Dynamics of Forest Fragment Project (BDFFP) study area in the Amazon, reside exclusively within the matrix (Gascon *et al.* 1999). Species that exist in the matrix, such as exotic plants and animals and native species that take advantage of the matrix may invade remnant habitat and compete or prey on patch inhabitants (Andrén 1994; Laurance 1994; Brown and Hutchings 1997; Malcolm 1997; Tocher *et al.* 1997). Patch residents that are not able to tolerate increased levels of disturbance are likely to decline, while more resilient species or those that are able to take advantage of the changed conditions may increase (Brook *et al.* 2003; Cox 2003).

The type of matrix habitat will strongly influence landscape connectivity, the intensity of edge effects, species invasions, and the frequency and intensity of disturbances (Laurance *et al.* 2002). In general, the more closely the matrix resembles the structure and microclimate of the primary forest within patches, the more likely that fragmentation-sensitive species will be able to utilise it (Laurance *et al.* 2002). Stouffer and Bierregaard (1995) showed that edge avoidance by birds was reduced when patches were surrounded by regrowth rather than open pasture.

The ability for species to use the matrix surrounding patches will affect their vulnerability in fragmented landscapes (Gascon *et al.* 1999). Empirical studies have shown that species that avoid the matrix will decline or disappear from patches, while species that are able to tolerate or exploit the matrix will often remain constant or increase (Laurance 1990, 1991a, 1994, 1997;

Malcolm 1991; Laurance and Laurance 1999; Laurance *et al.* 2002). For example, Laurance and Laurance (1999) found the matrix-avoiding lemuroid ringtail possum was the species that suffered the greatest effects of habitat fragmentation. The long-term persistence of populations within habitat patches will be determined by the species' ability to cross the matrix (Laurance 1991a; Laurance 1997; Pavey 1998; Gascon *et al.* 1999). Differences in species' abilities will lead to altered species composition. Over time, small fragmented communities are likely to be dominated by generalist species that tolerate the matrix, disturbance-adapted opportunists, and species with small area requirements (Laurance *et al.* 2002).

·OPEN WOODLAND·

·OPEN WOODLAND·

·TROPICAL SAVANNAH·
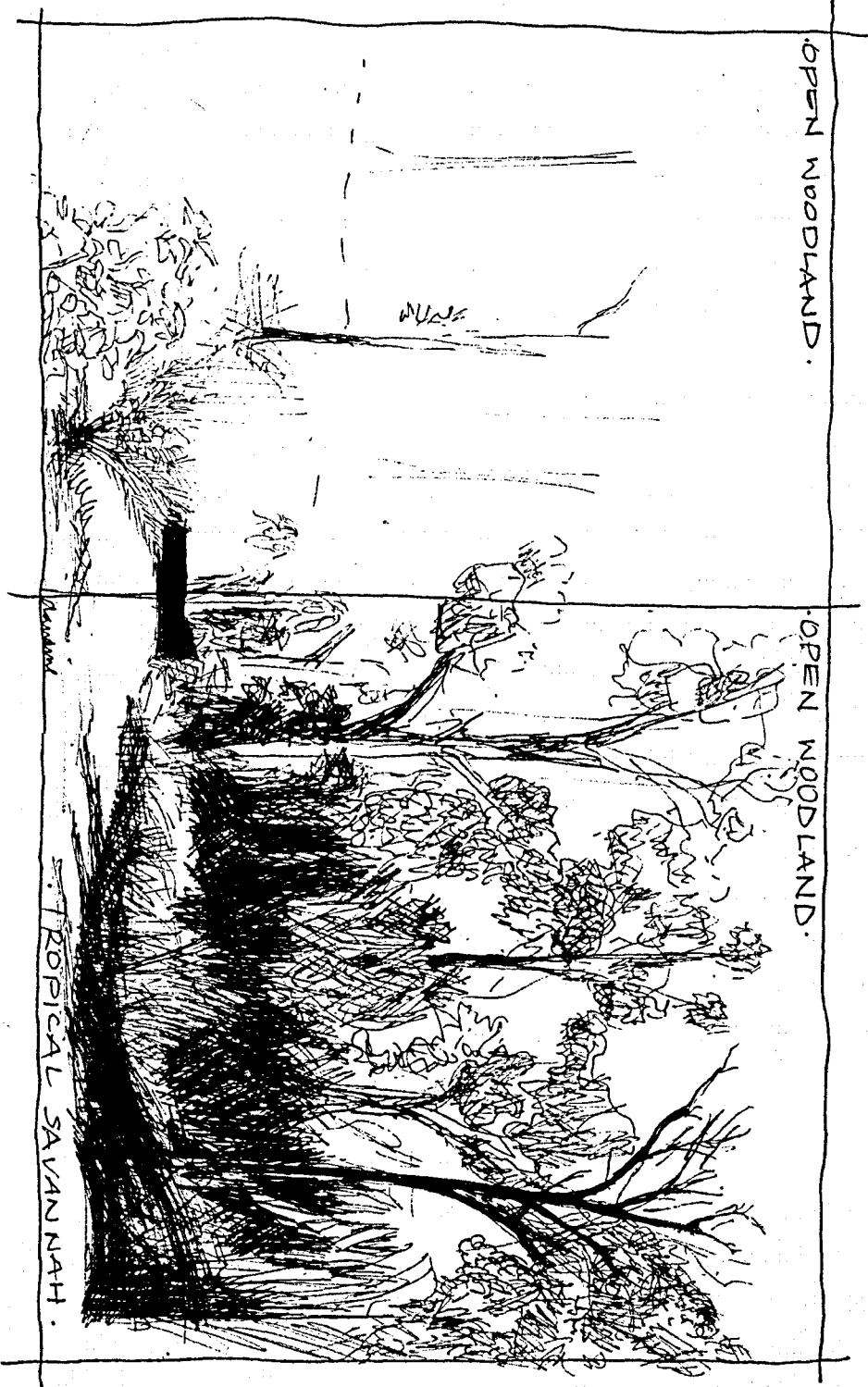
CHAPTER 2

Australia's Tropical Savannas: An Overview

Tropical Savannas

Defined as any tropical community characterised by a continuous herbaceous layer with a discontinuous tree and/or shrub layer (Bourlière and Hadley 1983; Sarmiento 1984; Johnson and Tothill 1985; Cole 1986; Solbrig 1996), tropical savannas differ from other ecosystems because of the dual significance of grasses and woody vegetation (Huntley and Walker 1982; Walker 1985). Savanna vegetation occupies approximately 40% (23 million km^2) of the world's tropics, including areas in Central and South America, Africa, India, southeast Asia and Australia (Cole 1986) (Figure 2.1). Spanning the landscape between rainforests and deserts, savannas are the result of a distinctive seasonal wet/dry climatic pattern (Johnson and Tothill 1985; Fox et al. 2001). In covering such large areas, rainfall extent and seasonality, or the length of the dry season, are the major determinants of the type of vegetation that will occur. Open shrublands and grasslands dominate areas with lower precipitation while woodlands and open forests occur in areas of high precipitation (Solbrig 1996).

Tropical savannas are some of the world's most important wildlife ecosystems. The savannas of Africa and Asia contain a rich diversity of mega-herbivores and predators, with the savannas of East Africa containing the largest diversity and biomass of large herbivores and their predators in the world (Cox 1997). In contrast, Australian and South American savannas have few large herbivores, but support a large proportion of endemic fauna (Cox 1997).

Frequent fire is characteristic of savanna ecosystems worldwide and is an integral part of the cultural and ecological landscape (Dyer et al. 2001). The frequent occurrence of fire is the result of an annual cycle of abundant herbaceous production during the wet season, followed by seasonal drought (Huntley and Walker 1982; Andersen 2003). Frequent fires have played an integral role in the evolution of savannas around the world and have been a major factor in the development of savannas from other vegetation types (Dyer et al. 2001; Andersen 2003).

Savannas in all areas except perhaps Australia contain a large and rapidly growing human population that is placing these ecosystems under threat (Werner 1991; Cox 1997). Most savannas are experiencing increased land use pressures, exposed to large-scale changes for agricultural development and changed fire regimes.
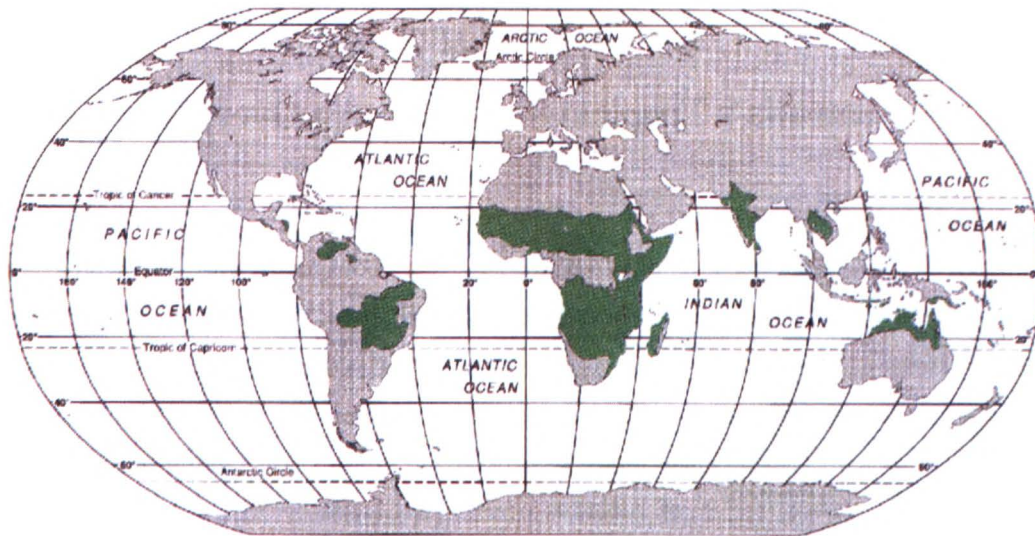
Figure 2:1: Location of the world's tropical savannas, indicated in green (taken from Cox 1997).

Australian Savannas

In Australia, tropical savannas cover approximately one-fifth of the continent (see Figure. 2.3), approximately 190 million hectares (Fox *et al.* 2001), and occur in a wide continental arc that includes the coastal and sub-coastal areas from south-eastern Queensland across northern Australia (Mott *et al.* 1985; Holmes 1996; Solbrig 1996). They have a dense tall-grass understorey of variable floristic composition with an upper stratum dominated by *Eucalyptus* species (Mott *et al.* 1985). In general, the world's savannas occur on old, weathered soils, poor in nutrients (Cole 1986; Walker 1985; Solbrig 1996). This is also the case in Australia (Walker and Gillison 1982; Gillison 1983; Fox *et al.* 2001), where in some areas leaching of nutrients from the soil during the wet season further reduces the productivity of the soils (Fox *et al.* 2001).

The climate is highly seasonal with an extended dry season over winter (May-September) and a short, but predictable wet season in summer (December-March). There is a buildup in humidity during October-November before the onset of the wet season, with the reverse occurring during April (McDonald and McAlpine 1991). Temperatures are generally high year-round with higher relative humidity during the wet and higher rates of evaporation during the dry season (McDonald and McAlpine 1991).

Vegetation

When compared to southern Australia, the tropical savannas of the north are relatively intact and in good ecological condition (Woinarski and Braithwaite 1990), and the natural vegetation remains extensive with limited modification (Woinarski and Dawson 2001; Woinarski et al. 2005). Eucalypt forests and woodlands dominate northern Australia extending over 180,000 km^2 in the Northern Territory (Wilson et al. 1990) (Figure 2.2). These forests are simple in structure and have similarity in species composition across a wide longitudinal range (Woinarski 1992; Woinarski et al. 2005). Strong rainfall gradients from higher rainfall in the north to lower less predictable rainfall in the arid areas of the south, and a complex distribution of soil types, are the driving forces influencing savanna composition and structure (Solbrig 1996; Williams et al. 1996). The tropical north also includes smaller areas of monsoon rainforest, often associated with areas of permanent water and/or areas protected from fire (Russell-Smith 1991). Areas of mangrove forests are associated with the coastline and intertidal areas of larger river systems, with extensive areas of open floodplain bordered by Melaleuca paperbark forests, which are typically inundated in the wet season (Figure 2.2).
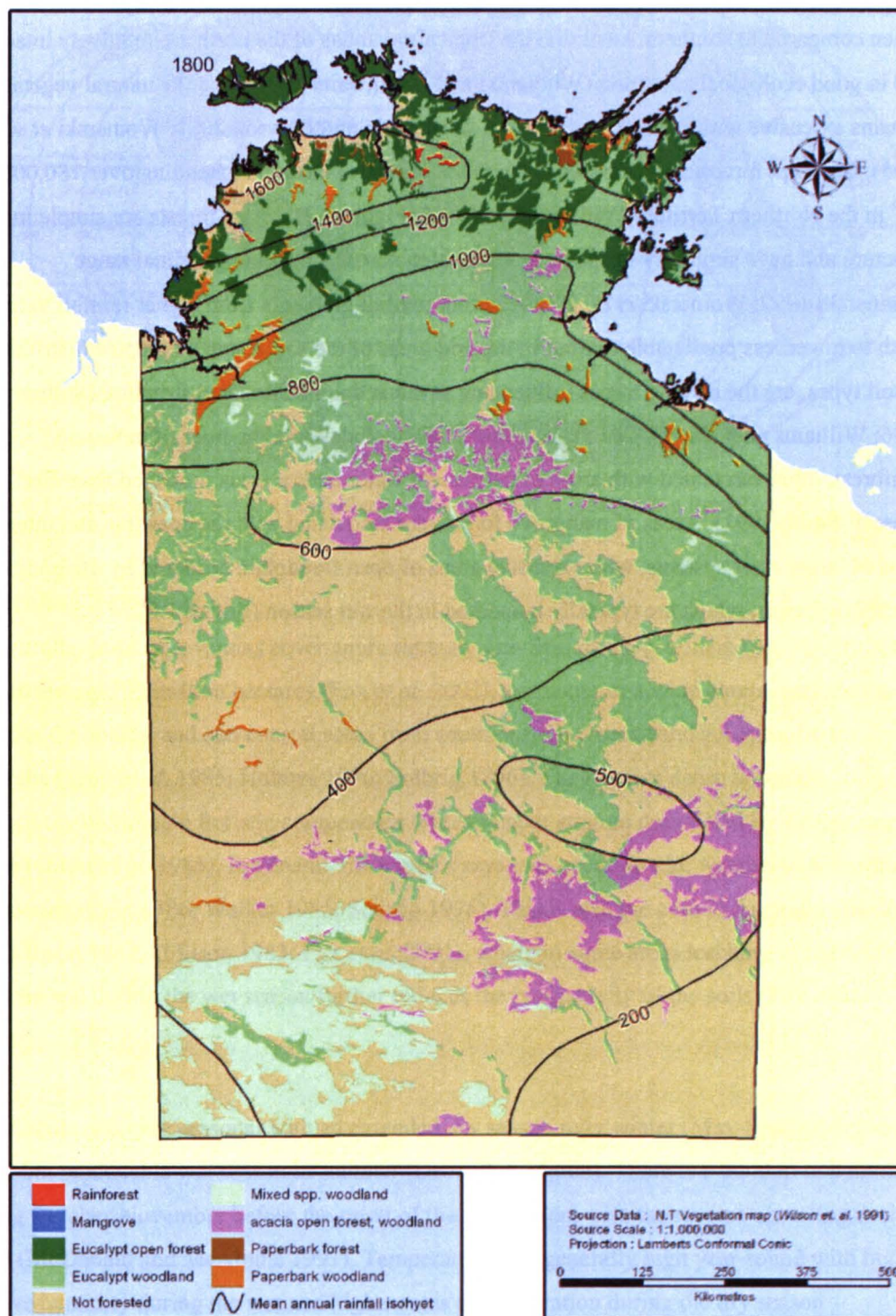
Figure 2:2: Location of broad forest communities within the Northern Territory.

Fire within Savanna Landscapes

Fire is an important ecological feature of savannas during the dry season, and like most Australian vegetation, the savannas are well adapted to regular burning (Huntley and Walker 1982; Walker and Gillison 1982). Primed for frequent fire with an extensive grass component that flourishes during the wet season, the tropical savannas of northern Australia have the largest and most frequent fires in the continent (Dyer *et al.* 2001) (Figure 2.3). Fire typically occurs annually or biannually at any one location (Braithwaite and Estbergs 1985; Russell-Smith *et al.* 1997) with up to 50% of the savanna landscape burnt each year (Russell-Smith *et al.* 1997; Gill *et al.* 2000; Edwards *et al.* 2001; Andersen 2003).
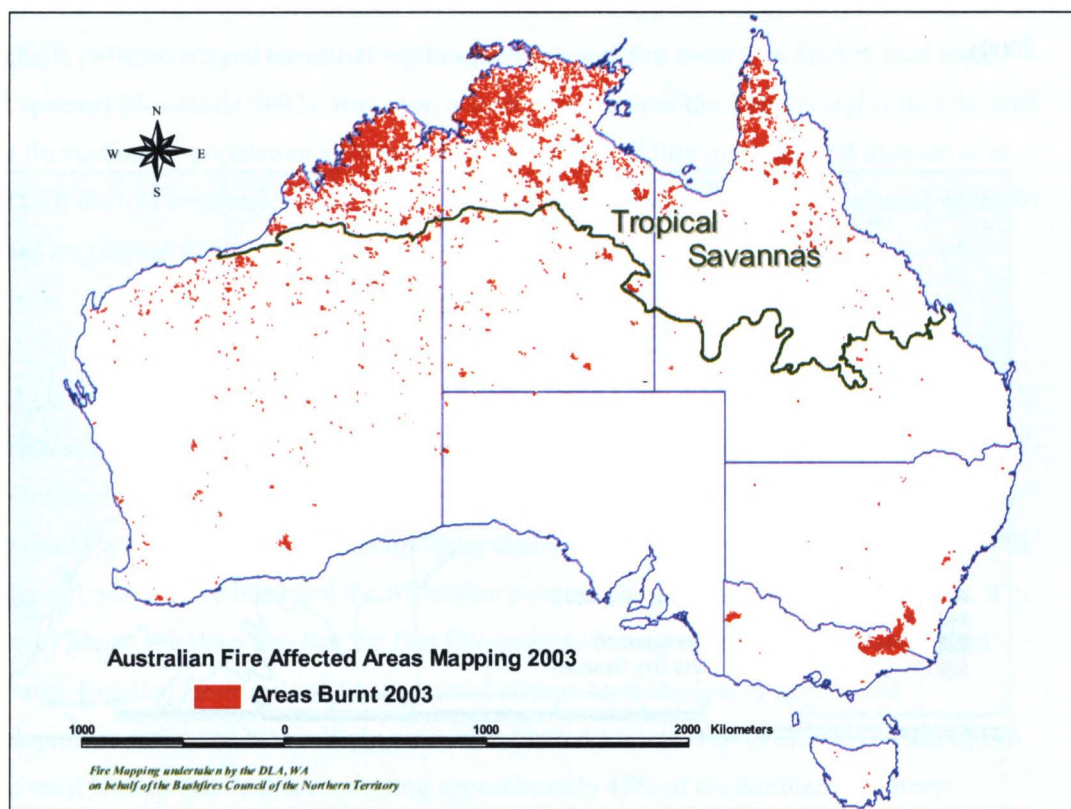
Figure 2:3: The location and extent of fires within Australia during 2003 (Map created by A. Edwards, NT Bushfire Council).

The effects of fire on vegetation will depend on the quantity and type of fuel available for combustion and the conditions under which the fire burns (Lacey *et al.* 1982). However in general, fires that occur in the early dry season (May-June) are low intensity leaving a mosaic of burnt and unburnt patches, while late dry season (July-October) fires are of greater intensity and more extensive (Lacey *et al.* 1982; Williams *et al.* 1999a).

Before the arrival of humans to the continent, lightning would have been the source of fire ignition (Stocker 1966). However, since Aboriginal people arrived on the Australian continent (approximately 50,000 years ago) fires have become mostly anthropogenic. Fire has been used by Aboriginal people for hunting, food gathering, signaling and ease of movement from place to place (Stocker 1966), and is an integral part of traditional Aboriginal lifestyle (Russell-Smith *et al.* 1997). Thus, burning by people has been an important part of the Australian savannas for tens of thousands of years. There is widespread agreement that since European settlement fire regimes in northern Australia have changed and fires are currently more frequent, intense and homogeneous than they were when Aboriginal people managed fire across the landscape (Lacey *et al.* 1982; Haynes 1985; Bowman and Panton 1993; Braithwaite 1996; Russell-Smith *et al.* 2000).
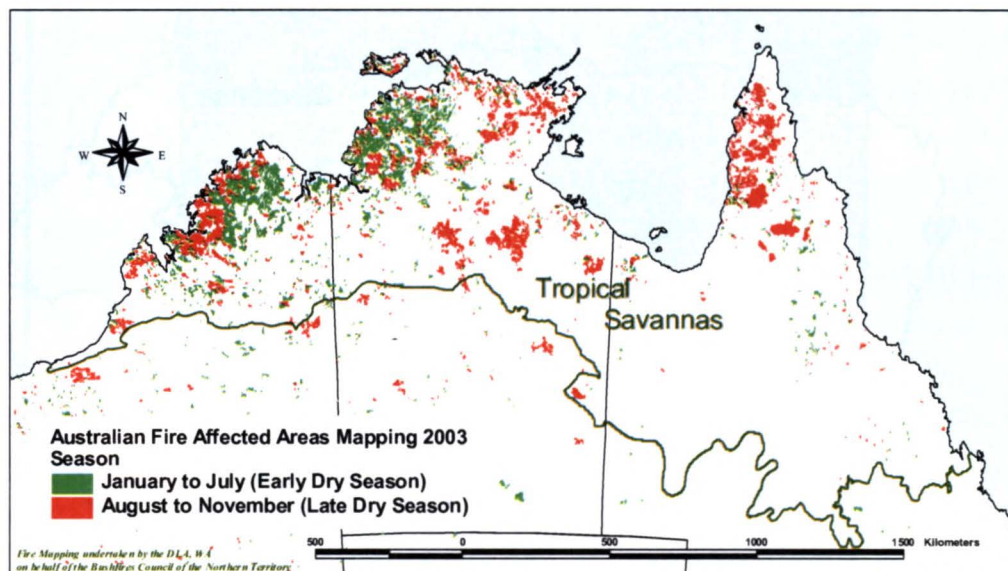
Figure 2:4: The location and extent of early and late dry season fires within the Tropical savannas of Australia during 2003 (Map created by A. Edwards, NT Bushfire Council).

Evidence suggests that these new fire regimes are damaging fire sensitive vegetation communities, including cypress pine *Callitris intratropica* (Bowman and Panton 1993; Price and Bowman 1994); escarpment heath habitat (Russell-Smith *et al.* 1998), and monsoon rainforests (Russell-Smith and Bowman 1992), which in turn is affecting certain faunal assemblages (Woinarski 1992). However, the responses of the biota of northern Australia to different fire regimes remains poorly known (Andersen *et al.* 2003).

Vertebrate Fauna

Compared to southern Australia, the natural vegetation remains extensive with limited modification, and has not suffered the loss of species that has plagued the rest of the continent since European settlement (Woinarski and Braithwaite 1990; Braithwaite 1991; Woinarski 1992). While no species from this region are known to have become extinct in recent times (Woinarski 1992), there are clear signs of significant biodiversity declines (Braithwaite and Griffiths 1994; Franklin 1999; Woinarski 2000; Woinarski *et al.* 2001b).

The *Eucalypt* open forests and woodlands of monsoonal Australia are rich in vertebrate species. Covering around 15% of the continent, the area is home to approximately 40% of Australian's mammals (94 species) and terrestrial reptiles (269 species) and more than 50% of land birds (252 species) (Woinarski 1992). However, a large proportion of the fauna is highly mobile, with huge fluctuations in population a characteristic feature of wildlife in the area (Woinarski *et al.* 1992). Of the 615 vertebrate species known from the area, 133 species are endemic, of which 91 species are reptiles (Woinarski 1992).

Land Uses

In contrast to most of the world's savanna ecosystems, Australia's savannas have not experienced extensive use by humans (Gillon 1983). Despite their extensive range, tropical savannas support a mere 1% of Australia's population (~200 000 people; Lindsay 1996). While Aboriginal people have inhabited the Australian continent for approximately 50 000 years, it was only about 100 years ago that the first European settlers (graziers) arrived in Australian savannas. Isolation, poor soils and hot seasonal climate have resulted in agricultural developments within the biome having met with limited success (Fox *et al.* 2001). Pastoralism is the most widespread land use, covering approximately 45% of the Northern Territory (Hosking 2002). Other uses include mining, tourism, military, agriculture, nature conservation and traditional use by indigenous people (Tothill *et al.* 1985; Winter and Williams 1996). Around 40 % of the Northern Territory is Aboriginal land, with only 4% of the territory conserved in National Parks or reserves (Woinarski *et al.* 1992) (Figure 2.5). In recent times, land use pressures are increasing and land managers are confronted with an increasing need to understand the ecological processes of savanna ecosystems, so sustainable land management decisions can be made (Winter and Williams 1996).

	Urban / Rural (1%)		Aboriginal Land (42%)
	Crown land (6%)		Pastoral Land (46%)
	Defence Land (1%)		Conservation Reserve (4%)

Source Data : N.T Tenure 2004
Source Scale : 1:1,000,000
Projection : Lamberts Conformal Conic

0   125   250   375   500
Kilometres
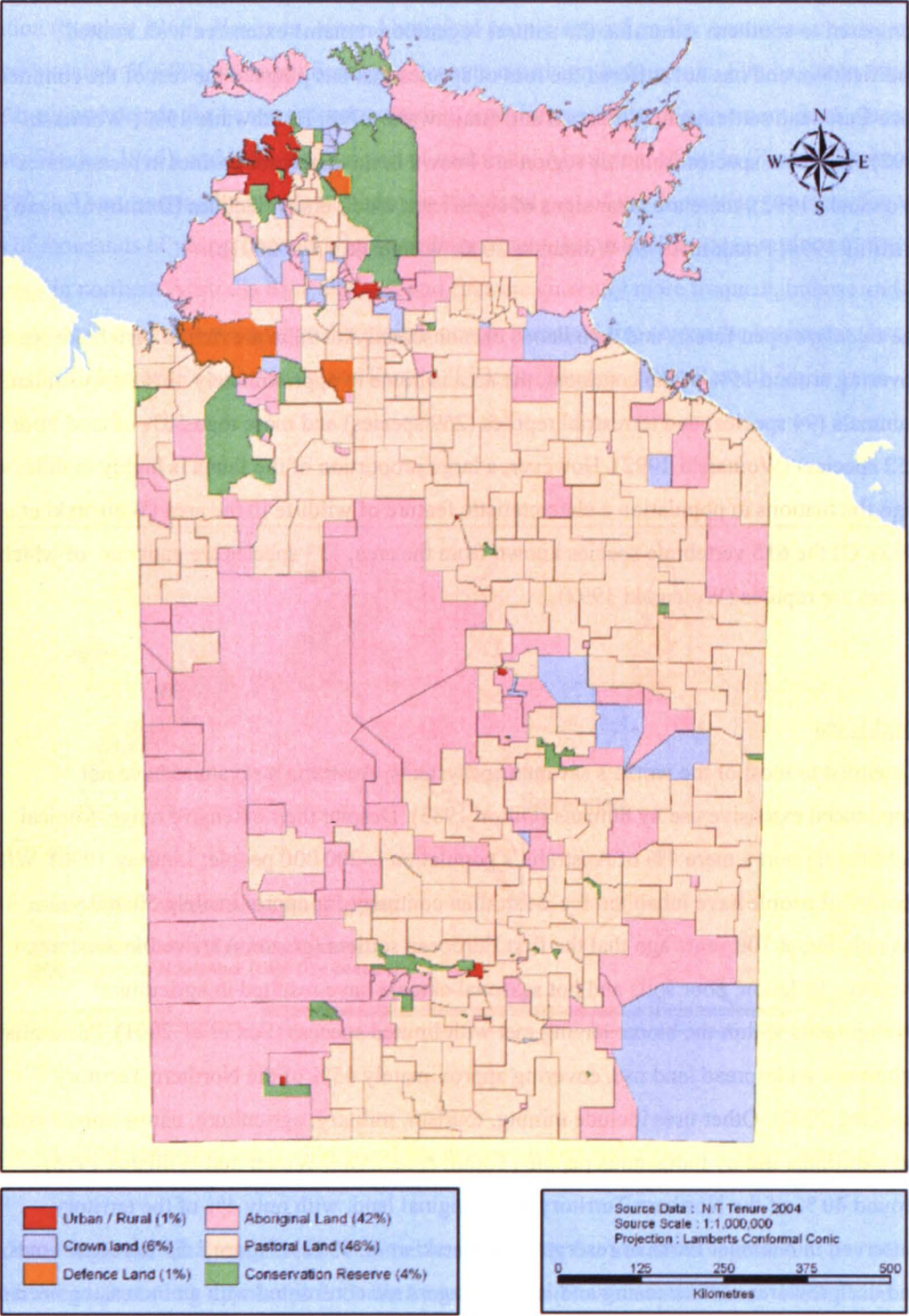
Figure 2:5: Location and percentage area of different land tenure in the Northern Territory.

Land Clearing

In Australia, the clearing of natural vegetation and habitat fragmentation is recognised as one of the principal threats to biodiversity (Williams *et al.* 2001). Agricultural development for stock grazing and crops has resulted in the clearing of vast areas of native vegetation (Saunders *et al.* 1991). In 2000 alone, over half a million ha of land was cleared in Australia, figures ranking Australia as the fifth highest country in the world in terms of the rate of land clearing (Williams *et al.* 2001).

In some regions of Australia, large scale clearing has resulted in particular ecosystems having been largely removed. For example, in the 140,000 km^2 wheatbelt of Western Australia, 93% of the native vegetation has been removed in the past 100 years, resulting in significant losses in native flora and fauna species (Saunders *et al.* 1993). In southern Queensland, brigalow *Acacia harpophylla* once covered more than 6 million ha. It has now been reduced to approximately 30,000 ha or 0.5% of its original cover, through clearing mostly in the 1960s (Conmmonwealth of Australia 1995).

In northern Australia, the destruction and degradation of the environment has been less pronounced than the rest of the continent. Fox *et al.* (2001) mapped changes in landcover for the region (Figure 2.6). As of 1997, 8.76 million hectares (4.61%) of the savannas had been cleared of native vegetation (Fox *et al.* 2001). As shown in Figure 2.6, most of this clearing has occurred in the south-east corner in Queensland, with limited patches across the rest of the area.
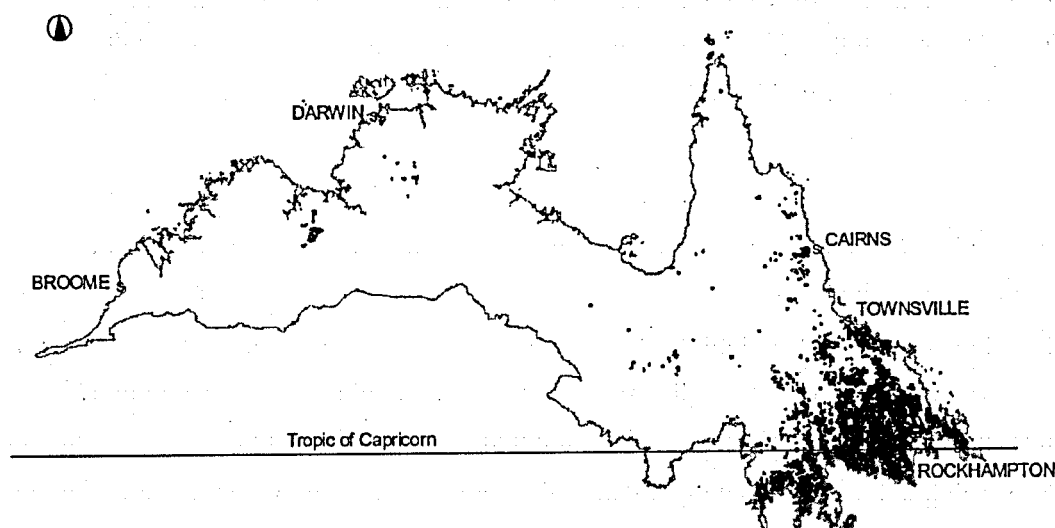
Figure 2:6: The extent and location of land clearing in Australian Tropical Savannas (taken from Fox et al. 2001).

Northern Territory

Since European settlement, the Northern Territory landscape has undergone limited land clearing. Containing approximately 20% of Australia's total extent of woodlands and forest (Woinarski 2004), the Northern Territory contributes less than 5% to the nation's land clearing. While trials of most agricultural schemes have failed in the past (Baskinski *et al.* 1985), in recent years this has changed with opportunities now emerging to exploit expanding markets for agricultural products (Brock 2001).

Although less than 0.5% of land within the Northern Territory has been cleared, clearing has been significant in some regions, being concentrated in the three main areas of Melville Island, the Darwin rural area (Litchfield Shire) and the Daly Basin. About 193,655 ha (9.3%) has been cleared in the Daly Basin (Hosking 2002). In the Darwin-Litchfield area 220 km^2 (14%) has been cleared (PWCNT unpub. data), due to expansions in urban development along with infrastructure development and expansion of the horticulture industry (Brock 2000). A number of extensive agricultural developments has been proposed or are being investigated for the Northern Territory, involving the Daly, Ord, Roper and Adelaide River catchments. This would see clearance of native vegetation on a scale not yet experienced in the region.

The first native vegetation clearing controls for freehold and Crown land in the Northern Territory were introduced in December 2002. Prior to this, no approval was required to clear native vegetation on freehold land, except in Litchfield Shire where approval was needed to clear more than 50% of a property. The new clearing controls require landholders to obtain a permit if they wish to clear more than 1 ha of native vegetation. This applies to freehold and Crown land greater than 2 ha, and excludes pastoral leases which are covered by similar controls under the Pastoral Land Act (1998).

This Study

Significance of this study

There is a substantial body of information for temperate Australia on the ecological effects of land clearing and fragmentation. Here I present the first study of how these processes affect the fauna in the tropical eucalypt forests of the Northern Territory. This is one of few studies conducted in tropical Australia. In contrast to the restoration works elsewhere in Australia, we have a rare opportunity to enact clearing controls informed by the principles of ecological sustainability, thus ensuring long-term maintenance of the Territory's native biodiversity. The configuration of habitat patches capable of maintaining viable wildlife populations can be pre-

determined, with guidelines being put into place before vegetation clearance occurs. Although this project studies habitat fragments or remnants, these remnants are used as surrogates to determine from the biodiversity perspective how landscapes targeted for future clearing should be structured and managed.

In 1999, funding was granted by the Natural Heritage Trust for a research project addressing the opportunities discussed above. This project stemmed from the Conservation Plan for the Daly Basin Bioregion (Price et al. 2003b), with the realisation that there was little understanding of how the fauna of this area was coping with clearing and habitat fragmentation and how that fauna was likely to cope the proposed broad-scale agricultural developments. This project was set up as a PhD study as a collaborative venture between the Charles Darwin University and the Parks and Wildlife Commission of the Northern Territory (PWCNT).

Study Area

The study was conducted in two regions in the monsoonal north of the Northern Territory. The reasoning behind the use of the two locations is discussed in detail in site selection.

Litchfield Shire

Litchfield Shire contains the rural area surrounding Darwin, including Howard Springs, Humpty Doo, Lambell's Lagoon, Fog Dam and Berry Springs. Although the shire covers an area of 300 000 ha, nearly half of this area is affected by seasonal flooding (Brock 2001). The Shire is bounded by the Adelaide River in the east, the ocean to the north and west and the Coomalie Shire to the south (Figure 2.7). This study was concentrated around the rural townships of Humpty Doo and Berry Springs.

Tipperary Station

Tipperary is a large cattle station located in the Daly Basin bioregion (latitude -13.736, longitude 131.040) approximately 150 km south of Darwin (Figure 2.7). One of the larger cattle stations in the area, Tipperary covers approximately 2733 km^2. The property is bounded by the Daly River to the south, a road to the north and other pastoral properties to the east and west. The Daly Basin bioregion is recognised as a high priority in terms of conservation initiatives, because its current extent of national parks and reserves is low, and imminent changes in land-use are likely to diminish some conservation values, unless they are afforded greater protection (Price et al. 2003a).

Selection of Study Areas and Sites

The majority of the study was conducted in the Litchfield Shire on the outskirts of Darwin, but land clearing here is still only localised and mostly recent, with the majority of clearing within the past 10 years. In order to obtain sites where land clearing has been more extensive and less recent, sites were selected at Tipperary Station 150 km south of Darwin. This is the closest location to Litchfield Shire that has undergone land clearing on this scale, with much of the clearing occurring in the 1960s and 1970s (Figure 2.7). Although the distance between the two study areas is approximately 150 km, the eucalypt forests of this region show unusually high homogeneity across very extensive areas (Woinarski *et al.* 2005), and extend almost unbroken across a wide range (Wilson *et al.* 1990; Woinarski 2004).

An ordination of vertebrate species composition at all study sites with native vegetation was conducted to assess the compatibility of the two main study areas.

The ordination included all species recorded in the study, abundances were not transformed, with compositional similarity of sites compared using the Bray-Curtis similarity index, with 10 random starts (refer to Chapter 3 for details on data collection and specifics on ordination alaysis). The relationship of study area to the resulting ordination patterns was examined using ANOSIM (see Chapter 3 for details). The results showed no marked difference in vertebrate species composition between the study areas (Figure 2.8) (R = 0.012, P > 0.05). This finding supports the use of the Tipperary study area, despite the distance between the two areas.

Unlike fragmentation studies conducted in most other areas, one of the initial challenges for this study was obtaining enough sites that could be defined as fragments. Limited and mostly small-scale land clearing meant that many of the patches are small in size (the majority are less than 5 ha), and are isolated from other wooded areas by small distances.
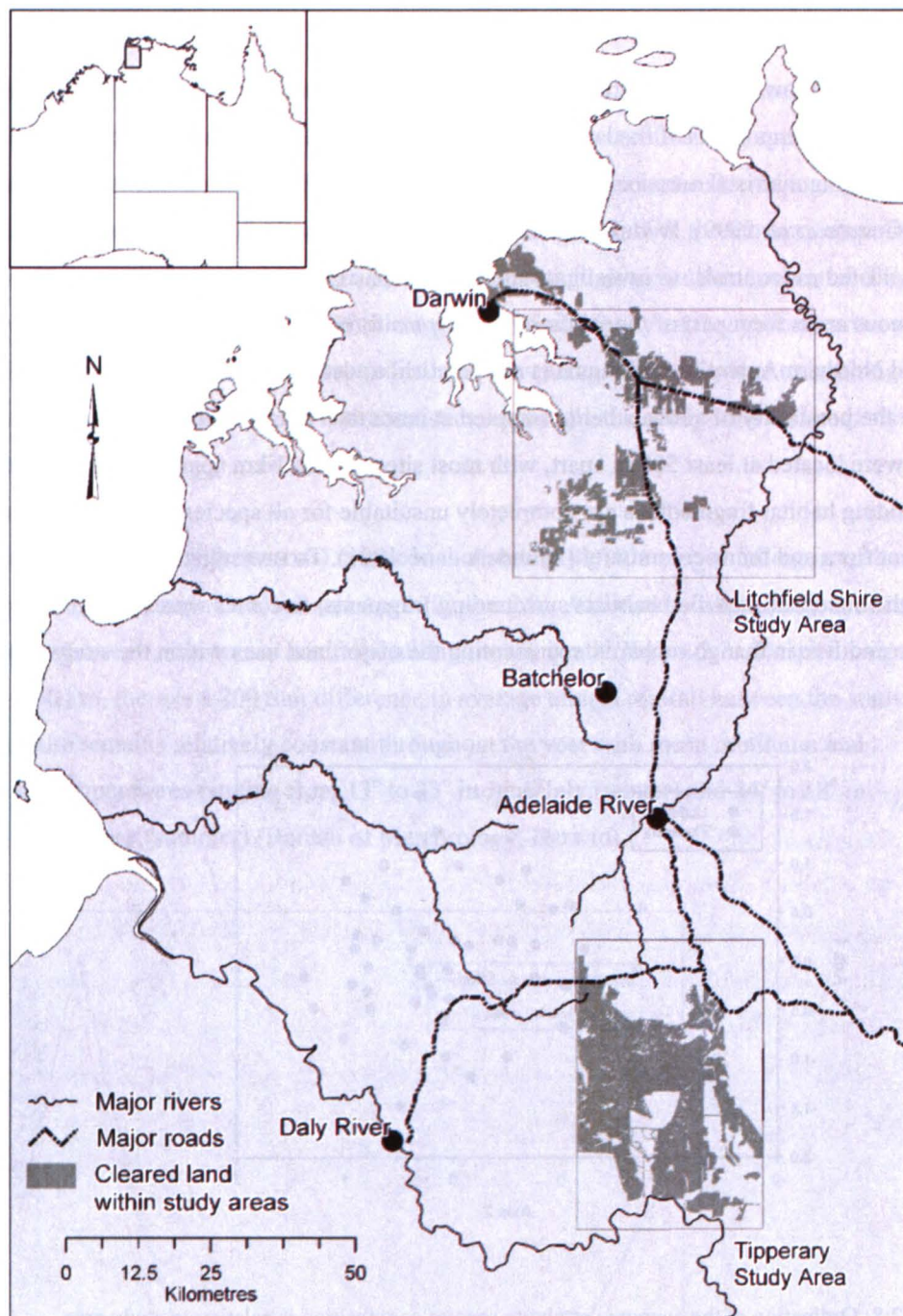
Figure 2:7: Location of the two study areas: Litchfield Shire and Tipperary Station, cleared area is dark grey.

Despite this, a total of 46 fragments of *Eucalyptus miniata/E. tetrodonta* forests were surveyed. Thirty-nine fragments were isolated from surrounding woodland by human-modified habitat and were not linked by corridors, which have been shown to mitigate the effects of fragmentation

for some species (Bennett 1990b; Laurance 1990). The other seven fragments were corridors of varying width (15 m – 100 m) and length (500 m to 7 km), that linked larger forested areas.

To understand how species are affected by fragmentation requires information on how they respond to all components of the landscape, i.e. habitat patches, areas of continuous forest and the intervening matrix (Laurance 1990; Laurance 1991a; Fahrig and Merriam 1994; Laurance 1994; Gascon *et al.* 1999). Within this study, seven sites in continuous intact *Eucalyptus* forest were selected as 'controls' to investigate species that may be absent from fragments. These continuous areas form part of the fabric of *Eucalyptus* forests that extend relatively intact across tropical Northern Australia, and thus it is not practical to define an exact figure for size. To reduce the possibility of animals being sampled at more than one site, sites within continuous forest were located at least 500 m apart, with most sites at least 1 km apart. Developed land surrounding habitat fragments is not completely unsuitable for all species, and will support a different flora and fauna community (Saunders *et al.* 1991). To investigate species capable of using the matrix of modified habitats surrounding fragments, five sites were surveyed in open pasture and five in mango orchards, representing the major land uses within the study areas.
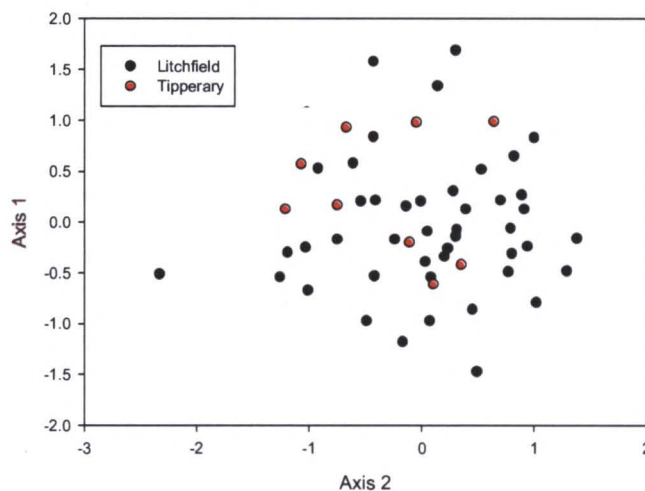
Figure 2:8: Ordination of the average vertebrate species composition in relation to study area.

Physical Environment

There is limited topographic variation within the study areas. The predominant landform at both areas is plain, with elevation ranging from 21 m in Litchfield Shire and reaching a maximum of 40 m above sea level at Tipperary. The surface is flat or gently undulating with slopes less than 3%. The soils of the Litchfield area are generally red and yellow massive earths (Wells and

Harrison 1978; Lucas and Czacharowski 1980; Lynch 1985). Sandy and sandy loam soils predominate and are often laterized.

The Daly Basin lies on a bed of Cambrian limestone and sandstone formations (Walpole *et al.* 1968), with surface formations of Cretaceous origin, associated with a long and variable history of deposition in the river basin (Price *et al.* 2003). The Daly area is considered to contain the largest area of soils suitable for crop production in the Top End, with the most common soils in the Basin being red earths, that are usually associated with high agricultural potential (Price *et al.* 2003). There are also large areas of siliceous sandy soils, sandy earths, yellow earths and podzols (often laterized). Many of these soils have low plant productivity due to leaching of nutrients, or unfavourable drainage characteristics, especially the sandy soils and podzols (Price *et al.* 2003).

The study area has a highly seasonal monsoonal climate with 90% of rain falling over the summer months, between October and April (Figure 2.9). A distinct rainfall gradient occurs across the area with total annual rainfall declining to the south (Figure 2.2). Despite a separation of only 150 km, there is a 200 mm difference in average annual rainfall between the study areas. Temperature remains relatively constant throughout the year with mean minimum and maximum temperatures ranging from 13° to 33° in June/July (winter) and 24° to 38° in December/January (summer) (Bureau of Meteorology, Darwin).
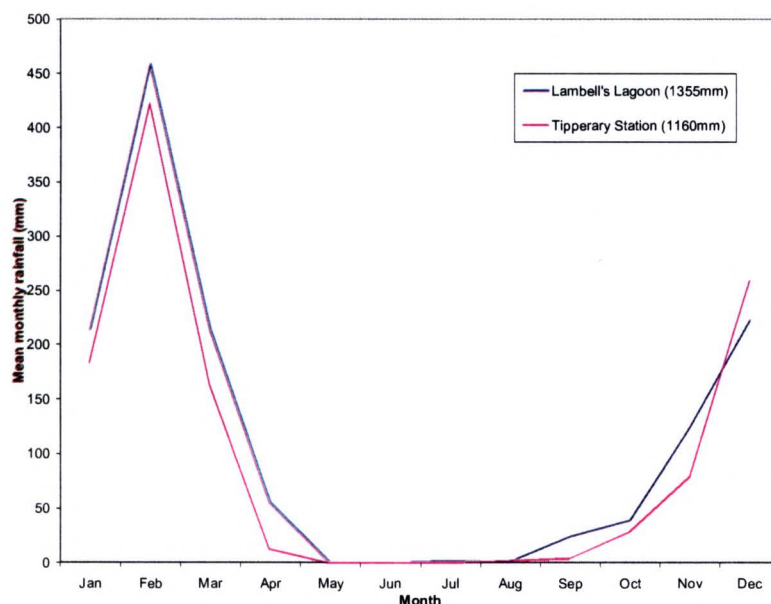
Figure 2:9: Mean monthly distribution of rainfall at the two study areas during the duration of the study (2001-2003). Mean annual rainfall for this period is given in brackets (Bureau of Meterology, Darwin).

Vegetation

Most land clearing in the Northern Territory occurs in the extensive Darwin woollybutt *Eucalyptus miniata* and Darwin stringybark *Eucalyptus tetrodonta* open forest, thus the study was confined to this vegetation type. As mentioned earlier, the eucalypt forests dominated by these two species extend over 180,000 km^2 in the Northern Territory (Wilson *et al.* 1990), and also cover large areas of northern Western Australia and northern Queensland (Woinarski 2004). These forests are simple in structure with a eucalyptus dominated canopy and a dense tall grass 'savanna" understorey and a sparse shrubby midlayer. The density and complexity of the midlayer is ultimately determined by the extent and frequency of fire at the site (Williams *et al.* 1999a; Woinarski *et al.* 2004).

Within the study areas the canopy is co-dominated by *E. miniata/E. tetrodonta*, with a scattering of other species including *Corymbi. bleeseri, C. porrecta, C. polycarpa, E. tectifica, C. foelscheana, C. confertiflora, C. polysciadia* and Ironwood *Erythrophleum chlorostachys*. The grassy understorey is dominated by perennial grasses, such as *Heteropogon spp.* and annual grasses like *Sorghum spp.* The midstorey contains a diverse array of fruiting shrubs that provide food resources for many vertebrate species, and include *Terminalia, Cycas, Pandanus, Planchonia* and *Livistona* species. The vegetation in the Tipperary area is structurally similar to that of the Darwin region, with high species overlap, but a variation in the dominant species at some locations.
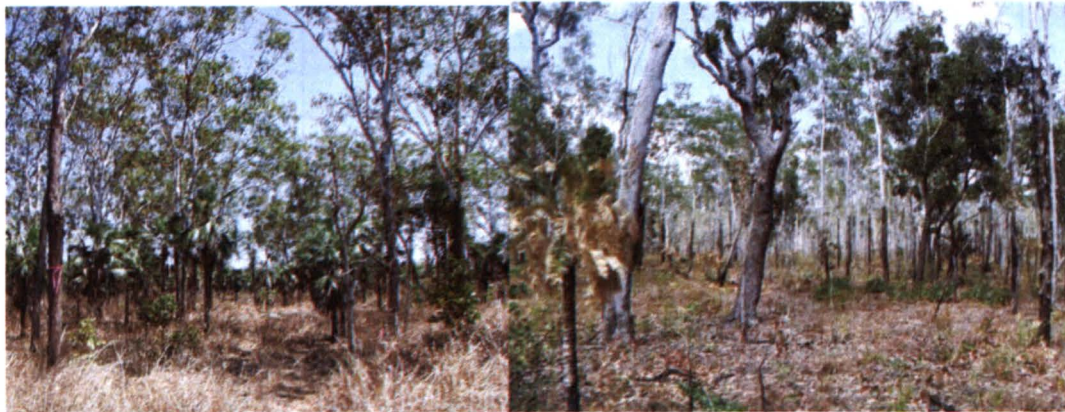
Figure 2:10: The typical habitat at (a) Tipperary and (b) Litchfield Shire.

Land uses

Urban expansion, infrastructure development and expansion of the horticultural industry account for significant vegetation clearing and recent increased rates of clearing in the Litchfield Shire (Whiteside 2000; Brock 2001). Horticulture is the main land use in the area with mango production dominating the industry, while other major crops include bananas and vegetable market gardens. As the dominant land use for this area, mango orchards were surveyed during the study (see chapter 3).

Pastoralism is the dominant land use in the Northern Territory and is the major land use at Tipperary Station. Tipperary has had a long history of agricultural development. The station was the site of the first large-scale clearing in the Northern Territory in 1967 (Hosking 2002). The large agricultural development scheme for grain sorghum production was a disaster (Woinarski and Dawson 2001). The scheme had initially planned to clear 79 000 ha over 5 years, however, poor management, and the unpredictable climate sent the company broke (Mollah 1980). An investment of $20 million for an expected annual production of 300 000 tonnes of grain sorghum, saw only 16 000 tonnes of sorghum harvested and approximately 10 000 ha of forest cleared, by the time the scheme was abandoned in 1973 (Woinarski and Dawson 2001). Further extensive clearing occurred on Tipperary in the late 1980s in areas with unsuitable landforms, which lead to erosion and land degradation, much of which remains in a poor condition (Brock 2001).

fragments

CHAPTER 3

Effects of Habitat Fragmentation on the Vertebrate Fauna of Eucalypt Open Forests in the Northern Territory

Most of this chapter has been published as:

Rankmore, B.R. and Price, O., (2004). "Effects of Habitat Fragmentation on the Vertebrate Fauna of Tropical Woodlands, Northern Territory." 2nd Ed. *Conservation of Australia's Forest Fauna*, edited by D. Lunney, Zoological Society of New South Wales.

Owen Price aided in the collection of field data and research design, provided advice on data analysis, created the connectivity index using GIS and supplied logistical support.

Introduction

There is no doubt that species will be lost locally when habitats become fragmented, but exactly which species depends on the size of the fragments, the mix of habitats they provide, the configuration of fragments in the vicinity and the management of the fragments (Saunders *et al.* 1991). The size of a patch will influence the possible size of the local populations. The number of individuals that can exist in a patch will depend on the area requirements and social structure of the species. Larger patches are likely to contain larger populations of most species, making them less likely to suffer from demographic and environmental fluctuations and natural catastrophes (Soulé 1987). Smaller populations will be more susceptible to these fluctuations and may also suffer from reduced genetic variability, because of genetic drift and inbreeding depression, which in turn will reduce fitness (Soulé and Simberloff 1986; Lande and Barrowclough 1987). The vulnerability of a particular animal or plant species will depend on many factors, including its ability to use the new habitat and to move among fragments (Laurance 1994; Gascon *et al.* 1999).

There is evidence that species loss from a landscape is slow in the early stages of habitat loss, and increases dramatically above a certain threshold (Andrén 1994; Fahrig 2001, 2002). A worldwide review of habitat fragmentation studies found that 30% habitat retention is a critical threshold below which species are rapidly lost from landscapes (Andrén 1994). The most likely reason for the threshold is that it occurs when landscape connectivity begins to break down and

movement and dispersal are interrupted, a conclusion supported by simulation modelling (Ims 1995; With and Crist 1995).

The effects of fragmentation can be reduced by the retention of habitat corridors between remaining fragments. Corridors are an important part of any fragmented landscape because they provide some species with habitat and also facilitate the movement of species between otherwise isolated populations (Bennett 1990b). Many studies have found that corridors are used by animals to move among fragments (Saunders and de Rebeira 1991; Haas 1995; Machtans et al. 1996). In a comparison of 20 fragmentation experiments, Debinski and Holt 2000) concluded that movement and species richness in fragments was positively affected by corridors and connectivity. However, corridors can also be avenues for invasion of disease, weeds and feral animals (Bennett 1990b). The linear shape of corridors also means that there is a high edge to area ratio, thus making corridors more susceptible to edge effects (Diamond 1975; Bennett 1990b; Saunders et al. 1991).

Although habitat fragmentation implies a loss of the natural habitat, it also means an increase in the area of new or modified habitats (Angelstam 1992; Andrén 1994). Some species will ultimately prosper from the modified habitats and thus there is no concern for their conservation. The fragments of habitat remaining in the Northern Territory following land clearing are not simply miniature versions of continuous woodland. The main difference is an increase in the amount of edge habitat, creating a diverse group of interactions that occur at the ecotone between two distinctly different habitats. These interactions are commonly termed 'edge effects' and may occur naturally, where two major habitat types connect (Harris 1988), or as a result of land clearing and habitat fragmentation. Studies have shown a range of physical and biological effects that occur along edge habitats, which in turn can affect wildlife, either directly or indirectly, through changes to habitat (Harris 1988; Angelstam 1992; Bierregaad Jr. et al. 1992).

Large-scale clearing of natural vegetation can modify radiation patterns and alter the fluxes of wind, water and nutrients across the landscape (Saunders et al. 1991; Hobbs 1992). These altered wind and water regimes can redistribute nutrients from agriculture across the landscape and into remnant vegetation. Increased nutrient levels can alter growth patterns of native vegetation and provide increased opportunities for weed invasion (Hobbs and Saunders 1993), which in turn alters fuel loads and therefore fire regimes (Panetta and Hopkins 1991). Many exotic plants have been introduced into northern Australia to increase pastoral productivity (Lonsdale 1994). The intentional establishment of exotic grasses and clearing of native vegetation has facilitated the spread of weeds into the remaining fragments (Fairfax and Fensham 2000), with many weed species being associated with areas of disturbance arising *

from human activities (Cowie and Werner 1993). The transfer of nutrients to remnant vegetation has been identified as a potential factor in the increased level of rural tree dieback, caused by an increased abundance of defoliating insects (Landsberg *et al.* 1990).

This Chapter describes a broad-scale investigation into the effects of habitat fragmentation on the vertebrate fauna of eucalypt open forests near Darwin in the Northern Territory. The study surveyed vertebrate species in open eucalypt forest fragments over a range of sizes and degrees of isolation, as well as continuous forest and completely modified sites. The specific aims of this chapter are:

- to determine the species that are capable of using the matrix of modified habitats within the area;
- to ascertain the species likely to use corridors;
- to evaluate the extent of edge effects on habitat structure and investigate impacts this may have on the vertebrate fauna.
- to determine the species that are affected by habitat fragmentation
- to determine which structural and landscape variables relate to the abundance of these species within a fragmented landscape.

Methodology

GIS Analysis

To select the study sites it was necessary to construct a map of all cleared land in the study areas. In the Tipperary area, aerial photographs were transferred into the GIS (1:50 000 scale, taken in 1994), and cleared areas were digitised onto the computer screen. In Litchfield Shire, aerial photographs (1:20 000 scale, from 1997) were used in conjunction with a GIS layer of property boundaries to classify each property as cleared, under horticultural use, a rural block (meaning that clearing is less than half of the property), or woodland (meaning no clearing could be seen). In larger properties (8 ha or more), cleared or horticultural areas were segregated from woodland within the property. Land clearing that has occurred since 1997 was added by referring to a Landsat 7 MSS satellite image from September 1999. Sites selected from the GIS imagery were then ground truthed to confirm vegetation type.

A range of fragmentation indices was calculated by GIS for each of the study patches. Three of the variables related to the estimated the percentage of woodland in the surrounding landscape, calculated from the central point of each fragment and measured in a circle around each fragment. The radii used by the three measures were 250 m, 1 km and 4 km. The area of the

fragment was not included in the estimate of woodland for the surrounding area. The amount of woodland within a 4 km radius of fragments (Bush 4 km) is mapped in Figure 3.1 for Litchfield Shire and Figure 3.2 for Tipperary. Similar measures have been used previously to investigate the distribution of species in patchy environments (Price *et al.* 1999; Fauth *et al.* 2000).

Connectivity with other woodland areas was estimated for each study site by calculating a least cost path from the site to all points on a circle, 2 km from the patch. In this method, we arbitrarily assumed that it is 10 times more costly to move across modified land than woodland. Cost is considered in terms of fitness: predation risk may be increased or food intake decreased by a factor of 10 in modified land compared to woodland. The GIS software calculates the route from the study site to all points on the circle minimising the cost rather than distance travelled. The actual route may be circuitous if corridors of woodland are present. Un-fragmented woodland gets a perfect score on this calculation, but fragments may come close to this score if there are many corridors and a large proportion of the circle perimeter is in woodland. Sites receive a low score if there were considerable blocks of modified land that had to be crossed to get to the perimeter.
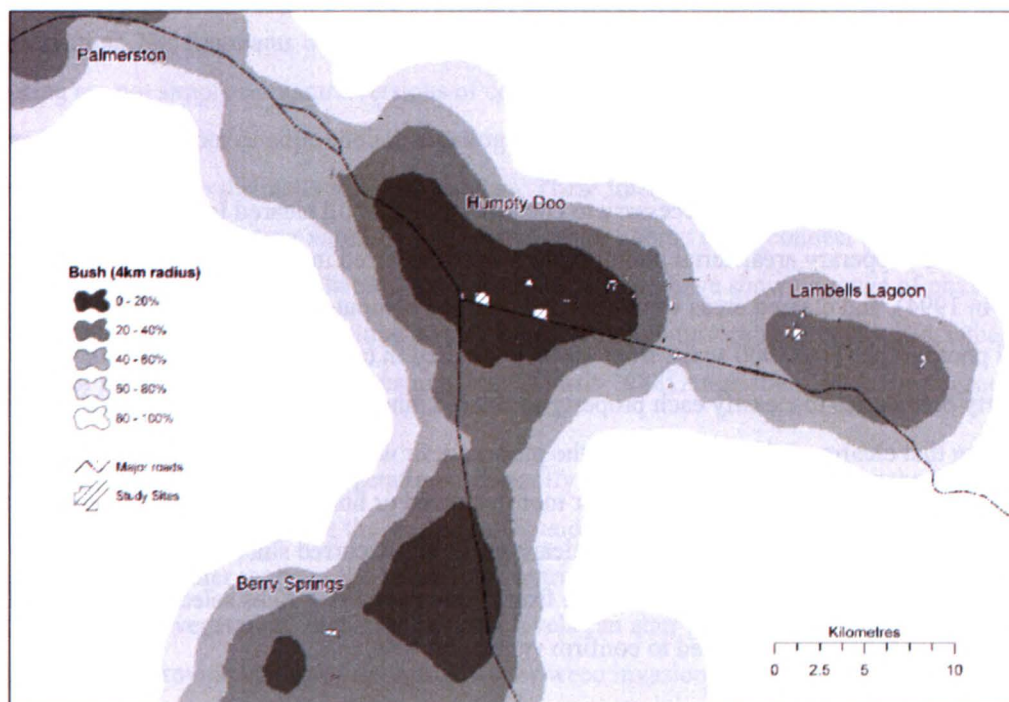
Figure 3.1: The amount of woodland within a 4 km radius of study sites (Bush 4 km) at Litchfield Shire. Dark grey = 0-20%, White = 80-100% of landscape. Roads and study sites are superimposed.
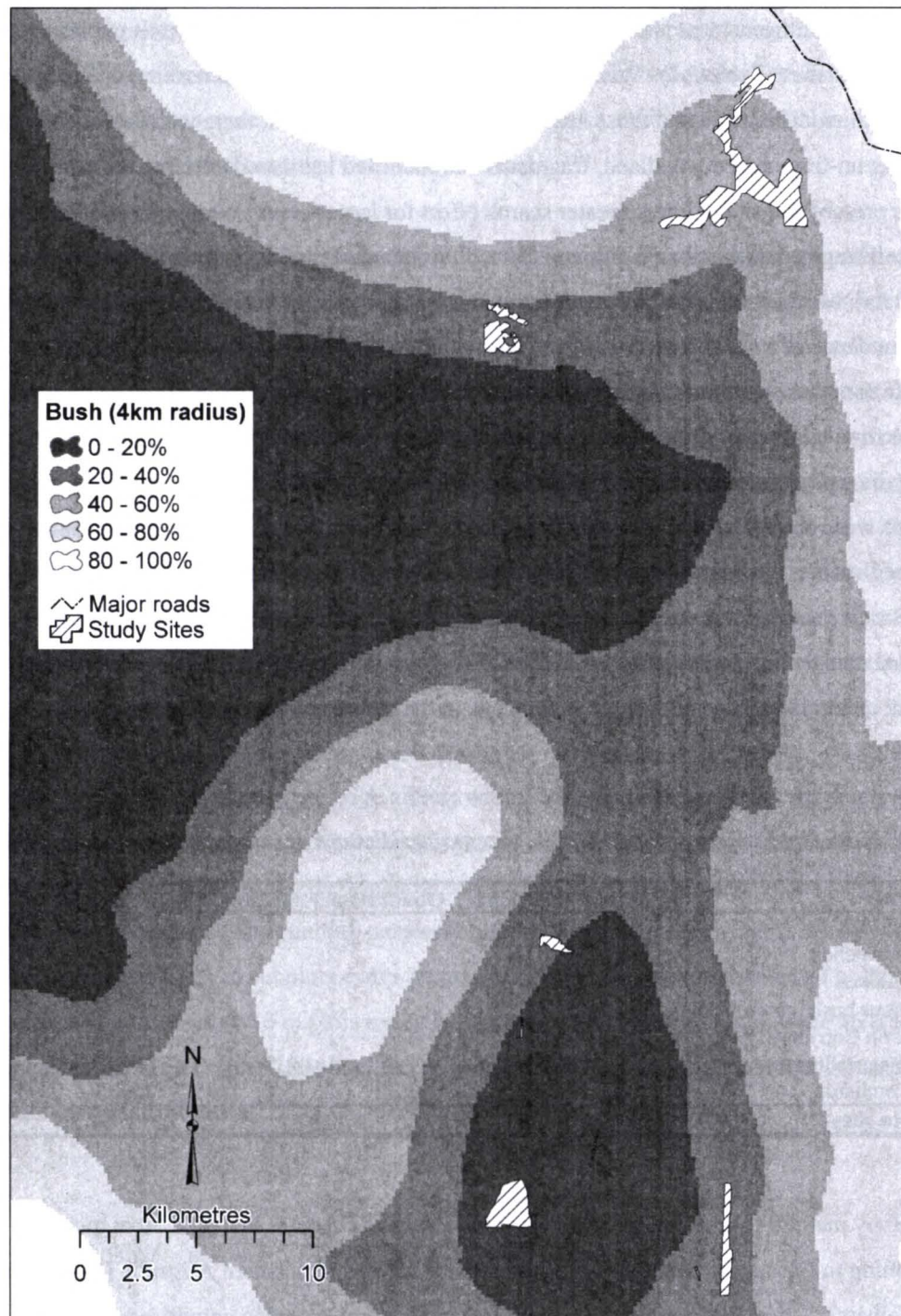
Figure 3.2: Woodland within 4 km (Bush4km) at Tipperary Station. Black = 0-20%, White = 80-100% Study sites are superimposed in diagonal stripping.

Field Methods

A wildlife survey was conducted over the dry season from July to September, in 46 fragments that ranged in size from 0.15 ha to 100 ha (median 5.1 ha), that were isolated to varying degrees (Table 3.1). In addition to the fragments, five sites were selected in mango orchards, five in

cleared land and eight in un-fragmented woodland. Seven of the fragments were corridors, ranging in width from 15 to 180 m and from 500 m to 7 km in length that connected larger woodland patches (Table 3.1). This combination of sites enabled us to determine which species occurred in modified land and those absent from fragments. In total, there were 64 sites, including un-fragmented woodland, fragments and modified habitats. Detecting most of the species present at a site requires greater search effort for larger areas (Woinarski *et al.* 2001a). For small fragments (less than 5 ha), one (50 x 50 m) quadrat was used, for medium fragments (5 – 10 ha), two quadrats, and for large fragments (greater than 10 ha), three quadrats were used. The abundance of a species recorded from a single quadrat in a small fragment is a more accurate estimate of the true fragment abundance than the abundance recorded in a single quadrat from a large fragment. This is because a larger proportion of the fragment area and habitat diversity has been surveyed in the small fragment. Thus, for larger fragments, more quadrats were needed to give an estimate of similar accuracy. In order to avoid the problem of increased species abundance in larger fragments resulting from increased survey effort, the mean for all quadrats was used for sites with more than one quadrat, and for animals only ever observed outside the quadrat, an abundance of 1 was used. In fragments with more than one quadrat, quadrats were positioned to include one at the centre and one at the edge of the fragment.

Table 3.1: Size dimensions, number of wildlife sampling quadrats per site type and replicates for habitat patches and cleared sites.

Site Types	Site Dimensions	Quadrats per site type	No. of Replicates
Small patches	< 5 ha	1	18
Medium patches	5 – 10 ha	2	8
Large patches	> 10 ha	3	13
Continuous bush (control sites)	N/A	1	8
Vegetation Corridors	15-180m	1	7
Cleared/agricultural	N/A	1	5
Mango orchards	N/A	1	5
Total No sites			64

The survey method focused on identifying all the vertebrate species in a 50 x 50 m quadrat, conforming to the standard methods for biodiversity surveys in northern Australia (Menkhorst and Woinarski 1992; Woinarski *et al.* 1999). In each quadrat, trapping comprised 20 small Elliott brand mammal traps (33 x 10 x 9 cm) and four larger cage traps (56 x 20 x 20 cm) placed around the perimeter of the quadrat, and four bucket pitfall traps (28 cm diameter x 36 cm depth) with 10 m of 28 cm drift fence within the quadrat. Traps were baited with a mixture of oats, peanut butter and honey, with all traps checked several times a day for three days. Two, 10-minute spotlight searches, two 10-minute reptile searches of undergrowth and fallen logs, and eight 5-minute bird surveys were also conducted. Bird surveys were stratisfied across the

day, with three surveys in conducted between sunrise and 9am, three between 4pm and sunset and two during the middle of the day. Reptile searches were conducted during the heat of the day when reptiles are most active. All surveys were spread across the length of the study. Microchiropteran bats were sampled with one, 10-minute Anabat recording taken within three hours of sunset. Anabat recordings were analysed using ???

A floristic inventory of all plant species present in each quadrat was made, and a number of environmental variables were recorded. The percentage ground cover of grass types, litter and bare soil were assessed using a point intercept method, by recording the value every 1 m along a 100 m tape placed in a 'v' pattern within the quadrat. The basal area of tree species was recorded using a bitterlich wedge. Trees counted using this method were identified and placed into four broad size classes (<5 cm, 5-20 cm, 20-50 cm, >50 cm DBH). Total canopy cover and cover at six different height classes (>10 m, 5-10 m, 3-5 m, 1-3 m, 0.5-1 m, 0-0.5 m) in the vegetation profile were visually estimated. The fire period was estimated from a visual assessment of time since fire and the cumulative impacts of past fires on vegetation structure at each site. This was then used to compare sites with unknown fire histories against sites where the fire history was known.

Transects were used to investigate edge effects within each fragment, with two transects sited in each small fragment, four for each medium fragment and six for each large fragment. Transects were evenly distributed through the fragment so that the distance to parallel edges and other transects was maximised and running perpendicular to the starting edge (Figure 3.3). Weed cover was assessed in 1 m subplots every 10 m while tree cover and the number of hollows and dead trees was assessed in 10 m plots every 30 m along the transect. In total, in the 46 sites, we sampled 133 transects with 1280 subplots for weeds and 503 plots for the number of dead trees, tree hollows and tree cover.
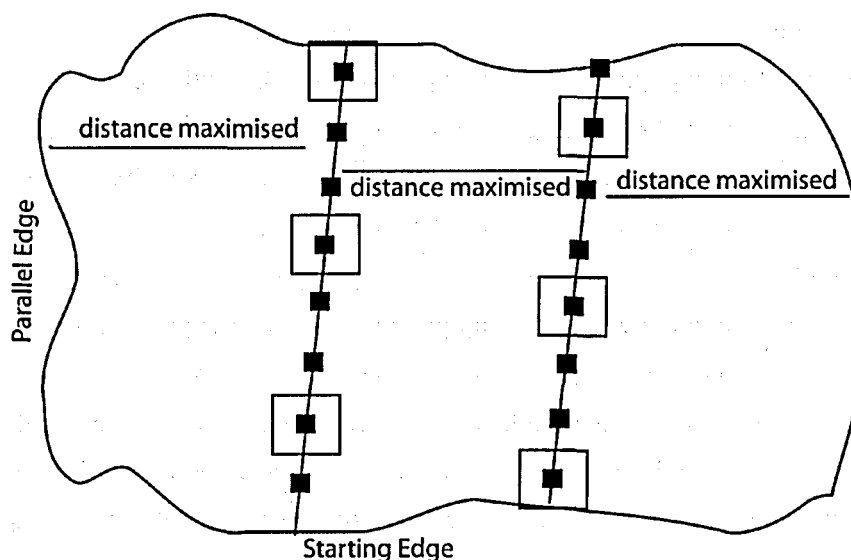
Figure 3.3: Layout of transects, plots and subplots used to measure edge effects within a small fragment. Small filled boxes represent 1 x 1m subplots to assess weed cover at 10m intervals, and larger open boxes representing 10 x 10m plots used to assess tree cover, hollows and dead trees at 30m intervals along the transect. (Note: diagram is a representation only and not to scale).

Statistical Analysis

Patterns of vertebrate species abundance based on habitat type were examined using ordination, in the program PRIMER (Clarke and Gorley 2001). Sites with 2 or less species were removed from the analysis. For this analysis fragments containing one quadrat were given the habitat category of 'patch edge'. For larger fragments with more than one quadrat, quadrats were positioned to include one at the centre and one at the edge of the fragment. These quadrats were categorised as 'patch centre' and 'patch edge'. This allows the investigation of potential differences in community patterns between the edge and centre of fragments. The surrounding matrix of modified habitats may influence or alter the habitat at the edge of fragments and hence the communities that occur there.

The ordination included all species recorded in the study. Abundances were not transformed, with compositional similarity of sites compared using the Bray-Curtis similarity index, with 10 random starts. The relationship of habitat type to the resulting ordination patterns was examined using an analysis of similarities ANOSIM. This procedure uses a test statistic (R) which is based on the difference between the average of all the ranked dissimilarities between species abundance between habitat types and the average of all the rank dissimilarities between species abundance within habitat types (Quinn and Keough 2002).

Species richness across different habitat types was investigated using a one-way ANOVA. Sites were pooled into the following habitat types (mango orchards, cleared paddocks, corridors, fragments and continuous woodland).

The habitat preference of each species was investigated using generalised linear modelling (GLM). The abundance of each species was tested as the dependent variable against site type as the explanatory variable. This analysis aimed to determine species capable of persisting in the modified matrix, hence site type was defined as Woodland or Modified. All 91 quadrats were used in the sample and a Poisson error distribution and log link function was assumed in the models. For species that did not occur in any modified quadrat, Fisher's exact test was used to compare whether their occurrence in unmodified quadrats was significantly higher. In practice, any species that occurred in at least 23 unmodified quadrats, and no modified sites, satisfied this test. This method was also used to identify species that were less likely to use corridors. In this analysis, a species must have occurred in at least 28 quadrats, of which none was in a corridor, in order to satisfy the threshold for a significant difference. The goodness-of-fit for each GLM (structural robustness) was checked by confirming that an adequate amount of deviance was explained by each model, with residuals approximating the form of the maximum likelihood distribution without any substantial bias from outliers.

In assessing edge effects, a GLM analysis was used to investigate the relationship between weed cover and distance to the edge of the fragment, with each of the 1280 1 m subplots as the sample. In this analysis, a normal error distribution was used. For statistical analyses, subplots were not truly independent because subplots in one transect or site might be expected to have similar values. To overcome this problem, we tested whether the distance relationship was still significant when site identity was added to the GLM model. GLM analysis was also used to investigate the relationships between the number of dead trees, the number of hollows and tree cover, with distance to the edge of the fragment, with each of the 503 10 m plots as the sample, with a normal error distribution being used. Although this analysis suffers from pseudo-replication, it provides us with insight into how edge effects are distributed through fragments. A Wilcoxon Pairs Test was used to investigate differences between edge and centre quadrats at each site for groundcover. The edge and centre quadrats for all transects at a site were combined to give an average value for the edge and centre. A one-way ANOVA was conducted to examine the effect of patch size on the observed differences between edge and centre quadrats. For this analysis, patch size was categorised into small, medium, large and corridors (see Table 3.1 for size classes of each category). Levene's test of normality was used to confirm normal distribution of the data. Tukey's HSD test was carried out to investigate where differences between size categories occurred.

An analysis was conducted among the 46 sites that were fragments to determine whether the extent of fragmentation affected the abundance of each species. GLM with a Poisson error distribution and log link function was used to relate one or more explanatory variables to one dependent variable, with the dependent variable here being the abundance of each individual species. In addition to fragmentation variables, a number of environmental variables were included to control for variation between the sites, and to determine the fragmentation response (Table 3.2). The fire variable, Fire history^2 was included because non-linear relationships with Fire history were expected. Correlation between variables was tested using Pearson's correlation coefficient, revealing variables that were inter-correlated. Where correlation between variables was greater than r = 0.80, one of the variables was eliminated from further analysis, with analyses being conducted on a subset of variables, avoiding those that were highly correlated (Table 3.3). In particular, time since clearing was closely and inversely correlated with the amount of woodland within 4 km of the site (Bush 4km), so the variable 'time since clearing' was omitted from further analysis.

Table 3.2: A list of the original set of explanatory variables assessed for correlation. A subset of variables (denoted by *) were used in the Generalised Linear Modelling Analysis.

Variable	Description
Site type	Five categories: fragment, corridor, bush (control), mango, cleared.
Area *	Ln (area) in m^2
Perimeter	The distance of the edge in meters
Shape *	0.282 * Perimeter / Area^2 . Ranges from 0 for circles to infinity for lines.
Bush1km *	Arcsine(proportion of bush in landscape within 1 km (excluding study patch)).
Bush4km *	Arcsine(proportion of bush in landscape within 4 km (excluding study patch)).
Connectivity *	Mean cost to move from 2 km perimeter to study patch using least cost path (as a proportion of the maximum achievable)
Basal 50 *	Basal area of trees with DBH >50 cm
Canopy cover *	Arcsine(Canopy cover) (by visual estimation)
Hollows *	Count of hollows in trees (from tree transects, see below)
Basal diversity *	Structural Diversity (Shannon Wiener diversity index for Basal Area of trees, <5cm dbh, 5-20, 20-50, >50 cm dbh.)
Structural diversity	Structural Diversity (Shannon Weiner diversity index for the cover of plants in layers > 10m, 5-10, 3-5, 1-3 m)
Ground diversity *	Ground Layer Diversity (Shannon Wiener diversity index for cover of perennial grass, annual grass, forbs, litter, bare ground and logs)
Weed cover *	Arcsine(Weed cover) (from ground transects, see below)
Perennial grass cover *	Arcsine(Ground cover of perennial grass) (using 100 point intercepts)
Fire history *	Estimated inter-fire period: 1, 2, 5 or 10 years (estimated from combination of fire impact score and time since last fire, assessed from evidence on site).
Fire history^2 *	Square of Fire_history
Clearing history	Time since clearing the area immediately surrounding the fragment: 1 = 1992-2000; 2 = 1981-1991; 3 = before 1981.
Basal ordination 1	First axis of ordination of fragments based on the basal area of each tree species recorded.
Basal ordination 2	Second axis of above.
Habitat ordination 1	First axis of ordination of fragments based on all of the environmental measurements taken at the site.
Habitat ordination 2	Second axis of above.

Table 3.3: Correlation matrix for explanatory variables (highlighted values indicate significant correlations).

	Area (ha)	Perimeter	Bush 1km	Bush 4km	Conne-ctivity	Basal 50	Perennial grass cover	Canopy Cover	Weed Cover	Hollows	Ground diversity	Structural diversity	Basal diversity	Fire History	Fire History[2]	Clearing History	Basal ordination 1	Basal ordina-tion 2	Habitat ordina-tion 1
Perimeter	-0.08																		
Bush 1km	0.12	-0.29																	
Bush 4km	-0.41	0.07	0.41																
Connectivity	-0.30	-0.55	0.41	0.37															
Basal 50	-0.08	-0.18	0.17	0.33	0.33														
Perennial grass cover	0.25	0.01	0.07	-0.07	-0.13														
Canopy Cover	-0.24	-0.06	0.15	0.21	0.27	0.23	-0.02												
Weed Cover	0.11	0.1	-0.07	-0.29	-0.30	-0.06	0.11	-0.28											
Hollows	-0.19	-0.16	-0.1	0.06	0.26	-0.02	-0.08	0.08	-0.14										
Ground diversity	0.19	0.22	0.07	0.18	-0.08	0.11	0.44	-0.37	0.06	0									
Structural diversity	-0.49	-0.27	0.03	0.42	0.34	0.16	-0.15	0.19	-0.31	0.24	-0.01								
Basal diversity	-0.26	-0.33	0.29	0.47	0.45	0.53	-0.1	0.23	-0.22	0.22	-0.05	0.49							
Fire History	-0.29	-0.55	0.05	0.08	0.54	0	-0.06	0.31	-0.06	0.25	-0.35	0.45	0.31						
Fire History	-0.31	-0.52	0.01	0.09	0.55	0.03	-0.12	0.31	-0.05	0.26	-0.36	0.43	0.32	0.99					
Clearing History	-0.36	0.13	0.29	0.81	0.28	0.21	0.01	0.36	-0.28	0.02	0.11	0.36	0.36	0.12	0.12				
Basal ordination 1	-0.03	-0.05	-0.43	-0.17	-0.06	-0.13	0.06	-0.07	-0.05	0.07	0.05	0.03	-0.37	-0.02	-0.04	0.02			
Basal ordination 2	0.08	0.12	0.32	0.25	-0.04	0.01	0.13	0.32	-0.29	0.1	0.21	0.17	0.11	-0.1	-0.16	0.41	-0.07		
Habitat ordination 1	0	0.09	-0.13	0.08	-0.04	-0.06	-0.51	-0.23	-0.45	0.14	0.16	0.18	0.01	-0.33	-0.30	0.05	0.08	0.07	
Habitat ordination 2	-0.42	-0.04	-0.02	0.28	0.29	-0.09	-0.09	0.12	-0.64	0.06	-0.12	0.44	0.29	0.25	0.24	0.2	-0.01	0.14	0.11

For each of the 67 species recorded from at least eight fragment sites, two analyses were conducted. A best-fit model was built by backward stepwise deletion. Here, all of the explanatory variables were included in the model at the start of the analysis, and were eliminated one by one in order of those with the least explanatory power until only variables with significant effects remained. This model provides the best description of the factors determining the abundance of each species. In the second analysis, a standard model was fitted for each species consisting of a subset of the seven variables that most commonly occurred in the best-fit models (Table 3.4). These included both fragmentation and environmental variables, with three fragmentation, two environmental and two fire variables. With this model, the species could be directly compared on the basis of their response to each of the explanatory variables. The standard model was used to compile a list of species that showed significant fragmentation effects, and the best-fit model was used to examine instances where the standard model missed out or mis-represented an important effect.

Table 3.4: Occurrence of explanatory variables in the best-fit models. A subset of seven variables included in the standard models is denoted by *.

Variable	Frequency in Models	Variable	Frequency in Models
Area *	12	Canopy cover *	15
Shape	8	Hollows	11
Bush 1km	9	Weed cover *	15
Bush 4km *	22	Perennial grass cover	7
Connectivity *	16	Ground diversity	10
Basal 50 DBH	8	Fire history *	18
Basal diversity	13	Fire history^2 *	13

Results

A total of 158 animal species were recorded in the survey. Analysis of individual species was conducted on two sets of species. The 75 species found in more than six sites were used to describe habitat use, and the 67 species present from at least eight fragments were examined to assess the impact of fragmentation.

Habitat Utilisation

Species Patterns

There was a distinct difference between modified (cleared and mango orchards) and unmodified (continuous, patches and corridor) habitats in their vertebrate species composition (Figure 3.4). With the inclusion of all habitat types (Figure 3.4a), the position of sites within ordination space for all vertebrate species was significantly related to habitat type (R = 0.33, P < 0.001). However, with the removal of the modified habitat types from the analysis (Figure 3.4b), this relationship became non significant (R = 0.064, P > 0.05). This pattern also occurred for birds

(Figure 3.5), with all habitat types (R = 0.23, P < 0.01), and forested sites only (R = 0.07, P > 0.05); and for mammals (Figure 3.6) in all habitat types (R = 0.18, P = 0.01) and forested sites only (R = 0.03, P > 0.372). The species composition of reptiles at sites showed no distinct difference between habitat types (Figure 3.7). The position of sites was not related to habitat type with and without the inclusion of modified habitats, (R = 0.12, P > 0.05) and (R = 0.02, P > 0.05), respectively.
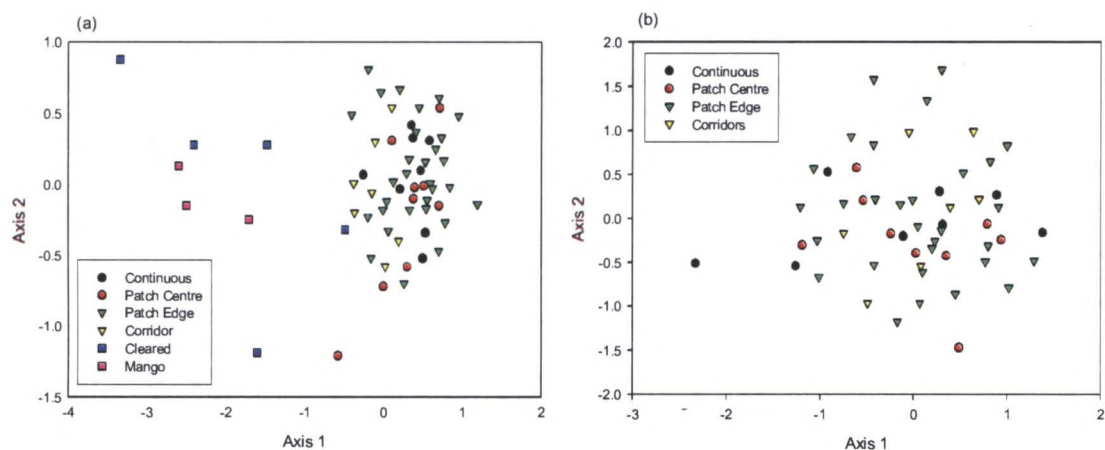
Figure 3.4: Ordination of sites by their vertebrate species composition in relation to (a) all habitat types (stress = 0.17); (b) forested sites only (stress = 0.24).
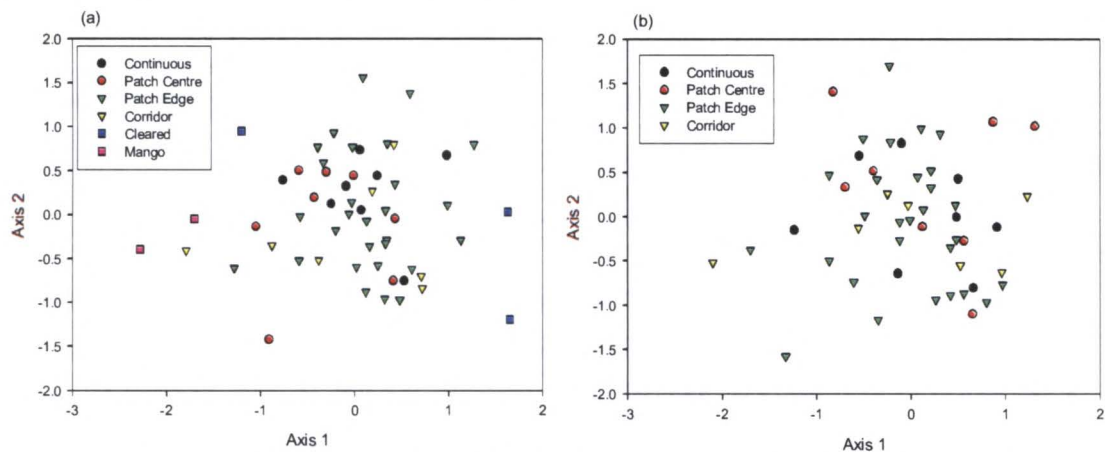
Figure 3.5: Ordination of sites by their bird species composition in relation to (a) all habitat types (stress = 0.22); (b) forested sites only (stress = 0.26).
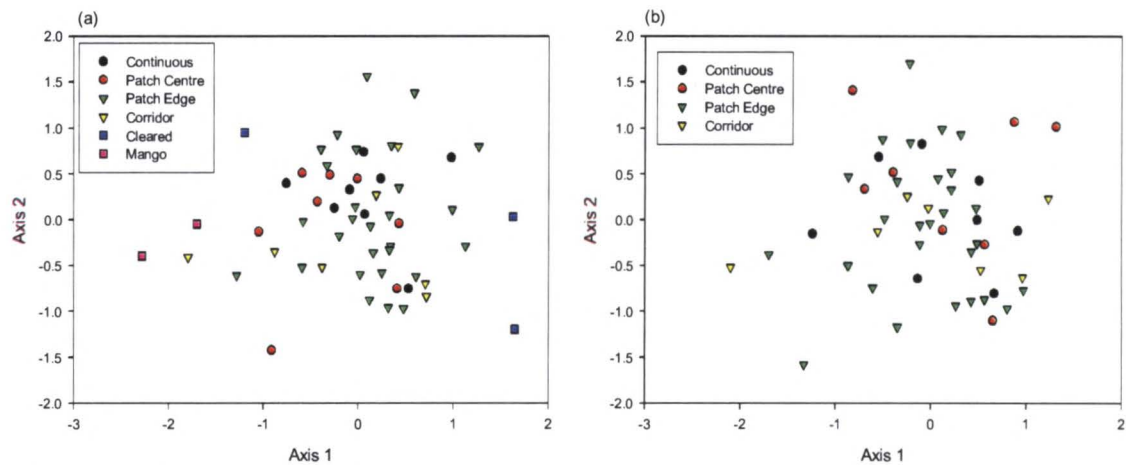
Figure 3.6: Ordination of sites by their mammal species composition in relation to (a) all habitat types (stress = 0.21); (b) forested sites only (stress = 0.21).
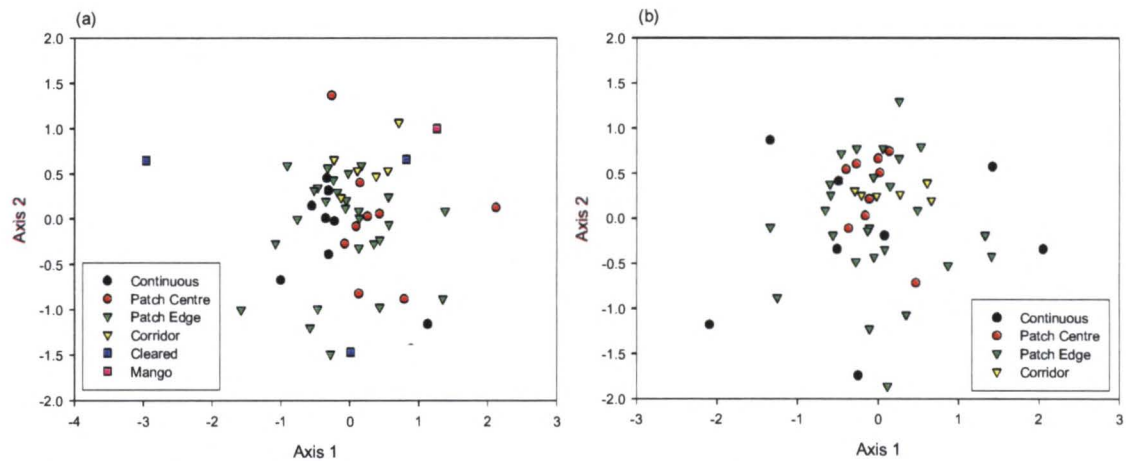
Figure 3.7: Ordination of sites by their reptile species composition in relation to (a) all habitat types (stress = 0.19); (b) forested sites only (stress = 0.2).

Species Richness

To assess species richness across the different habitat types (mango orchards, cleared paddocks, corridors, fragments and continuous woodland) sites were pooled into habitat types (Figure 3.8). A one-way analysis of variance (ANOVA) showed significant difference in species richness between the different habitats (P < 0.001). Tukey's HSD test was than used to identify significant differences between habitat types. Most habitat types showed significant differences in species richness (P < 0.05), but, no significant difference was observed between corridor and fragment habitats (P > 0.7), corridor and cleared habitats (P > 0.10), and cleared and mango habitats (P > 0.2) (Table 3.5).
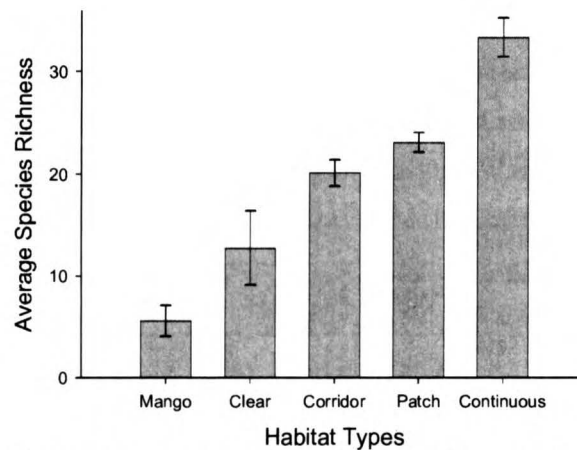
Figure 3.8: Average quadrat-level species richness (±SE) within different habitat types

Table 3.5: Variation in species richness between the different habitat types surveyed during the study (highlighted values indicate significant correlations).

Tukey HSD test Error: Between MS = 32.8, df = 59						
Taxonomic Group	Habitat Type	Cleared	Corridors	Continuous	Mangos	Fragments
Vertebrate species	Cleared					
	Corridors	0.18				
	Continuous	<0.01	<0.01			
	Mangos	0.29	<0.01	<0.01		
	Fragments	<0.01	0.75	<0.01	<0.01	
Birds	Cleared					
	Corridors	0.28				
	Continuous	<0.01	0.03			
	Mangos	0.35	<0.01	<0.01		
	Fragments	0.04	0.99	0.01	0.01	
Mammals	Cleared					
	Corridors	0.99				
	Continuous	0.04	0.06			
	Mangos	0.92	0.70	<0.01		
	Fragments	0.50	0.71	0.16	0.07	
Reptiles	Cleared					
	Corridors	0.46				
	Continuous	0.01	0.01			
	Mangos	0.95	0.12	<0.01		
	Fragments	0.03	0.81	0.01	<0.01	
Amphibians	Cleared					
	Corridors	0.97				
	Continuous	0.98	0.68			
	Mangos	1.00	0.97	0.98		
	Fragments	0.99	0.65	1.00	0.99	

Individual Species

Of the 75 species considered, 19 were recorded from two or more of the 10 mango orchard and/or paddock sites (Table 3.6). It should be noted that three of the cleared sites were selectively cleared, retaining scattered trees and within close proximity to wooded areas. Fifteen species showed no significant difference in abundance between woodland and modified sites (Table 3.6). Only one species, the northern freetail-bat *Chaerophon jobensis,* was more commonly recorded in modified sites. Fifty-five species were significantly more common in

woodland than modified sites. Of these species 14 were classified as unlikely to use modified habitats with statistical confidence ($P < 0.05$) as they were recorded from at least 23 sites of which none was modified. The confidence was stronger ($P < 0.01$) for seven of these species which were recorded in at least 30 sites (Table 3.6). All but one were birds, with most of these being highly arboreal, such as Weebill and honeyeaters.

Table 3.6: Habitat preference and corridor use for species from at least five sites in this study. The table includes the mean percentage occurrence in woodland sites (including controls and all fragments), and in cleared and mango sites combined. The Habitat preference column was calculated by comparing these two columns. Significant preferences (calculated using a GLM analysis) are indicated by asterisks at increasing probability levels (* = 0.05, ** = 0.01, *** = 0.001). A blank in this column means that the species uses both habitats and it was not possible to determine the preferred one. Corridor use is given as yes or no for the species that were recorded frequently enough to be confident that an absence in corridor sites means they do not use them. Unknown is given to species that were not recorded in corridors, but were recorded from <28 quadrats in woodland. BUSH is used as a surrogate term for woodland.

Scientific Name	Common Name	No. Obs	% Occurrence in Wood-land	Modified	Use Modified Land?	Habitat preference (abundance)	Use Corridors?
Amphibians							
Limnodynastes convexiusculus	Marbled Frog	12	11.1	20	YES		UNK
Birds							
Coturnix ypsilophora	Brown Quail	8	8.6	10			YES
Geopelia striata	Peaceful Dove	27	30.9	20	YES	BUSH**	YES
Geopelia humeralis	Bar-shouldered Dove	60	70.4	30	YES	BUSH***	YES
Burhinus grallarius	Bush Stone-curlew	13	13.6	20	YES		YES
Haliastur sphenurus	Whistling Kite	28	30.9	30	YES	BUSH***	YES
Milvus migrans	Black Kite	9	9.9	10			YES
Trichoglossus haematodus	Rainbow Lorikeet	43	51.9	0	NO**	BUSH***	YES
Calyptorhynchus banksii	Red-tailed Black-Cockatoo	28	34.6	0	NO*	BUSH**	YES
Cacatua galerita	Sulphur-crested Cockatoo	22	23.5	20	YES	BUSH*	UNK
Aprosmictus erythropterus	Red-winged Parrot	27	30.9	10		BUSH***	YES
Platycercus venustus	Northern Rosella	7	8.6	0		BUSH***	UNK
Eurystomus orientalis	Dollarbird	11	12.4	0		BUSH***	UNK
Dacelo leachii	Blue-winged Kookaburra	44	54.3	0	NO**	BUSH***	YES
Todiramphus macleayii	Forest Kingfisher	8	8.6	10			UNK
Merops ornatus	Rainbow Bee-eater	41	46.9	30	YES	BUSH**	YES
Cacomantis variolosus	Brush Cuckoo	11	13.6	0		BUSH***	YES
Centropus phasianinus	Pheasant Coucal	15	17.3	0		BUSH***	YES
Hirundo nigricans	Tree Martin	13	12.4	30	YES	BUSH***	UNK
Rhipidura leucophrys	Willie Wagtail	16	18.5	10			YES
Myiagra rubecula	Leaden Flycatcher	14	14.8	20	YES	BUSH*	UNK
Pachycephala rufiventris	Rufous Whistler	16	19.8	0		BUSH***	YES
Grallina cyanoleuca	Magpie-lark	38	38.3	70	YES		YES
Coracina novaehollandiae	Black-faced Cuckoo-shrike	25	30.9	0	NO*	BUSH***	YES
Coracina papuensis	White-bellied Cuckoo-shrike	58	65.4	40	YES	BUSH***	YES
Lalage leucomela	Varied Triller	21	23.5	20	YES	BUSH**	UNK
Sphecotheres viridis	Figbird	16	18.5	10		BUSH*	YES
Pomatostomus temporalis	Grey-crowned Babbler	23	27.2	0	NO*	BUSH***	UNK
Smicrornis brevirostris	Weebill	45	54.3	0	NO**	BUSH***	YES
Malurus melanocephalus	Red-backed Fairy-wren	23	28.4	0	NO*	BUSH***	YES
Dicaeum hirundinaceum	Mistletoebird	21	25.9	0		BUSH**	UNK
Melithreptus albogularis	White-throated Honeyeater	45	54.3	10		BUSH***	YES
Myzomela obscura	Dusky Honeyeater	8	9.9	0		BUSH***	UNK
Lichmera indistincta	Brown Honeyeater	47	56.8	0	NO**	BUSH***	YES
Lichenostomus unicolor	White-gaped Honeyeater	27	33.3	0	NO*	BUSH***	UNK
Manorina flavigula	Yellow-throated Miner	52	61.7	10		BUSH***	YES
Entomyzon cyanotis	Blue-faced Honeyeater	52	64.2	0	NO**	BUSH***	YES
Philemon argenticeps	Silver-crowned Friarbird	27	33.3	0	NO*	BUSH***	YES
Philemon citreogularis	Little Friarbird	52	61.7	10		BUSH***	YES
Taeniopygia bichenovii	Double-barred Finch	19	22.2	10		BUSH**	UNK
Poephila acuticauda	Long-tailed Finch	12	13.6	10			YES
Oriolus sagittatus	Olive-backed Oriole	16	19.8	0		BUSH***	YES
Oriolus flavocinctus	Yellow Oriole	27	33.3	0	NO*	BUSH**	UNK
Dicrurus bracteatus	Spangled Drongo	8	8.6	10			UNK
Chlamydera nuchalis	Great Bowerbird	12	14.8	0		BUSH***	YES
Corvus orru	Torresian Crow	33	37	30	YES	BUSH**	YES
Cracticus nigrogularis	Pied Butcherbird	18	22.2	0		BUSH***	YES
Cracticus torquatus	Grey Butcherbird	50	60.5	0	NO**	BUSH***	YES
Pardalotus striatus	Striated Pardalote	56	67.9	10		BUSH***	YES
Mammals							
Dasyurus hallucatus	Northern Quoll	14	17.3	0		BUSH*	UNK

Scientific Name	Common Name	No. Obs	% Occurrence in Wood-land	Modified	Use Modified Land?	Habitat preference (abundance)	Use Corridors?
Sminthopsis virginiae	Red-cheeked Dunnart	12	12.4	20	YES		YES
Isoodon macrourus	Northern Brown Bandicoot	71	85.2	10		BUSH***	YES
Trichosurus vulpecula	Common Brushtail Possum	55	65.4	10		BUSH***	YES
Macropus agilis	Agile Wallaby	33	37	30	YES		UNK
Chaerophon jobensis	Northern Freetail-bat	13	13.6	20	YES	CLEARED***	YES
Scotorepens greyii	Little Broad-nosed Bat	12	12.4	10			UNK
Rattus tunneyi	Pale Field-rat	13	14.8	0		BUSH*	YES
Mesembriomys gouldii	Black-footed Tree-rat	25	30.9	0	NO*	BUSH**	YES
Pseudomys delicatulus	Delicate Mouse	14	14.8	20			YES
Melomys burtoni	Grassland Melomys	13	12.4	30	YES		UNK
Reptiles							
Heteronotia binoei	Bynoe's Gecko	16	19.8	0		BUSH**	YES
Oedura rhombifer	Zig-zag Gecko	7	8.6	0			YES
Delma borea		10	12.4	0		BUSH*	YES
Diporiphora bilineata	Two-lined Dragon	27	30.9	20	YES	BUSH*	YES
Lophognathus temporalis		13	17.3	0		BUSH*	UNK
Varanus tristis		10	12.4	0			UNK
Carlia gracilis	Slender Rainbow Skink	8	9.9	0		BUSH***	UNK
Carlia munda	Striped Rainbow Skink	59	70.4	20	YES	BUSH***	YES
Carlia tricantha	Three-spined Rainbow Skink	7	7.4	10			
Cryptoblepharus plagiocephalus	Arboreal Snake-eyed Skink	31	37	10		BUSH**	UNK
Ctenotus essingtonii	Port Essington Ctenotus	25	29.6	10		BUSH***	YES
Menetia greyii	Grey's Menetia	44	54.3	10		BUSH***	YES
Morethia storri	Storr's Snake-eyed Skink	15	18.5	0		BUSH*	YES
Glaphyromorphus darwiniensis	Darwin Skink	26	29.6	20	YES		YES
Glaphyromorphus douglasi	Douglas' Skink	7	8.6	0			UNK

Corridors

Of the 75 species recorded in more than 6 sites, 50 were found to use corridors. The proportion of species using corridors was comparable across faunal groups, namely 71% of birds, 64% of mammals and 73% of reptiles (Table 3.6). There were no species recorded in at least 28 woodland sites that were not recorded in corridors.

Edge Effects

Weed cover varied greatly among sites, but averaged 12% on the edges of fragments with a consistent decline away from the edge (Figure 3.9), stabilising at approximately 5%, 20 m from the edge. This decreasing trend was significant ($p < 0.001$), but captured only 1.4% of variation in weed cover. When site identity was added to the GLM model, the distance relationship became more significant with deviance = 821 compared to 345. Eighty-nine percent of fragments had some weeds, but for the majority, the average cover was below 3% and weeds did not penetrate far into fragments (Figure 3.9). The fragmentation analysis found nine vertebrate species responded negatively to weed cover in the standard model, while seven species responded positively (Table 3.8). It is noted that weed cover remained constant at 5% in the interior of fragments, although it is likely that the value would decrease further several hundred metres from a patch edge. However, no data on weed cover were collected in the control sites for comparison.
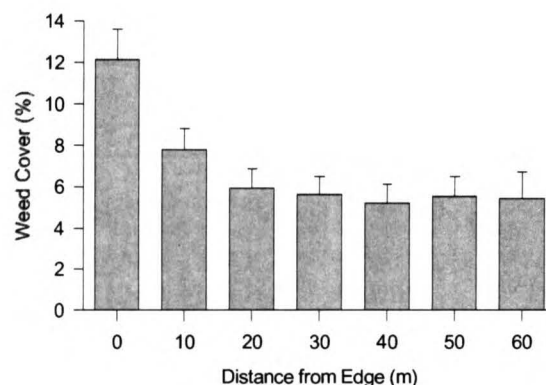
Figure 3.9: Mean % weed cover in fragments (+SE) at increasing distance from fragment edge, measured in 1 m quadrats along 60 m long transects (n = 1280). Leaf litter cover was the predominant groundcover in fragments, with an average percentage cover of 40 % at the edge of fragments and 53% at the centre. Forbs and annual grasses were the least represented groundcover categories, making up approximately 5% cover (Fig 3.10). Significant differences between the edge and centre quadrats of fragments were observed for four of the six ground cover categories; bare ground (P = 0.01); litter (P < 0.001); weeds (P < 0.1); and forbs (P < 0.01). Annual and perennial grass cover showed no significant differences between edge and centre quadrats, with (P > 0.1) and (P > 0.6) respectively (Fig 3.10). Differences between the edge and centre of fragments was not influenced by fragment size for all groundcover variables except bare ground (Table 3.7), which was significant at (P < 0.01) with significantly more bare ground at the edges of fragments (Fig 3.11a). Weed cover showed no significant difference between edge and center quadrats in fragments (Fig 3.11b).
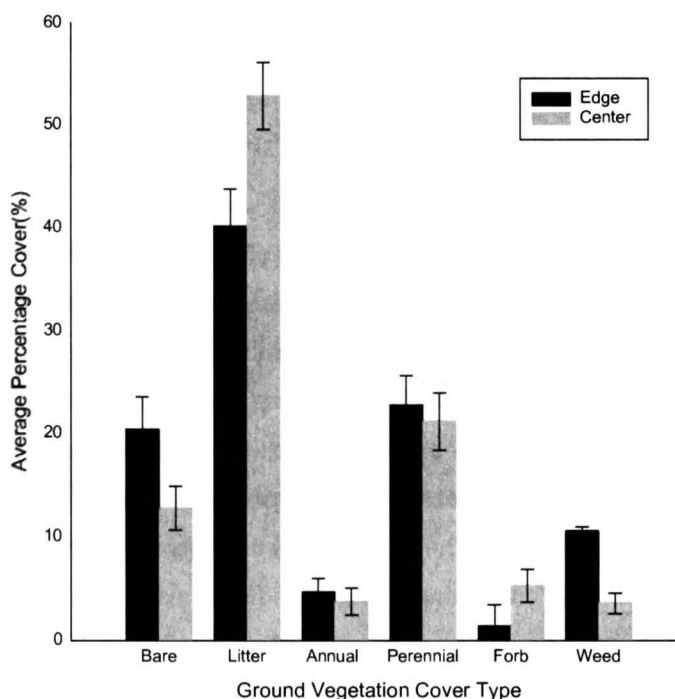
Figure 3.10: Average percentage cover of each groundcover type at the edge and centre of fragments. Whiskers represent one standard error

Table 3.7: Variation in the average percentage cover of groundcover categories in edge and centre quadrats within woodland fragments; $P < 0.01$; †F-values are from a one-way ANOVA for the fragment size, S = small, M = medium, L = large and C = corridor.

Groundcover Category	Difference in Percentage Cover between Edge and Centre Quadrats	
	†F	Tukeys HSD
Bare	3.07$^{\phi\phi}$	S = M = L =C
Litter	0.36	S = M = L =C
Annual grass	2.03	S = M = L =C
Perennial grass	0.22	S = M = L =C
Forbs	1.28	S = M = L =C
Weeds	0.28	S = M = L =C
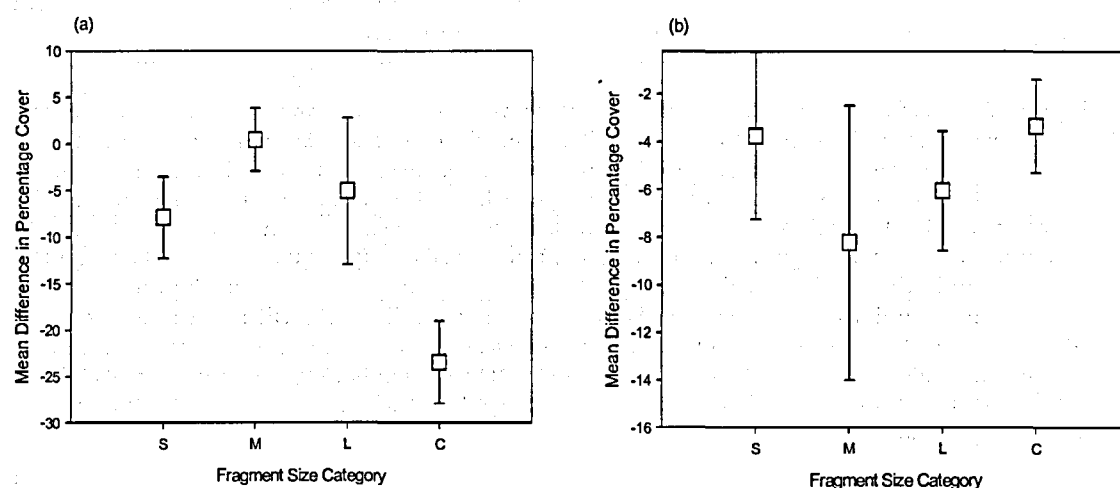
Figure 3.11: The mean difference between edge and centre 1 x 1 m quadrats for the percentage cover of (a) bare ground; (b) weed cover. Whiskers represent one standard error. Fragment size, S = small, M = medium, L = large and C = corridor.

The fragmentation analysis included 18 fragments where an edge and a centre quadrat were surveyed. It was not possible to identify any animals that were convincingly edge specialists or edge avoiders. Of the 75 species recorded in more than six sites, only four were not found in the 18 paired edge sites, and none in more than four of the centre quadrats. Conversely, five species were absent from the centre quadrats, and none was in more than three of the edges. An ordination of the average abundance of vertebrate fauna at each wooded site was not significantly related to habitat type (Figure 3.4b). There was no difference in the composition of vertebrate species between the edge and centre of fragments for all major taxonomic groups (see Figures 3.5; 3.6; 3.7).

The number of hollows (p<0.05) and cover of trees above 10 m (p<0.001) increased significantly with distance from the edge, while the number of dead trees decreased significantly (p<0.01) (Figure 3.12).
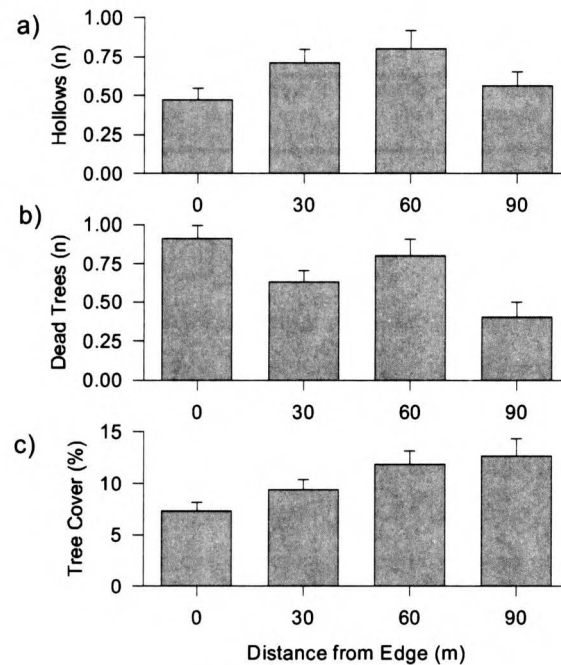
Figure 3.12: Mean number of hollows (a), dead trees (b) and % cover of trees above 10 m height (c) (+SE) at increasing distance from fragment edge, measured in 10 m quadrats along 60 m long transects (n = 503).

Environmental Variables

Seventeen species (25%) showed a significant response to fire in the standard model, and of these, 14 preferred sites with an intermediate (5-10 years) fire frequency (Table 3.8). These species were less abundant, or did not occur, on sites burned annually or that had been unburnt for a long period (20-30 years). One species was found to prefer extreme fire regimes (i.e. regularly burnt and long unburnt sites), while two species preferred frequently burnt sites (Table 3.8). The density of trees was also a significant factor in the models, whether expressed as canopy cover, the number of hollows or basal area measures.

Table 3.8: The significance of variables in the standard model for each species. In the columns Area to Weed-cov, the sign of the response is indicated by "+" or "-", with one sign indicating significance at p < 0.05, two at p < 0.01. % Dev. Exp. is an estimate of the percentage of deviance explained by the model. In the fire column "short" indicates species who prefer short fire intervals, "int" intermediate fire intervals, and "extr" extreme fire intervals (i.e. frequently or long unburnt) "*" indicates level of significance, with one sign indicating significance at p < 0.05, two at p < 0.01 (see Appendix 1 for scientific names).

Species	Site Count	% Dev. Exp.	Fragmentation Variables Area	Bush 4km	Conne-ctivity	Habitat Variables Canopy Cover	Weed Cover	Fire
Amphibians								
Limnodynastes convexiusculus	6	0				++		
Birds								
Brown Quail	6	67			++		++	
Peaceful Dove	16	10						
Bar-shouldered Dove	32	50		–				
Bush Stone-curlew	8	34	+					
Whistling Kite	19	79				--	++	
Black Kite	7	30						SHORT*
Rainbow Lorikeet	28	29				--	--	
Red-tailed Black-Cockatoo	13	15						
Sulphur-crested Cockatoo	10	36						INT*
Red-winged Parrot	18	46		++	++			SHORT**
Blue-winged Kookaburra	24	17						
Rainbow Bee-eater	24	47	++	–	+			
Pheasant Coucal	12	6						
Willie Wagtail	9	73						
Leaden Flycatcher	6	27	+				+	
Rufous Whistler	11	78		–	–			INT*
Magpie-lark	23	26				--		INT**
Black-faced Cuckoo-shrike	18	24						
White-bellied Cuckoo-shrike	33	10						
Varied Triller	10	57				+	++	
Figbird	12	42				+		
Grey-crowned Babbler	14	26			+			INT**
Weebill	24	31	++	–	++			
Red-backed Fairy-wren	13	62	++	++		--		INT**
Mistletoebird	12	41				++		
White-throated Honeyeater	25	48	++		++			INT*
Dusky Honeyeater	6	47	+					
Brown Honeyeater	28	25		–	+			INT**
White-gaped Honeyeater	17	47						
Yellow-throated Miner	30	24			++		--	
Blue-faced Honeyeater	29	15						INT**
Silver-crowned Friarbird	18	37			-	--	--	
Little Friarbird	33	24			–	--	--	
Double-barred Finch	11	18	+				+	
Long-tailed Finch	7	70						
Olive-backed Oriole	10	32						
Yellow Oriole	15	45				+		
Great Bowerbird	8	26					+	
Torresian Crow	20	31			–			
Pied Butcherbird	17	21		-				
Grey Butcherbird	30	35		++	+	-	--	INT*
Striated Pardalote	33	48	+	++	–		--	INT**
Mammals								
Dasyurus hallucatus	6	53		+				
Sminthopsis virginiae	8	46						INT**
Isoodon macrourus	39	20		–				
Trichosurus vulpecula	31	35		+	++	+		
Macropus agilis	15	30	++		+			
Rattus tunneyi	7	76		-				
Mesembriomys gouldii	16	40	++		+			
Pseudomys delicatulus	9	64		++	-			INT**
Melomys burtoni	9	71		+		++	++	
Chaerophon jobensis	8	53						EXTR*
Scotorepens greyii	9	38	-					
Melomys burtoni	9	71		+		++	++	
Reptiles								
Heteronotia binoei	12	34			+			
Oedura rhombifer	6	20						
Delma borea	6	24						

Species	Site Count	% Dev. Exp.	Fragmentation Variables			Habitat Variables		
			Area	Bush 4km	Conne-ctivity	Canopy Cover	Weed Cover	Fire
Diporiphora bilineata	12	69		--			--	INT*
Lophognathus temporalis	11	17						
Varanus tristis	8	14						
Cryptoblepharus plagiocephalus	24	22		-	++			
Ctenotus essingtonii	14	38		++	-			INT**
Menetia greyii	28	22				--	--	
Morethia storri	8	20						
Glaphyromorphus douglasi	6	47				+		
Glaphyromorphus darwiniensis	15	23			-			
Carlia munda	35	39	--	--				--

The Effect of Fragment Area and Isolation

In the best-fit models, the most common variable included was the amount of woodland with 4 km of the site (Bush 4km) (Table 3.4). The other fragmentation variables, Fragment Area and Connectivity, were also commonly included (Table 3.4). The standard model used seven explanatory variables (Area, Bush 4km, Connectivity, Canopy cover, Weed cover, Fire history and Fire history^2). A total of 24 species showed significant negative responses to fragmentation variables in the standard model, while another four species showed significant negative responses in the best-fit model. These are identified in Table 3.8, with a "+" relationship with Fragment Area, woodland within 4 km or Connectivity. In the standard model, Fragment Connectivity was present most commonly (15 models), followed by Area (12 models) and Bush 4km (9 models). It should be noted that of the nine species that showed a significant Bush 4km relationship, six were still significant when the Tipperary sites were removed from the analysis. This data reduction procedure was tested because the Tipperary sites were geographically removed from the other sites.

In contrast, 13 species showed a significant positive effect of fragmentation. Many of these species are among the most common and broadly distributed animals in the Top End. They included the Bar-shouldered Dove *Geopelia humeralis*, Torresian Crow *Corvus orru*, Silver-crowned and Little friarbirds *Philemon buceroides* and *P. citreogularis*, Brown Honeyeater *Lichmera indistincta*, Northern Brown Bandicoot *Isoodon macrourus* and three of the most common lizards. However, this positive effect was unexpected for several species, such as the Rufous Whistler *Pachycephala rufiventris*, and the Pale Field-rat *Rattus tunneyi*. The bat *Scotorepens greyii* may prefer to forage in fragmented or cleared areas, but it must roost in trees. For this species, the dependence on woodland may act at a larger scale than the study could reveal.

Five of the nine species with a significant negative relationship with the amount of woodland within 4km (Bush 4 km) were absent from fragments with less than 25% of woodland in the

landscape (Figure 3.13), and the abundance of another two species in such isolated patches, was less than one fifth of that in un-fragmented woodland. Three of these species were still absent in fragments with less than 50% Bush 4km. The Northern quoll *Dasyurus hallucatus* was not recorded in patches with less than 65% woodland within 4 km of the fragment.

Of the 11 species with a significant positive Area relationship, the Bush Stone-curlew *Burhinus grallarius* and Black-footed tree-rat *Mesembriomys gouldii* were not found in fragments smaller than 1 ha (Figure 3.14). The abundance of the Leaden Flycatcher *Myiagra rubecula* and Agile wallaby *Macropus agilis* fell to approximately one tenth of that of the un-fragmented woodland in the smallest fragments, while the other species showed either gradual declines with decreasing area or erratic patterns.
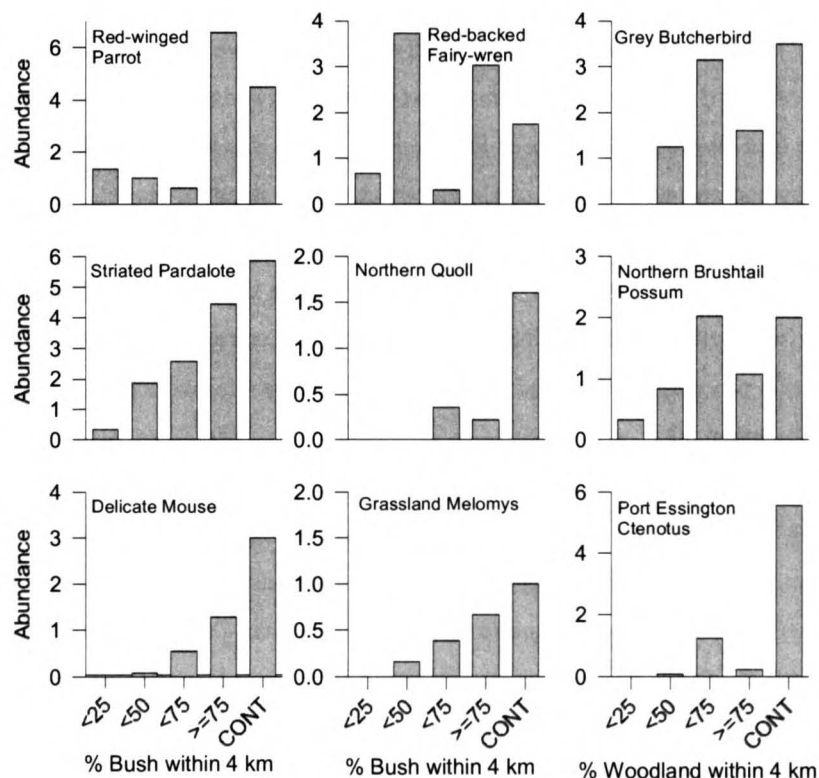
Figure 3.13: The mean abundance of species in sites grouped by the percentage of woodland within 4 km of each site (Bush 4 km). The mean abundance in continuous woodland sites "Cont" is also included. Only species that showed a significant positive effect of the factor in the standard model are shown.

Fourteen species showed a significant positive relationship with Connectivity. Four of these species were not present in fragments where connectivity was below 0.2 (Figure 3.15). Another three species declined to numbers less than one fifth of that in un-fragmented woodland, while five of these seven were at very low numbers in fragments with less than 0.4 connectivity. Connectivity allowed many species to be present in fragments that otherwise would be too small to have maintained them. For example, Agile Wallabies and Black-footed Tree-rats were found in small fragments, 0.8 ha and 2.0 ha respectively, but the connectivity of these fragments was above 0.6. Specific examples from different taxa of some responses to fragmentation are presented here using species that displayed the strongest effects.
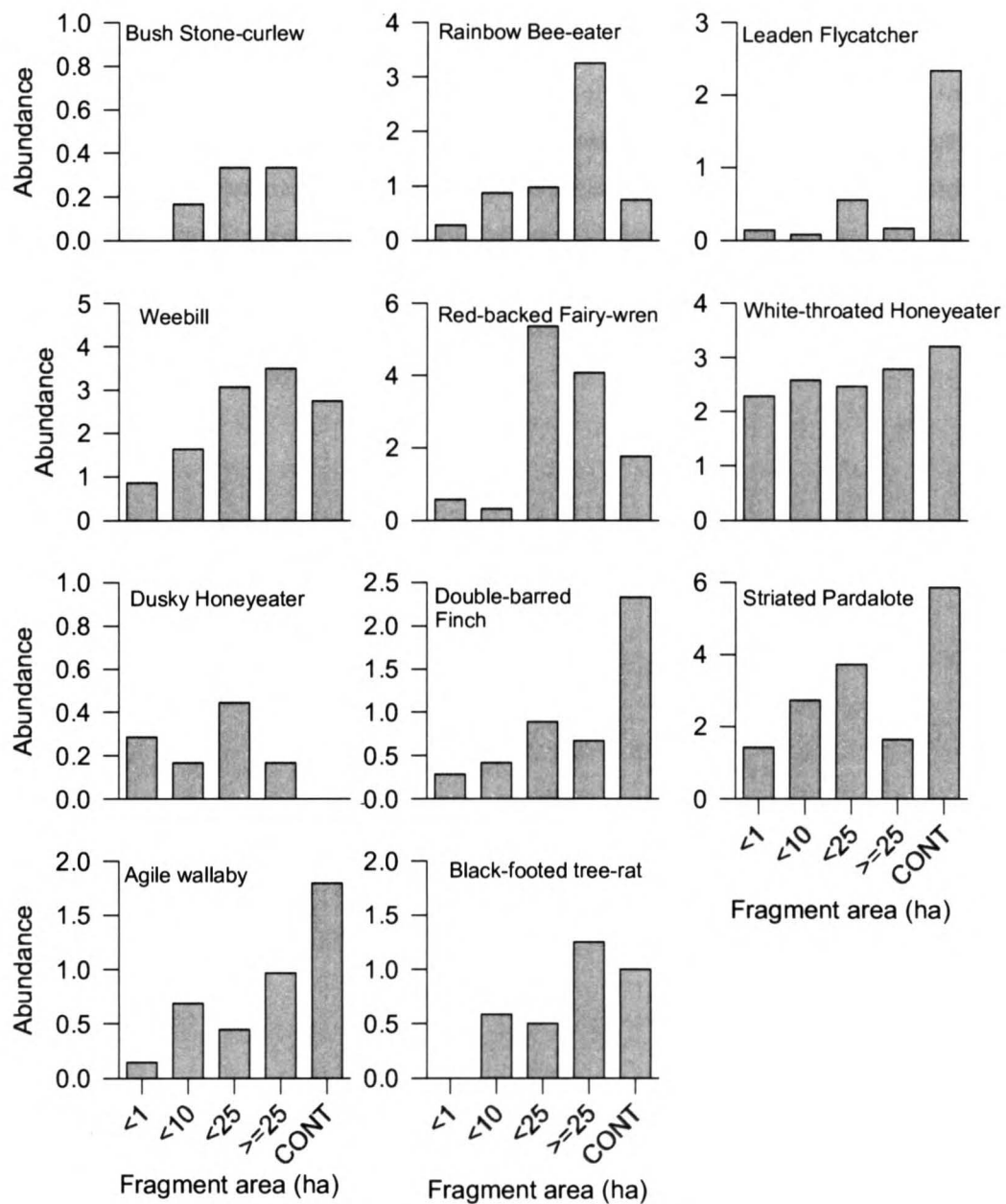
Figure 3.14: The mean abundance of species in sites grouped by fragment area. The mean abundance in continuous woodland sites "Cont" is also included. Only species that showed a significant positive area effect in the standard model are shown.
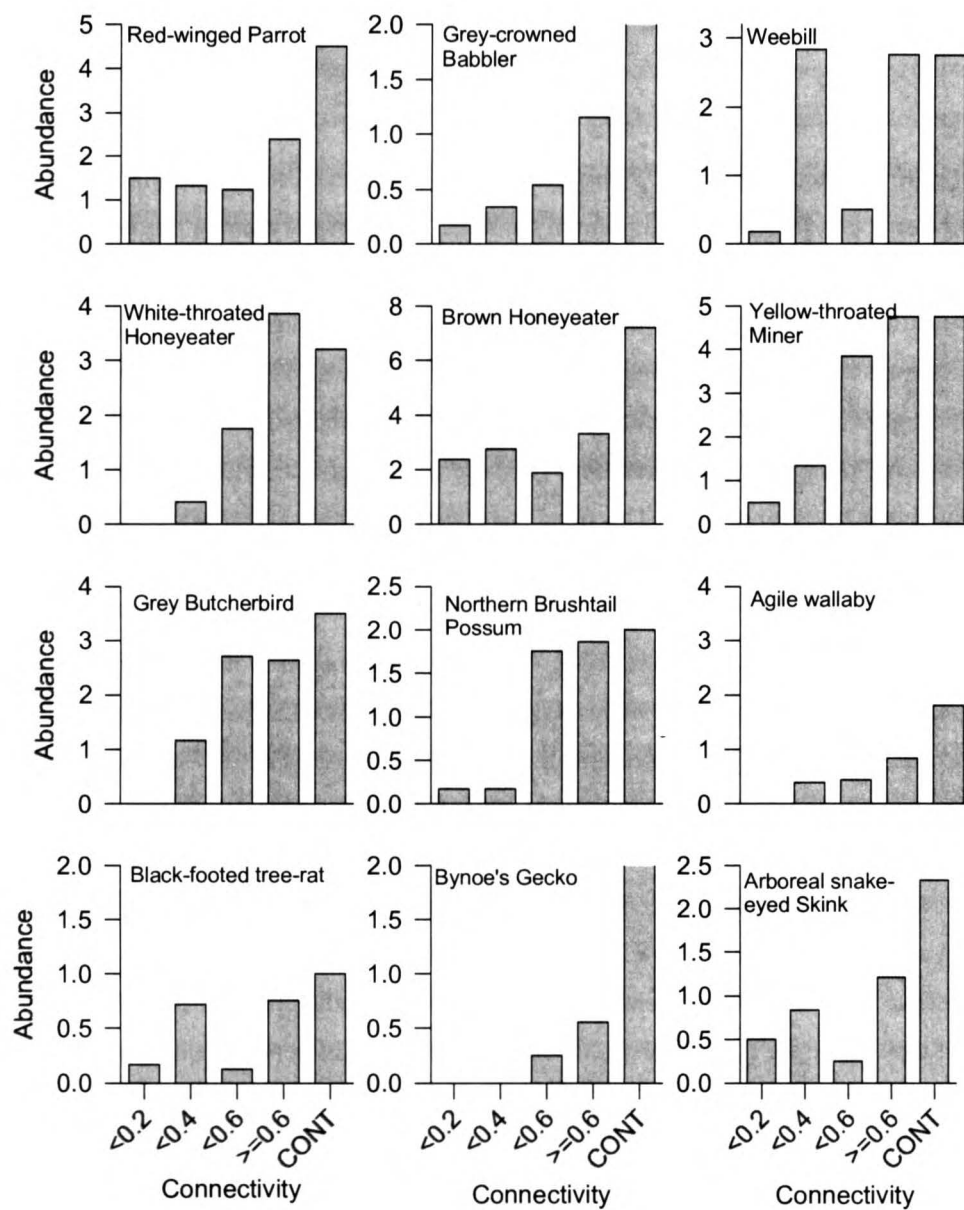
Figure 3.15: The mean abundance of species in sites grouped by connectivity to other woodland. The mean abundance in continuous woodland sites "Cont" is also included. Only species that showed a significant positive area effect in the standard model are shown.

Effects of Fragmentation on Individual Species

Specific examples of some fragmentation responses representing species with the strongest

effects, and/or representing species from different major taxanomic groups are given below.

Mammals

Northern Quoll: The northern quoll *Dasyurus hallucatus* is the smallest of Australia's four quoll

species (Strahan 1995). Nocturnal and primarily arboreal, quolls mostly den in tree hollows.

Weight ranges from 400-900g for males and 300-500g for females (Strahan 1995). Northern

quolls have suffered a substantial decline from their former broad distribution across the Top

End and they may be particularly vulnerable to catastrophes because of their short life-span

(Braithwaite and Griffiths 1994; Chapter 4). In this study the northern quoll showed a strong

negative response to fragmentation, with none recorded from fragments with less than 65%

woodland within 4 km (Figure 3.13). This trend has continued with a 2-year mark-recapture of

mammal species at a selection of these sites supporting this finding (see chapter 4).

Black-footed tree-rat: The black-footed tree-rat *Mesembriomys gouldii* is one of Australia's

largest native rodents weighing up to 900 g (Rankmore 2003). It is restricted to tropical

woodlands near the coastal areas in northern Queensland, the Top-End of the Northern Territory

and the Kimberley in Western Australia (Strahan 1995; Rankmore 2003). Black-footed tree-rats

are considered to be fairly common in the Northern Territory but rare in the rest of their range.

This species showed independent effects of fragment area and connectivity (Figures 3.14 and

3.15), being absent from patches below 2 ha and from sites with connectivity smaller than 0.15.

They only occur in the smaller fragments if connectivity is high, and in poorly connected

fragments if they are large. This suggests that black-footed tree-rats depend on a certain amount

of woodland to maintain a population, and this may be achieved either in a single large patch, or

in several connected patches.

Agile Wallaby: The agile wallaby *Macropus agilis* is the most common macropod in the coastal

areas of tropical Australia. This species showed a very similar pattern to the black-footed tree-

rat. The wallaby will occur in patches as small as 1 ha (Figure 3.14) if connectivity is above 0.7

and in fragments with less than 0.5 connectivity (Figure 3.15) if they are at least 10 ha in size.

Wallabies will use cleared land as well as woodland and this is the main difference between

them and black-footed tree-rat. However, the similarity between the two species suggests that

whatever use wallabies make of cleared land, it is the extent of woodland that determines how

many can live in an area.

Northern Brushtail Possum: The common brushtail possum *Trichosurus vulpecula* is widely distributed across Australia (Strahan, 1995). Animals in the tropical north of Australia are smaller and have less brushlike tails than their southern cousins. Possums appear to be able to persist in low abundance in sites small in area (approx 2 ha) with less than 23% of woodland remaining within a 4 km radius of the patch and low connectivity of 0.15. However, abundance increases with increased connectivity and bush within 4 km (Figures 3.15 and 3.13).

Birds

Of the smallest 13 bird species encountered during the study, eight showed significant fragmentation effects. This suggests that, in comparison to the larger birds, many of these species are unable to move far enough to overcome the landscape effects of fragmentation, being more like mammals in their response.

Striated Pardalote: A small bird weighing less than 10 g, the striated pardalote *Pardalotus striatus* occurs within woodland and open forests of much of Australia. The Striated Pardalote increased in abundance with an increasing amount of woodland within 4 km of the patch (Figure 3.13) and with patch area (Figure 3.14). It occurred in patches as small as 0.57 ha if there was more than 73% woodland within a 4 km radius of the patch. However, numbers were highest in continuous woodland. A study by Seddon *et al.* 2001) in eastern Australia also found a positive relationship with remnant area.

Weebill: The weebill *Smicrornis brevirostris*, weighs less than 10 g that occurs in eucalypt woodlands. Abundance of the weebill showed a strong correlation with patch area (Figure 3.14), being found in patches as small as 0.5 ha only if they were well connected. This finding is supported by the work of Seddon *et al.* 2001), who also found a positive relationship with patch areas for this species.

Grey-crowned Babbler: The grey-crowned babbler *Pomatostomus temporalis* is a sedentary bird, living and breeding in co-ordinated communal groups containing as many as 12 individuals (Schodde and Tidemann 1986). Groups generally consist of one breeding pair, its siblings and its offspring, with pairs mating for life. The group as a whole defend and maintain a territory of approximately 12 ha (Schodde and Tidemann 1986). The abundance of the Grey-crowned Babbler was significantly related to connectivity (Figure 3.15). It occurred in patches with low connectivity (0.14) only if the patch was large (about 100 ha). Along with its absence from modified habitats, these results identified that babblers prefer to move via connected corridors rather than across the cleared matrix. Studies of the White-browed babbler

Pomatostomus superciliosus in highly fragmented environments in southern Australia have found that this species uses wooded corridors for dispersal and as breeding habitat (Cale 2003), and is capable of traversing gaps of at least 270 m (Brooker *et al.* 1999).

Red-Tailed Black Cockatoo: The red-tailed black cockatoo *Calyptorhynchus banksii* is a large, widely distributed and highly nomadic bird. It is granivorous, feeding high in the trees or on the ground. They nest in trees with a hollow of suitable size, laying eggs from March to July in the Northern Territory (Schodde and Tidemann 1986). The model for the red-tailed black cockatoo, a bush-dependent species, did not show any response to fragmentation. Rather, the significant variables were the number of hollows and fire frequency. This is consistent with what is known about the ecology of the bird: it requires hollows in large trees for its nests and it often feeds in recently burned country. The absence of a fragmentation response may reflect the scale at which this species operates. Capable of covering large distances it may respond to the amount of woodland over much larger areas (such as within 20 km).

Reptiles

Bynoe's Gecko: Bynoe's gecko *Heteronotia binoei* is perhaps the most widely distributed lizard in Australia. Lacking pads on its toes like other geckos, this species rarely climbs, preferring to shelter in rock crevices and under logs (Cogger 1996). Connectivity was found to be an important factor in the presence of Bynoe's Gecko within fragments. Abundance increased with increasing connectivity (Figure 3.15). Although the Bynoe's Gecko showed no association with the amount of woodland within 4 km of the site, the gecko was found in patches of lower connectivity (0.48) only if the amount of woodland within a 4 km area of the site was high.

Port Essington Ctenotus: The Port Essington ctenotus *Ctenotus essingtonii* is a medium sized slender skink. It is distributed along the coast and islands of the Northern Territory, extending inland from the Gulf of Carpentaria and across Cape York Peninsula in Queensland (Cogger 1996). The Port Essington Ctenotus was found to have a significant relationship with connectivity (Figure 3.15) and the amount of bush within 4 km of the site (Figure 3.13). They occurred in patches with low connectivity (0.21) only if there was more than 89% bush within a 4 km radius of the site. This suggests that the Port Essington Ctenotus may move across open ground over short distances, but prefers to move via connected corridors than across the cleared matrix.

Scenarios to illustrate the results

The design of landscapes to achieve the maximum retention of wildlife will require three aspects of the spatial distribution of fragments to be considered: the overall proportion of the landscape retained; the size of fragments; and their connection with corridors. To illustrate how

these combine to influence the species present, three scenarios are shown in Figure 3.6. The first is the actual landscape, where three fragments differ in size and isolation. Our results predict that if corridors were added, several species would return to particular patches (scenario 2), and if the percentage of woodland within 4 km was raised from around 50 to 65% (scenario 3), other species, including the quoll, would return. It should also be noted that it may not be possible to design a connected corridor system capable of conserving all species (especially those that are uncommon or rare), and considered vulnerable to habitat fragmentation. However, the principle remains clear. As agricultural development proceeds in the tropical north, considerable areas of woodland need to be retained and they should be connected with corridors. It should also be noted that although we are able to create these scenarios illustrating the results, they only take into account spatial aspects of the landscape. Other factors, such as the nature of the surrounding matrix and the quality of habitat remaining would also have an affect.

Figure 3.16: Scenarios illustrating the effect of Connectivity and Bush4k on the predicted occurrence of selected mammal species. Picture 1) is the true landscape, dark = woodland, pale = modified land. Three fragments, A, B and C have different values for the three fragmentation variables:

Scenario/	Fragment		
Variable	A	B	C
Scenario 1)			
Area	100	9.7	0.8
Bush4k	49	37	56
Connect	0.4	0.17	0.22
Scenario 2)			
Area	100	9.7	0.8
Bush4k	50	37	56
Connect	0.8	0.7	0.8
Scenario 3)			
Area	100	11	0.8
Bush4k	62	46	64
Connect	0.8	0.75	0.8
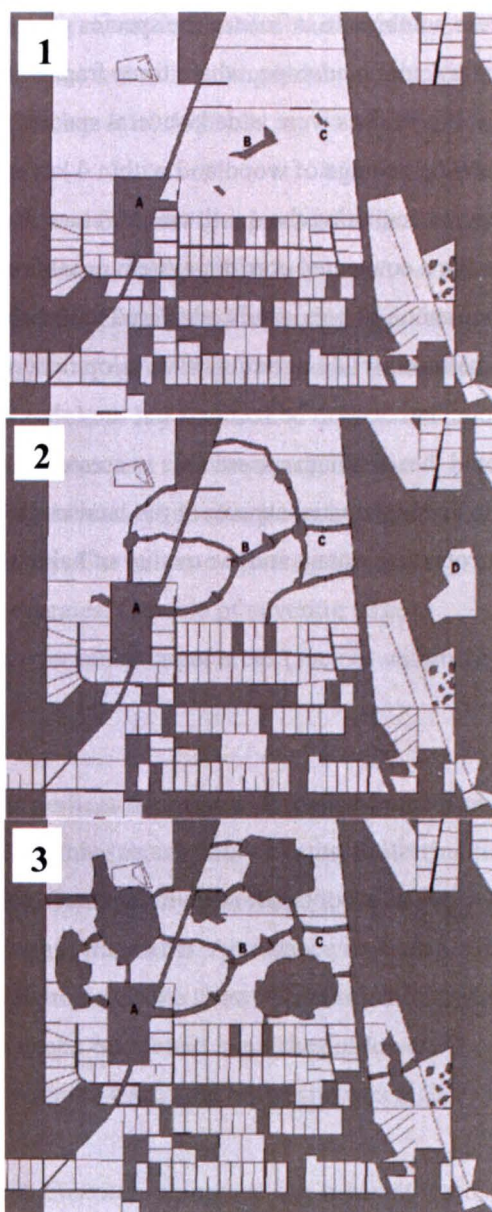
In scenario 2), the fragments in the large clearing are connected with corridors. A cleared area is added at D to keep the overall cleared area the same as in 1). In 3), large internal fragments are added and no additional clearing is present, to increase Bush4k by about 10%.

Based on the results of this study, it is predicted that in scenario 1), quolls do not occur at all in the 3 remnants, tree-rats and wallabies occur only in fragment A, and possums occur in A and B. In Scenario 2), fragment C gains possums, and fragment B gains wallabies and tree-rats. In scenario 3), fragment C gains wallabies, and A gains quolls. Several bird and reptile species would also return to the fragments in scenarios 2) and 3).

Discussion

There are a number of species that actively use or prefer the new matrix of modified habitats. These species tend to be generalists that prefer open areas (e.g. Torresian crow *Corvus orru*). Most (83 species) were recorded too infrequently to analyse individually statistically. Rare species are likely to be the first to suffer from fragmentation due to their already low population densities and the loss of available habitat (Bennett 1990; Saunders *et al.* 1991).

The edges of fragments differ from the interior, but in this study edge effects did not penetrate far into the fragment. Weed cover stabilised after about 20 m into the fragment at about half the edge value, and tree cover after about 60 m at twice the edge value. I found that 89% of fragments contained weeds, but for most the average weed cover was below 3%. Cowie and Werner 1993) also recorded similarly low cover values in un-fragmented woodlands in Kakadu National Park. Many weeds are spreading in Litchfield Shire, and so it is expected that weed invasion into fragments will become worse over time (Kean and Price 2003). In particular Gamba grass *Andropogon gayanus* and Mission grasses *Pennisetum polystachion* and *P. pedicellatum* are rapidly spreading species that increase the fuel levels in open forest, thereby increasing fire intensity (Rossiter 2001; Kean and Price 2003). Most fragments in the study have been isolated only since 1980, but some at Tipperary were cleared in the 1960s and have weed cover above 20%. These trends do not suggest that edges are swamped by weeds, or have lost all of their large trees. Animal species that are affected by weeds or prefer large trees will avoid fragment edges or be absent from small patches altogether. On the other hand, species that prefer weeds or open habitats might be expected to be more common in edges. In this study almost all species made no distinction between edges and interiors of fragments. This is consistent with the minor edge effects found in the habitat variables. It is possible that the sample of fragment sizes used in this study was too small to detect possible edge and interior species, as large fragments (those containing an edge and a centre quadrat) were those larger than 10 ha.

The width of a corridor influences which species will use it and how serious the edge effects will become. In general, a corridor is likely to be more effective where animals can live in the corridor as well as move through it. Therefore it is better to maximise the width of corridors where possible, potentially incorporating a greater diversity of habitats and thereby making the corridor acceptable for more specialised species (Bennett 1990). Because of the small number of corridors sampled in the study, and the large variation in corridor width, we are unable to define an appropriate corridor width. Most species occurred within corridors, confirming that corridors have an important role in maintaining wildlife in the landscape. Incorporating habitat corridors

into landscape plans will be an increasingly important component of the conservation of wildlife in Australia's tropical woodlands.

A primary finding of this study was that the bird, mammal and reptile species living in the Northern Territory tropical woodlands and forests fall into three groups in relation to their response to fragmentation. Many species actively use the new matrix, and therefore at this point in time there is no need to implement measures for their conservation. Others do not use the matrix, but appear to remain at their previous levels in woodland fragments. Where fragmentation is severe, these populations may become non-viable as too few individuals will be left in the landscape. For these species, it is probably not necessary to implement specific conservation measures, as they will benefit from the measures needed to conserve the third group of species, namely those that showed a negative response to fragmentation. These species have not only been lost from areas that have been cleared, they have also declined in remaining fragments. Note that of the 158 species recorded in this study (83 species) were recorded too infrequently to analyse statistically. Rare species are likely to be the first to suffer from fragmentation due to their already low population densities and the loss of available habitat (Bennett 1990; Saunders *et al.* 1991).

The 13 species that responded positively to habitat fragmentation would be secure under moderate fragmentation, as exemplified by the Litchfield Shire study sites. However, it is doubtful that they would survive under conditions of extreme fragmentation. Most depend on woodlands for some part of their needs, whether it be food, shelter or nesting sites, and so these species will need some woodland retained in the landscape. For the 28 species that showed negative fragmentation effects, land uses must be planned to avoid losing them from the landscape. For this second group, it is noted that their populations are being reduced by the removal of woodland and lowered abundance from demographic and/or genetic effects of small population sizes in fragments. For example, when more than 75% of the woodland is cleared within a 4 km radius of a fragment, the abundance of brushtail possums *Trichosurus vulpecula* in the remaining fragments is about 25% of their abundance in un-fragmented woodland. A combination of these two factors yielded a decline in the possum population to 6% of that in an un-fragmented landscape. For the 26 species that showed no relationship with the fragmentation indices, I expect their populations to decline in line with the amount of woodland cleared.

Implication for landscape design

The design of future landscapes needs to focus on optimising the three important fragmentation indices: the amount of woodland within 4km of the fragment, Fragment Area, and Connectivity.

Although not able to support a high diversity, small fragments provide useful habitat for some species. Most species, even those that are affected by fragment size, occur in some small fragments. Thus fragments of any size are useful, but larger ones are better than smaller ones.

Connectivity allows many species to be present in fragments that would otherwise be too small to maintain them. Agile Wallabies and Black-footed Tree-rats were found in small fragments 0.8 ha and 2.0 ha respectively, but in these cases connectivity was high, above 0.6 (with 1.0 representing un-fragmented woodland). The width of a corridor influences which species will use it and how serious the edge effects will become. In general, a corridor is likely to be more effective where animals can live in the corridor as well as move through it. Therefore it is better to maximise the width of corridors where possible, potentially incorporating a greater diversity of habitats and thereby making the corridor acceptable for more specialised species (Bennett 1990). Because of the small number of corridors sampled in the study, and the large variation in corridor width, I was unable to define an appropriate corridor width. Most species occurred within corridors, confirming that corridors have an important role in maintaining wildlife in the landscape. Incorporating habitat corridors into landscape plans will become an increasingly important component of the conservation of wildlife in Australia's tropical woodlands.

Management of Fragments

Several management issues that affect wildlife in fragments were identified in this study, and their consideration is important to maintaining the value of retained fragments. The GLM analysis highlighted several environmental variables that consistently influenced the abundance of species. The most important of these was fire frequency.

Fire: There is widespread agreement that fire regimes in northern Australia are currently more frequent, intense and homogeneous than they were when indigenous people routinely managed fire across this land (Haynes 1985; Bowman and Panton 1993; Braithwaite 1996; Russell-Smith *et al.* 2000). It is not possible from the nature of this study to provide an optimum fire frequency, and arguably there is no such ideal that encompasses all species. However, the results are consistent with other studies, which suggest that a mosaic of fire histories is a better goal (Russell-Smith *et al.* 1997; Bowman 1999; Gill *et al.* 2000; Woinarski *et al.* 2001b; Yibarbuk *et al.* 2001; Williams *et al.* 2002b; Price *et al.* submitted). Price *et al.* submitted) suggest that low levels of habitat fragmentation may actually increase habitat heterogeneity in the landscape, in the form of new vegetation types and a variety of fire regimes. In one region of the study area (Lambell's Lagoon), fauna diversity and abundance was very high. Here many of the sites surveyed had not been burnt in over 20 years, while other sites had been burnt either

twice during that time or were annually burnt. This variety of fire regimes provides species with a greater diversity of habitats and resources.

Trees, shrubs and ground cover: Several species need large trees either for nesting or roosting, with 40% of mammals, 18% of birds, 20% of reptiles and 13% of frogs in the Top End of the Northern Territory using tree hollows (Taylor *et al.* 2003). Others favour them because they provide abundant resources (e.g. nectar or insects). Williams *et al.* 1999a) found that fire reduces the survival of large trees (> 40 cm DBH), those most likely to contain hollows, so fragments need to be managed to conserve large trees by avoiding fires late in the dry season. It is important that landholders and managers do not cut down large trees, and actively support measures for their conservation.

Weeds: Weed cover was important to fauna, but most species were still present in sites with up to 20% weed cover. It is likely that weeds will become an increasingly major issue in the management of fragments as the time since isolation increases. At present weeds do not appear to be a major issue. It is noted that while this is true of vertebrates, invertebrates and plants are more likely to have been affected by weeds

Exotic animals: Exotic animals affect native species, either by predation, competition for resources or habitat degradation. Although wild and domestic dogs and cats are known to be plentiful in the rural area, they are evasive and were not observed frequently enough to analyse statistically. It can be predicted that the symptoms of exotic species will increase as fragmentation continues. Fragments are likely to be degraded by exotic species (pigs, cattle, and horses), and exotic predators (domestic and wild dogs and cats) will have ever-increasing effects as the fragments become smaller and increasingly isolated by time as well as distance.

Conclusion

This chapter describes the habitat preferences of fauna recorded in tropical woodlands near Darwin in the Northern Territory, identifying those species capable of utilising modified habitats and woodland corridors. A total of 158 animal species were recorded in the survey, but most were not recorded frequently enough to analyse. Analysis was conducted on a set of 75 species found in more than six sites.

Only a small proportion of species (25%) used modified land, but most (69%) were recorded in corridors. No species could confidently be classified as edge specialists, i.e. preferring the interface between woodland and modified land. Faunal species richness was highest in continuous woodland and lowest in mango orchards.

Habitat at the edge of fragments was different to the interior with approximately twice the cover of weeds and only 50% of the tree cover. However, both effects dissipated quickly inside the fragments.

The open forest and woodland fragments in this study were all isolated within the last 30 years, and many of them within the last 10 years. This is insufficient time for populations of animals or plants to adjust to the new landscape. Studies of fragmentation around the world show that species continue to disappear from fragments more than 70 years after isolation (Diamond *et al.* 1987; Sieving and Karr 1997). The speed with which species re-adjust depends on generation time (Brook *et al.* 2003), so small rodents and dasyurid marsupials will adjust quickly while longer-lived species such as cockatoos and wallabies may take several decades to adjust. In this study I could not discern time since isolation as a factor affecting the occurrence of species, as the variable was so highly correlated with the percentage of woodland within 4 km of the fragment. Consequently, our results are an optimistic assessment of the impact of fragmentation because time since isolation is yet to have an impact. Thus the conclusion drawn here is that many animals are likely to continue to decline in abundance in the open forest and woodland fragments in the Northern Territory.

For every species analysed, there was another that was recorded too infrequently for individual analysis. It is likely that some of these species also show a fragmentation response. Being uncommon, their populations are already at low levels and the further reduction caused by habitat fragmentation may not be sustainable. Uncommon or rare species are often the first ones lost when a habitat is fragmented (Diamond *et al.* 1987; Laurance 1994). There have also been 339 other vertebrate species recorded in Litchfield shire that were not recorded in this study (PWCNT unpublished atlas data).

Most habitat fragmentation studies have been conducted in areas where large-scale clearing has resulted in an extreme loss of native vegetation. For these areas, the aim of was to report on the effects that habitat fragmentation and loss has had on the biota of the region and to suggest the best ways to restore and manage the remaining vegetation (Brook *et al.* 2003). In contrast, the main aim here was to determine the requirements of the region's fauna in order to guide the design of future agricultural landscapes. The amount of land clearing in the Northern Territory has increased markedly since the early 1990s, although it is still limited compared to southern Australia. Consequently, planners in the Northern Territory have a rare opportunity to enact clearing controls, informed with the principles of ecological sustainability, to help ensure the long-term maintenance of the Northern Territory's native flora and fauna.

This chapter has investigated how the vertebrate species inhabiting the open eucalypt forests of the monsoonal Northern Territory are being affected by habitat fragmentation. However this has only provided us with the situation at one snapshot in time, and cannot provide us with information on how habitat fragmentation is affecting species survival. To explore this aspect, a selection of fragments in areas with varying degrees of fragmentation intensity were surveyed for medium-sized mammals over a 2 year period. The effects of habitat fragmentation on the survival of medium-sized mammals are assessed in the next two chapters.

Appendix 3.1: A list of all study sites, identifying habitat type, area (ha), connectivity and the amount of Bush (%) within 4 km of the site. Site numbers are listed to identify the sites on the maps of the study areas in Appendix 2.

Site No.	Site Name	Habitat Type	Area (ha)	Connectivity	Bush4km
1	HUMP1	PATCH	6.031	0.725	47.44
2	HUMP2	PATCH	49.707	0.805	46.17
3	HUMP2/7	PATCH	0.581	0.704	53.75
4	HUMP2/3	PATCH	0.145	0.668	53.93
5	HUMP2/6	PATCH	13.233	0.645	47.78
6	HUMP3	PATCH	45.848	0.707	48.9
7	WAN1	PATCH	0.934	0.558	48.58
8	HUMP2/5	PATCH	2.042	0.71	46.93
9	WAN2	PATCH	2.023	0.705	47.09
10	WAN3	PATCH	1.28	0.726	47.44
11	HUMP4	PATCH	1.833	0.751	51.04
12	PION4	PATCH	0.712	0.736	57.53
13	WAN4	PATCH	0.525	0.709	58.31
14	PION5	PATCH	5.969	0.718	55.54
15	PION6	MANGO	0.098	0.607	54.45
16	PION3	PATCH	13.715	0.689	56.71
17	PION2	PATCH	2.016	0.771	61.67
18	HUMP2/4	PATCH	5.148	0.714	58.72
19	WAN5	PATCH	5.3	0.617	71.89
20	WAN6	CORRI	1.065	0.466	80.72
21	WAN7	CLEAR	0	0.434	81.5
22	WAN8	BUSH	2500	0.772	84.5
23	WAN10	BUSH	2500	0.837	88.4
24	WAN9	BUSH	2500	0.82	87.96
25	PION1	PATCH	9.797	0.45	72.87
26	HUMP2/2	CORRI	1.699	0.74	75.85
27	HUMP2/1	CORRI	2.705	0.744	74.9
28	ARN2	PATCH	16.254	0.787	81.26
29	ARN1	PATCH	2.391	0.587	86.67
30	ARN4B	CORRI	7.895	0.212	77.86
31	ARN4A	CORRI	10.08	0.182	76.94
32	ARN3A	PATCH	0.391	0.329	76.25
33	ARN3B	CLEAR	0	0.283	76.39
34	ARN5B	BUSH	2304	0.806	73.58
35	ARN5A	BUSH	2304	0.953	74.42
36	LAM1	PATCH	1.253	0.485	71.67
37	LAM5	PATCH	8.341	0.711	71.45
38	LAM4	PATCH	3.534	0.732	66.86
39	LAM2	PATCH	7.851	0.694	66.16
40	LAM3	PATCH	29.648	0.692	66
41	FOGG5	CLEAR	0	0.589	68.77
42	LAM6	PATCH	0.862	0.689	71.57
43	FOGG4	BUSH	441	0.799	64.01
44	FOGG3	BUSH	441	0.616	62.84
45	FOGG1	MANGO	470	0.265	67.56
46	FOGG2	MANGO	470	0.418	64.87
47	FOGG6	PATCH	0.57	0.289	67.02
48	FOGG7	CLEAR	0	0.365	66
49	FOGG9	PATCH	1.485	0.677	81.62

Site No.	Site Name	Habitat Type	Area (ha)	Connectivity	Bush4km
50	FOGG8	PATCH	15.598	0.451	66.58
51	BERR1	PATCH	16.657	0.529	68.25
52	BERR2A	MANGO	0.111	0.449	67.38
53	BERR2B	MANGO	0.111	0.355	67.28
54	BERR3B	PATCH	4.945	0.593	64.29
54	HONY1	PATCH	18.206	0.328	42.29
55	HONY2	PATCH	52.505	0.308	35.07
57	HONY4	BUSH	343.411	0.369	55.26
58	BLAIN1	PATCH	1.401	0.169	32.46
59	BLAIN2	CORRI	57.184	0.203	34.37
60	BLAIN3	CLEAR	0	0.116	9.45
61	BLAIN4	CORRI	1.949	0.126	10.7
62	BLAIN5	PATCH	100.878	0.137	13.71
64	BLAIN6	PATCH	2.22	0.148	23.15
65	BLAIN7	PATCH	18.781	0.199	28.76

Appendix 3.2: A map showing location of study areas and location of sites within each area. Individual maps of each location follow; (a) Humpty Doo, (b) Berry Springs, (c) Tipperary.
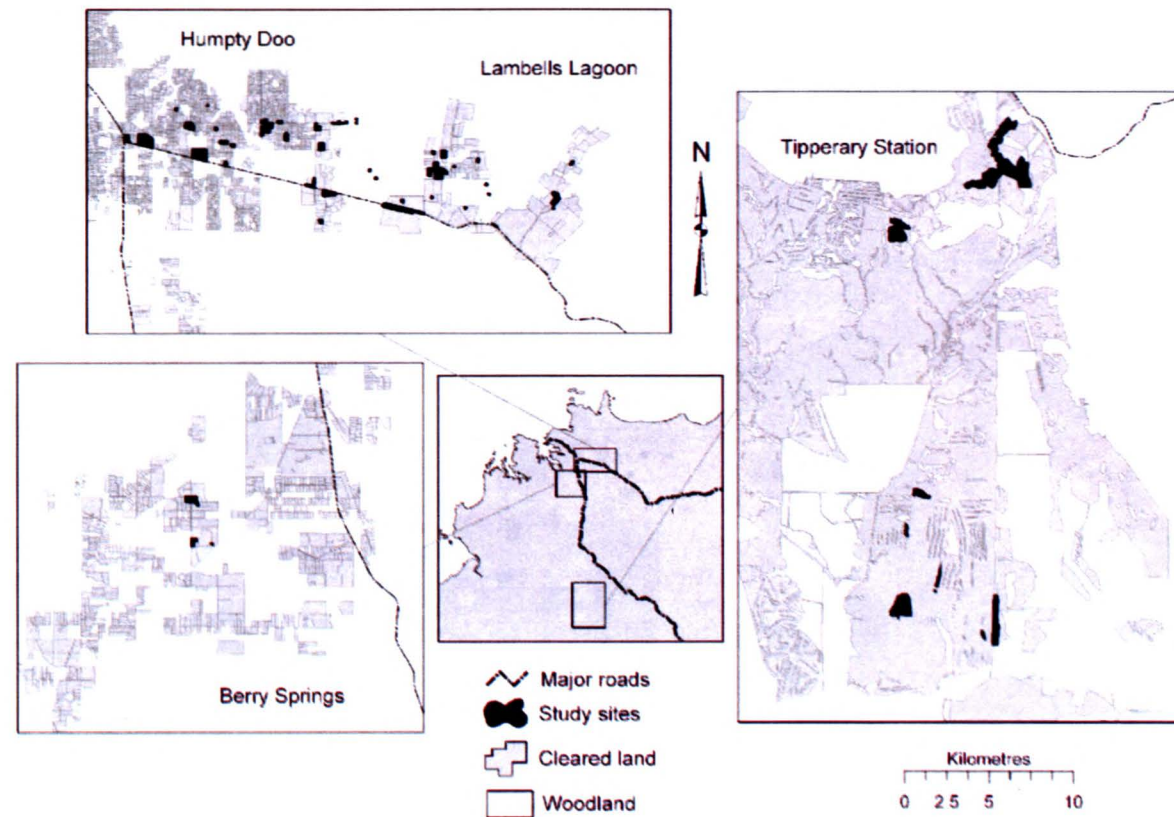
(a): Map of Humpty Doo in the Litchfield Shire study area, with study sites identified by number.
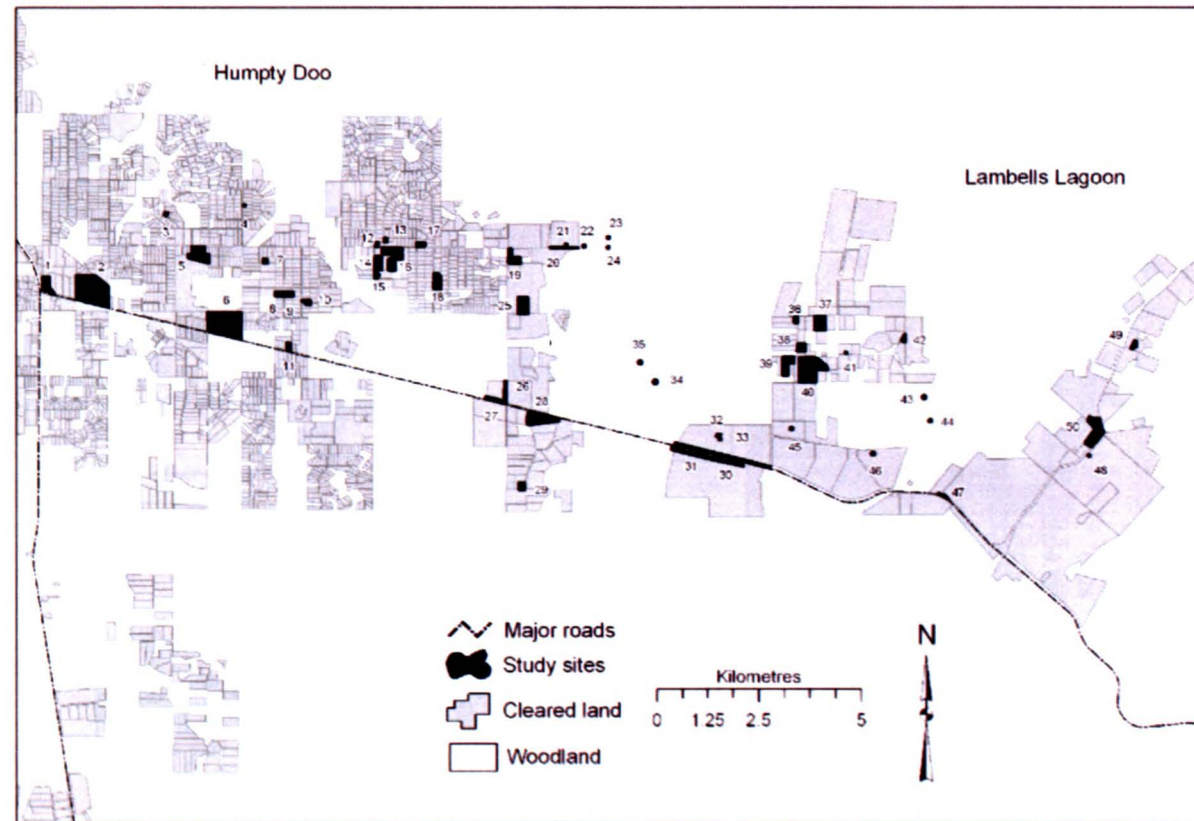
(b): Map of Berry Springs in the Litchfield Shire study area, with study sites identified by number.
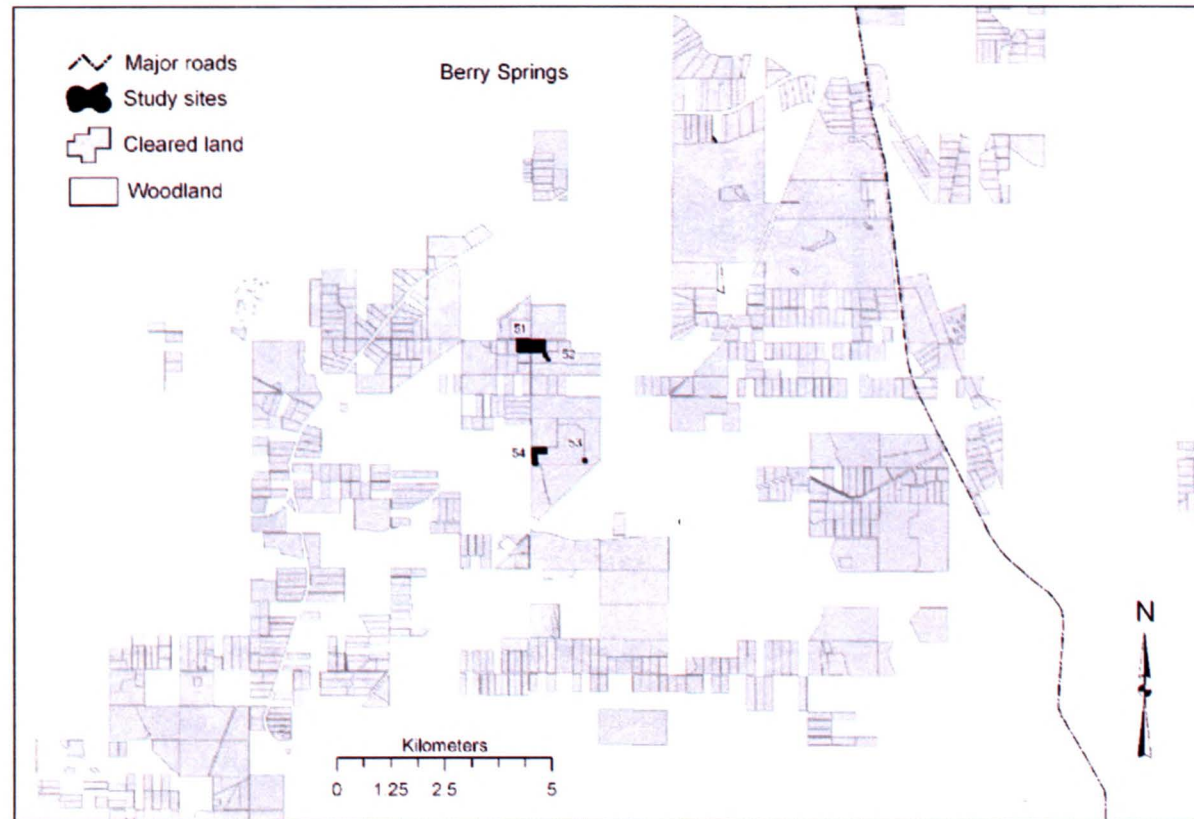
(c): Map of Tipperary Station in the Daly Basin study area, with study sites identified by number.

Appendix 3.3: A list of all species recorded during the study showing the number of times they were observed, the number and location of sites, the number of fragmented sites and the minimum area from which they were recorded

Common Name	Scientific Name	No. observations	No. of sites	No. fragment sites	Minimum Area (ha)
Amphibians					
Marbled Frog	Limnodynastes convexiusculus	12	9	6	0.57
Desert Tree Frog	Litoria rubella	2	2	2	9.8
	Uperoleia inundata	4	3	3	7.85
	Uperoleia lithomoda	6	6	4	0.57
Birds					
Australian Owlet-nightjar		5	4	3	0.93
Banded Honeyeater		1	1	1	18.78
Bar-breasted Honeyeater		1	1	1	0.86
Barking Owl		1	1	1	0.86
Barn Owl		2	2	1	100
Bar-shouldered Dove	Geopelia humeralis	60	42	32	0.15
Black Kite	Milvus migrans	9	8	7	1.7
Black-breasted Buzzard		2	2	1	5.3
Black-faced Cuckoo-shrike	Coracina novaehollandiae	25	19	18	0.57
Black-faced Woodswallow		3	2	2	2.22
Black-tailed Treecreeper		1	1	0	100
Blue-faced Honeyeater	Entomyzon cyanotis	52	36	29	0.53
Blue-winged Kookaburra	Dacelo leachii	44	31	24	0.53
Brown Falcon		3	3	2	18.78
Brown Goshawk		2	2	2	1.4
Brown Honeyeater	Lichmera indistincta	47	33	28	0.57
Brown Quail	Coturnix ypsilophora	8	8	6	1.07
Brush Cuckoo	Cacomantis variolosus	11	9	5	1.95
Bush Stone-curlew	Burhinus grallarius	13	12	8	4.95
Common Bronzewing		2	2	1	52.51
Crested Pigeon		2	2	1	1.95
Crimson Finch		1	1	1	15.6
Dollarbird	Eurystomus orientalis	11	5	4	4.95
Double-barred Finch	Taeniopygia bichenovii	19	15	11	0.57
Dusky Honeyeater	Myzomela obscura	8	6	6	0.86
Figbird	Sphecotheres viridis	16	14	12	0.58
Forest Kingfisher	Todiramphus macleayii	8	8	5	2.39
Galah		6	6	5	1.95
Golden-headed Cisticola		2	1	1	52.51
Great Bowerbird	Chlamydera nuchalis	12	11	8	1.95
Green-backed Gerygone		1	1	1	15.6
Grey Butcherbird	Cracticus torquatus	50	34	30	0.15
Grey Fantail		3	3	1	7.85
Grey Shrike-thrush		2	2	1	18.78
Grey-crowned Babbler	Pomatostomus temporalis	23	17	14	1.28
Horsfield's Bronze-Cuckoo		1	1	1	18.78
Leaden Flycatcher	Myiagra rubecula	14	11	6	0.86
Lemon-bellied Flycatcher		3	3	2	0.86
Little Corella		2	2	2	0.93
Little Friarbird	Philemon citreogularis	52	39	33	0.57
Long-tailed Finch	Poephila acuticauda	12	11	7	1.07
Magpie-lark	Grallina cyanoleuca	38	33	23	0.1
Masked Finch		4	4	1	0.57

Common Name	Scientific Name	No. observations	No. of sites	No. fragment sites	Minimum Area (ha)
Masked Lapwing		3	3	0	100
Mistletoebird	Dicaeum hirundinaceum	21	16	12	0.86
Nankeen Kestrel		2	2	1	1.7
Northern Fantail		1	1	1	7.85
Northern Rosella	Platycercus venustus	7	7	4	2.39
Olive-backed Oriole	Oriolus sagittatus	16	13	10	0.58
Orange-footed Scrubfowl		2	2	2	0.86
Peaceful Dove	Geopelia striata	27	23	16	0.86
Pheasant Coucal	Centropus phasianinus	15	12	12	1.25
Pied Butcherbird	Cracticus nigrogularis	18	17	17	0.53
Pied Imperial Pigeon		6	5	5	0.58
Rainbow Bee-eater	Merops ornatus	41	31	24	0.58
Rainbow Lorikeet	Trichoglossus haematodus	43	30	28	0.15
Rainbow Pitta		1	1	1	15.6
Red-backed Fairy-wren	Malurus melanocephalus	23	17	13	0.93
Red-backed Kingfisher		4	2	2	52.51
Red-tailed Black-Cockatoo	Calyptorhynchus banksii	28	21	13	1.95
Red-winged Parrot	Aprosmictus erythropterus	27	21	18	0.71
Restless Flycatcher		4	4	3	0.86
Rose-crowned Fruit-Dove		2	2	2	0.86
Rufous Whistler	Pachycephala rufiventris	16	13	11	0.71
Rufous-throated Honeyeater		6	5	5	0.86
Sacred Kingfisher		4	4	2	1.49
Silver-crowned Friarbird	Philemon argenticeps	27	21	18	0.58
Southern Boobook		1	1	0	100
Spangled Drongo	Dicrurus bracteatus	8	7	5	0.86
Spotted Nightjar		1	1	0	100
Striated Pardalote	Pardalotus striatus	56	41	33	0.15
Sulphur-crested Cockatoo	Cacatua galerita	22	18	10	0.71
Tawny Frogmouth		5	4	4	0.15
Torresian Crow	Corvus orru	33	28	20	0.86
Tree Martin	Hirundo nigricans	13	9	5	1.25
Varied Lorikeet		3	3	2	16.25
Varied Triller	Lalage leucomela	21	17	10	0.86
Weebill	Smicrornis brevirostris	45	28	24	0.15
Whistling Kite	Haliastur sphenurus	28	25	19	0.71
White-bellied Cuckoo-shrike	Coracina papuensis	58	43	33	0.15
White-breasted Woodswallow		1	1	0	100
White-gaped Honeyeater	Lichenostomus unicolor	27	19	17	0.86
White-throated Gerygone		1	1	1	1.95
White-throated Honeyeater	Melithreptus albogularis	45	31	25	0.1
White-winged Triller		1	1	1	100
Willie Wagtail	Rhipidura leucophrys	16	11	9	0.57
Yellow Oriole	Oriolus flavocinctus	27	18	15	0.71
Yellow-throated Miner	Manorina flavigula	52	35	30	0.15

Mammals

Dog *	Canis familiaris	4	4	3	1.07
Northern Quoll	Dasyurus hallucatus	14	11	6	1.25
Cat *	Felis catus	1	1	1	0.58

Common Name	Scientific Name	No. observations	No. of sites	No. fragment sites	Minimum Area (ha)
Northern Brown Bandicoot	Isoodon macrourus	71	48	39	0.53
Agile Wallably	Macropus agilis	33	23	15	0.86
Grassland Melomys	Melomys burtoni	13	13	9	0.86
Black-footed tree-rat	Mesembriomys gouldii	25	17	16	2.02
House mouse *	Mus musculus	2	2	2	0.15
	Petaurus breviceps	3	2	2	29.65
Common Planigale	Planigale maculata	5	5	4	1.4
Delicate Mouse	Pseudomys delicatulus	14	12	9	0.57
Western Chestnut Mouse	Pseudomys nanus	3	2	2	18.21
	Pteropus alecto	2	1	1	29.65
	Pteropus scapulatus	3	2	2	3.53
Dusky Rat	Rattus colletti	1	1	1	7.85
Pale field rat	Rattus tunneyi	13	7	7	1.95
Red-cheeked Dunnart	Sminthopsis virginiae	12	11	8	0.57
Pig *	Sus scrofa	2	2	0	100
Northern Brushtail Possum	Trichosurus vulpecula	55	38	31	0.15
Northern Freetail-bat	Chaerophon jobensis	13	13	8	1.25
Little Broad-nosed Bat	Scotorepens greyii	11	11	8	0.57
	Pipistrellus adamsi	1	1	1	0
	Pipistrellus westralis	4	4	3	5.15
	Pseudechis australis	1	1	1	1.4
	Rhinoplocephalus pallidiceps	1	1	1	2.02
	Saccolaimus flaviventris	1	1	1	1.4
	Scotorepens greyii	12	11	9	0.15
	Simoselaps semifasciatus	1	1	1	4.95
Reptiles					
Northern Death Adder	Acanthophis praelongus	1	1	1	18.21
	Carlia amax	5	5	4	5.3
Slender Rainbow Skink	Carlia gracilis	8	6	5	0.53
Striped Rainbow Skink	Carlia munda	59	43	35	0.15
Three-spined Rainbow Skink	Carlia triacantha	7	6	2	5.15
	Chalinolobus gouldii	1	1	1	52.51
	Chalinolobus nigrogriseus	2	2	1	1.28
Frillneck Lizard	Chlamydosaurus kingii	4	5	5	0.58
Arboreal Snake-eyed Skink	Cryptoblepharus plagiocephalus	31	28	24	0.15
Port Essington Ctenotus	Ctenotus essingtonii	25	22	14	0.57
	Ctenotus storri	5	3	2	16.66
	Delma borea	10	7	6	2.02
Spiny-tailed Gecko	Diplodactylus ciliaris	1	1	1	2.22
Two-lined Dragon	Diporiphora bilineata	27	21	12	1.4
Orange-naped snake	Furina ornata	1	1	1	0
Northern Dtella	Gehyra australis	3	3	3	0.53
Darwin Skink	Glaphyromorphus darwiniensis	26	21	15	0.57
Douglas' Skink	Glaphyromorphus douglasi	7	6	6	0.15
	Glaphyromorphus isolepis	1	1	1	0.86
House Gecko *	Hemidactylus frenatus	1	1	1	0.86
Bynoe's Gecko	Heteronotia binoei	16	14	12	0.53
Burton's snake-lizard	Lialis burtonis	1	1	1	52.51
Water Python	Liasis fuscus	1	1	1	15.6
Olive Python	Liasis olivaceus	1	1	1	0.86
	Lophognathus temporalis	13	12	11	0.57

Common Name	Scientific Name	No. observations	No. of sites	No. fragment sites	Minimum Area (ha)
Grey's Menetia	Menetia greyii	44	33	28	0.53
	Menetia maini	1	1	1	13.72
Storr's Snake-eyed Skink	Morethia storri	15	13	8	1.07
	Mormopterus beccarii	2	2	2	0
	Nyctophilus walkeri	5	5	3	7.85
Zig-zag Gecko	Oedura rhombifer	7	6	6	0.53
	Tiliqua scincoides	3	3	3	6.03
	Varanus panoptes	1	1	1	5.15
	Varanus tristis	10	10	8	0.15

BRUSH TAIL POSSUM.

BANDICOOT.
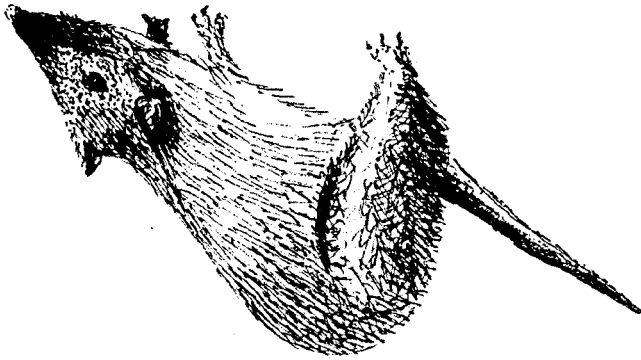
NORTHERN QUOLL.

BLACK-FOOTED TREE RAT.

CHAPTER 4

Survival of Four Mammal Species in a Fragmented Savanna Woodland.

Introduction

The transformation of once continuous expanses of native vegetation into fragmented remnants has a wide range of impacts on the population dynamics of individual species that are able to persist in remaining fragments. Many demographic changes have been reported in fragmented populations, including variations in population size (Lande and Barrowclough 1987; Diffendorfer *et al.* 1995; Collins and Barrett 1997; Dooley and Bowers 1998), recruitment (Brooker and Brooker 2002), reproductive output and sex ratios (Collins and Barrett 1997) and rate of emigration (Johannesen and Ims 1996).

When natural vegetation is removed species populations go through two distinct phases, with short and long term effects. Initially, loss in the amount of habitat available may lead to increased population densities and over crowding in the habitat patches that remain (Lovejoy *et al.* 1986; Saunders *et al.* 1991). This 'crowding effect' may lead to increased predation and competition pressure, followed by over- utilization of resources, altered behaviour and social structure of populations. As resources are exhausted there is a collapse in abundance, with species dropping out of the system as time goes on, and inevitably fragments will suffer a reduction in species richness. Soulé *et al.* (1988) showed that survival probabilities of species within the patch were negatively associated with time since isolation.

In this Chapter, I use the results of a 2 year mark-recapture study to investigate the effect of habitat fragmentation on the survival of four small mammal species in savanna woodlands, the northern brown bandicoot *Isoodon macrourus,* common brushtail possum *Trichosurus vulpecula,* northern quoll *Dasyurus hallucatus,* and black-footed tree-rat *Mesembriomys gouldii.* This assemblage of mammal species includes arboreal and ground-dwelling species that have different diet and resource requirements, baseline abundance and responses to habitat fragmentation (see Chapter 3). Their requirements are believed to be representative of, and encompass the needs of, many other mammal species in the area, and thus a landscape designed and managed to meet their needs should also encapsulate the requirements of many other species.

The specific aims of this chapter are:

- to investigate how habitat fragmentation affects the survival of each of the four species.
- evaluate the hypothesis that survival rates decrease as the level of habitat fragmentation increases.
- to assess differences in survival rates between sexes; and
- to assess survival and recapture rates in relation to temporal and environmental influences.

Study Species

Black-footed tree-rat

The black-footed tree-rat is a large (500-900g), nocturnal, murid rodent, restricted to open forests and woodlands near coastal areas in the Kimberley, Western Australia; the Northern Territory and Cape York Peninsula, Queensland (Figure 4.1a) (Friend and Calaby 1995; Rankmore 2003). The species is considered to be uncommon to rare in the Kimberley and Queensland and still common but patchily distributed in the Northern Territory (Rankmore 2003). Early distribution records from Eastern Arnhem Land and the Gulf of Carpentaria suggest that distribution has contracted in the Northern Territory (Friend and Calaby 1995) (Figure 4.1a).

The black-footed tree-rat is one of Australia's largest rodents and has been described as the Australian equivalent of a squirrel (Friend and Calaby 1995). They have a robust body with grizzly grey fur, large black feet and ears. Their most distinctive feature is a long hairy tail, 30-40cm in length that has a brush of white hairs at the end.

Tree-rats are aseasonal breeders, with a peak in breeding in the late dry season (Friend 1987). They have a relatively long gestation period of 43-44 days, with one to three young per litter. Young grow rapidly and are weaned at 4-5 weeks, when they weigh approximately 400g (Crichton 1969). Few details are known about the diet of black-footed tree-rats, however they are frugivorous, appearing to prefer fleshy and hard fruits and seeds, with pandanus fruit a particular favourite (Friend and Calaby 1995; Rankmore 2003). The patchy distribution of many suitable fruiting species is believed to be one factor responsible for the patchy distribution of black-footed tree-rats (Friend and Calaby 1995). Being nocturnal, black-footed tree-rats prefers to nest in tree hollows during the day, but they have also been recorded nesting in Pandanus where hollows are limited (Pittman 2003; Chapter 6).

Northern quoll

The northern quoll *Dasyurus hallucatus* is the smallest of Australia's four quoll species (Braithwaite and Begg 1995). It has suffered a substantial decline from a broad distribution across northern Australia (Figure 4.1b). Indeed, this map does not show the true extent of decline for this species, as it is disappearing from much of northern Australia as the cane toad *Bufo marinus* continues to invade the area.

A carnivorous marsupial, the quoll's diet includes a wide range of vertebrate species, invertebrates and fleshy fruits (Oakwood 1997). Nocturnal and primarily arboreal, quolls den in tree hollows. Their weight ranges from 400-900g for males and 300-500g for females (Braithwaite and Begg 1995). Northern quolls have a highly synchronous breeding cycle with mating occurring in late May/early June each year (Oakwood 2000). Young are born from mid June to July, with a litter size of one to eight (Braithwaite and Begg 1995; Oakwood 2000). Males show complete post-mating mortality, with most males dying within a few weeks of mating (Dickman and Braithwaite 1992; Oakwood 2000; Oakwood *et al.* 2001). Hence, males only live for 1 year while females may live for 2-3 years. Braithwaite and Griffiths (1994) suggested that the short lifespan of these animals makes them particularly susceptible to extinction.

a)

Mesembriomys gouldii

b)

Dasyurus hallucatus

c)

Trichosurus vulpecula

d)

Isoodon macrourus
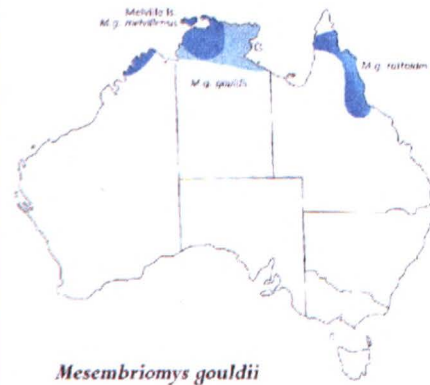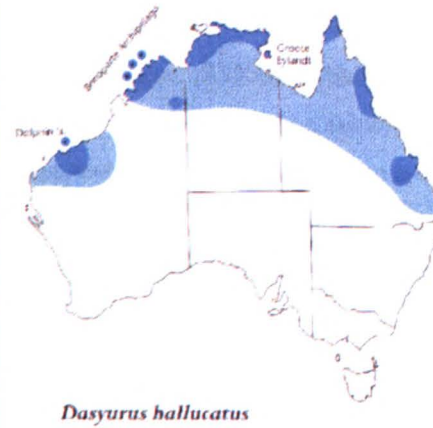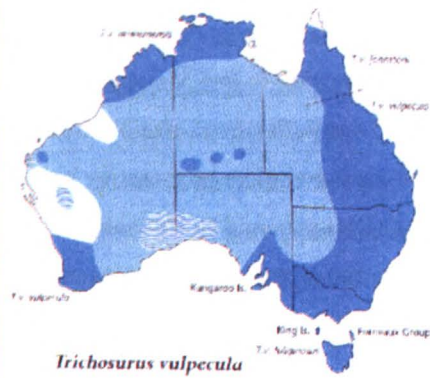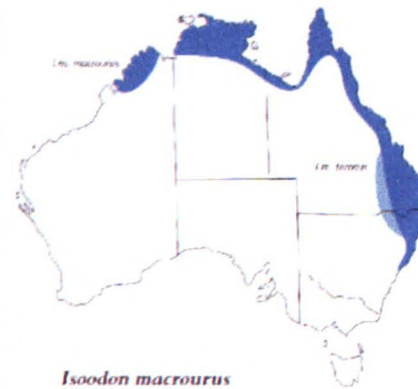
Figure 4:1: The distribution of a) black-footed tree-rat; b) northern quoll; c) common brushtail possum; d) northern brown bandicoot. Area of current distribution is in dark blue and light blue areas represent previous distribution or areas where the species has declined. The maps also show the location of each subspecies (all photos by M. Armstrong, except bandicoot by B. Rankmore, maps taken from Strahan 1995).

Northern brushtail possum

The common brushtail possum *Trichosurus vulpecula* is widely distributed across Australia, but has declined from the arid zone where it is now considered rare (Kerle *et al.* 1992; Figure 4.1c). Large variations in size and colour occur across its range (Howe and Kerle 1995), with the northern subspecies *Trichosurus vulpecula arnhemensis* being smaller with less brush-like tails than other subspecies (Kerle and Howe 1992; Howe and Kerle 1995). The brushtail possum is a nocturnal, arboreal marsupial, denning in hollow trees and logs. The diet varies across its wide distribution, with the majority of the diet consisting of leaves as well as some flowers and fruits (Howe and Kerle 1995). In the Northern Territory they are known to feed on flowering *Eucalyptus miniata,* the leaves of the toxic Cooktown ironwood *Erythrophleum chlorostachys,* and on flowers and fruits from the midstorey (Kerle and Burgman 1984; Kerle 1985).

Northern brown bandicoot

The northern brown bandicoot is one of Australia's most common bandicoots (Friend 1990; Gordon 1995). It has a largely coastal distribution from Sydney on the east coast up to the tip of Cape York in Queensland, across the Northern Territory and through the Kimberley in Western Australia (Gordon 1995, see Figure 4.1d). Although still considered common, the northern brown bandicoot has declined from the drier inland margins of its range (Gordon 1974; Johnson and Southgate 1990).

A medium-sized (<2.5 kg) ground-dwelling omnivorous marsupial, bandicoots mostly feed on insects and other invertebrates such as earth-worms, but also include berries, grass seeds and other plant material in their diet (Gordon 1995). It prefers areas of low ground cover which provide shelter and nests in a den constructed of ground litter over a shallow depression (Gordon 1995). The time of breeding varies geographically. In the Northern Territory breeding occurs between August and April. At my study sites breeding co-incided with the first rains and continued throughout the wet season. Early maturity, polyoestrous breeding, a short gestation period and minimal maternal care of young allow the species to have a high reproductive rate (Friend 1990; Gordon 1995).

Methods
Site Selection
To conduct a comprehensive investigation into the survival of small mammals within the fragmented landscape of the open forests of the greater Darwin region, a subset of the 64 sites surveyed in Chapter 3 was selected to represent four classes of fragmentation; high, medium,

low and un-fragmented, and were based on the amount of woodland within four km of the fragment (see Chapter 3, Figure 3.1). Of the four species being studied the black-footed tree-rat and northern quoll were the species of most interest, as they were among the group of species that showed strong negative relationships with habitat fragmentation in a previous correlative study (Chapter 3). Within each cluster of sites representing differing degrees of fragmentation, fragments were selected based on fragment size and the presence of black-footed tree-rats or northern quolls during the initial biodiversity survey (Figure 4.2). Sites were also selected at the Tipperary study area (Figure 4.3) and it was planned that these sites would be categorized as high level fragmentation. However these sites could not be included in the analysis, because of a lack of data. From this point on, all analyses include only data from Litchfield Shire (Table 4.1), with the data from Tipperary discussed separately.

Table 4.1: The characteristics of fragments from the Litchfield study area, selected from the initial survey (chapter 3) for the mark-recapture study; the original site number, the level of habitat fragmentation used as a group variable in the mark-recapture analysis is shown.

Site Number (from initial study – chapter 3)	Area (ha)	Level of Fragmentation	% Bush within 4km	No. of quadrats (used for mark-recapture study)
1	6.03	medium	47.4	1
2	49.7	medium	46.2	4
5	13.2	medium	47.8	2
35	2304	continuous	84.4	6
36	1.3	low	71.7	1
37	8.3	low	71.5	1
39	7.9	low	66.2	1
40	29.7	low	66.0	2
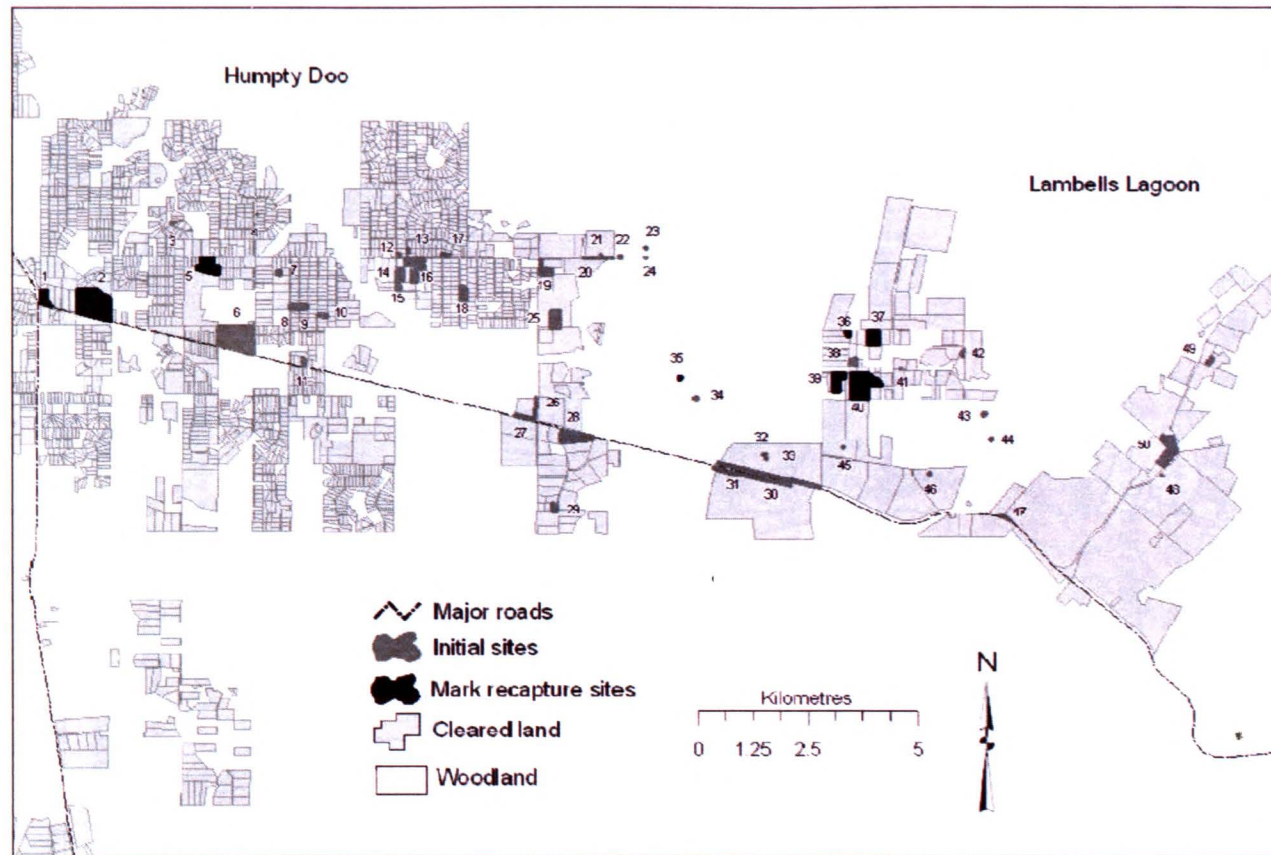
Figure 4:2: Map of Humpty Doo and Lambells Lagoon in the Litchfield Shire, all sites from the initial study (Chapter 3) are shown, with sites selected for the medium-sized mammal mark-recapture study identified in black.
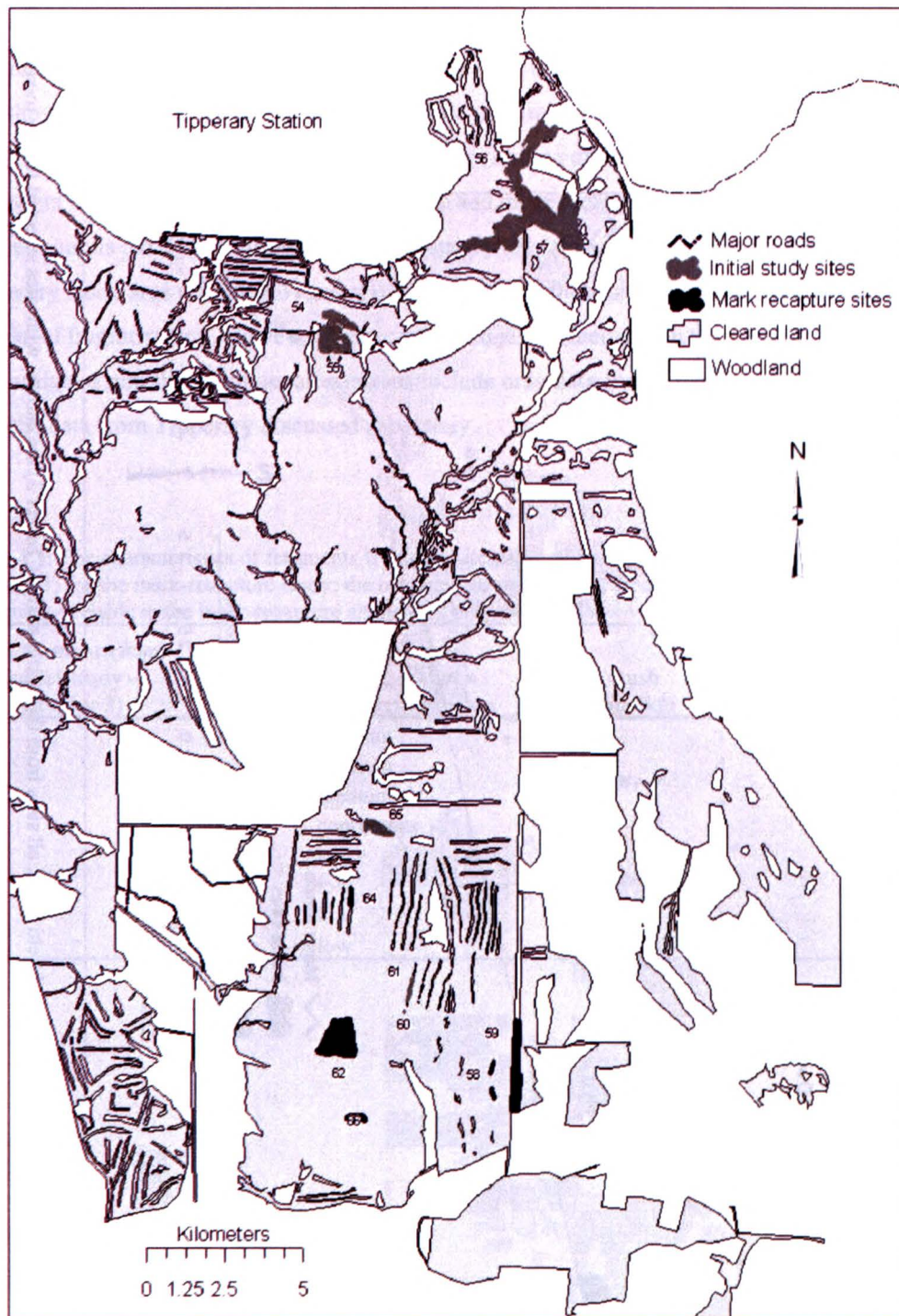
Figure 4:3: Map of Tipperary Station, all sites from the initial study (Chapter 3) are shown, with sites selected for the medium-sized mammal mark-recapture study identified in black.

Trapping protocol

Mammals were captured in large cage traps (56 x 20 x 20 cm) placed on the perimeter of one hectare quadrats. Each quadrat consisted of 16 traps placed at 25 m intervals and baited with a mixture of peanut butter, rolled oats and honey. Within fragments quadrats were positioned to cover most of the fragment, with the assumption that a quadrat could capture all animals within a 100m radius of the quadrat. Therefore, trapping effort increased with increasing patch size. Within the continuous site six quadrats were placed in two rows of three, with a distance of 200m between quadrats. Trapping was conducted at three month intervals from May 2001 to February 2003 at Litchfield Shire and from June 2002 to March 2003 at Tipperary. This provided eight trapping occasions for Humpty Doo/Lambells Lagoon and four occasions for Tipperary.

During each trapping session traps were placed at the same locations, identified by flagging tape. Traps were placed on the ground in a shaded location or covered with leaf litter, and were left open for three nights at each site and checked each morning. A total of 10 days was required to complete trapping at all Litchfield Shire study areas during each of the eight trapping periods. At Tipperary, trapping sessions were divided into two sections because of the distance between sites. A total of ten quadrats were surveyed, six in the first section and four in the second. On average, five days were required to complete trapping of all Tipperary sites during each of the four mark-capture sessions.

Handling

Two different handling protocols were used during this study, based on the species captured. Brushtail possums and bandicoots were processed at the site of capture and then released. At first capture, each individual was given an ear-tag, sexed, weighed and the reproductive condition recorded. For subsequent recaptures only the sex and ear-tag were recorded. Ear-tags did fall out; however, on 47 of the 59 occasions I was able to identify the individual based on sex, weight, trap location and characteristics. If an ear-tag was in poor condition a new ear-tag was given and the old ear-tag recorded. For the 12 animals that had lost their ear-tag and could not be identified a new ear-tag was given and it was recorded that they had been previously marked. Theses animals were not included in further analysis.

As black-footed tree-rats and northern quolls were the target species of this survey they underwent a different procedure. Each individual was given a passive integrated transponder or

PIT-tag. These tags are a microchip that is inserted under the skin near the shoulder blades using a hyperdermic syringe and when detected with a scanner provide an individual ten digit barcode. PIT-tags are permanent, ensuring that marks are not lost (Rogers *et al.* 2002). However care must be taken when recording the barcode as they can be misread – a potential source of error in mark-recapture studies (Pollock *et al.* 1990). PIT tags were not used for all animals as they are relatively expensive and could not be justified for the large number of possums and bandicoots captured during the study. The sex, weight, reproductive status and a selection of body measurements were recorded at each capture to investigate changes in growth and condition. Scat samples of black-footed tree-rats were collected from the cages and bags for diet analysis (not presented in this thesis). No animals died during capture or handling, so the number trapped was the same as the number released.

Mark-recapture analysis

The Cormack-Jolly-Seber (CJS) model is an open population capture-recapture method that permits separate estimation of survival and recapture probability and was used to determine survival and population estimates. Combining the CJS model with statistical extensions by Lebreton et al. (1992), allowed survival and recapture probabilities to be modelled as functions of explanatory variables, including environmental, temporal and individual covariates. These probabilities are estimated by determining the values that best fit the observed histories of captures and non captures of marked individuals (Lindenmayer *et al.* 1998). Capture histories for marked animals are represented as a series of ones and zeros. For example, in this study possum #1529 has the following capture history (10100101); thus over the eight trapping sessions this animal was first captured during the first trapping session, and subsequently recaptured in the third, sixth and eighth trapping sessions. From these data we know that the animal survived the length of the study (being caught in the first and last trapping session) and although not captured during the fourth and fifth sessions the animal was known to be alive, as it was detected during the sixth session. So the capture history provides information on the probability that an animal known to be alive will be captured in any given trapping session.

Using the CJS approach, recapture probability p_t is the probability of a previously marked individual that is known to be present in the population being recaptured at time t and survival probability Φ_t is the probability that an individual known to be alive at time t survives to time t + 1 (Williams *et al.* 2002a). Despite the fact that this approach does not assume the population is closed to immigration or emigration and although recapture rates account for temporary emigration, permanent emigration cannot be differentiated from survival probability. Hence, in this context, survival really refers to local persistence at the study site (Pardon *et al.* 2003).

The incidences of captures of animals with each possible capture history allow survival and recapture probabilities to be calculated. Despite this, p_1 cannot be calculated for any of the trapping records, as there are no animals marked prior to this trapping session. Also, as we are not able to know if our failure to trap an animal during the last trapping period is because it has died or just wasn't trapped, the survival and recapture rates for the last interval are not individually identifiable, and are estimated as a product of $\Phi_7 p_8$ (Lebreton *et al.* 1992; Cooch and White 2005).

$$
\begin{array}{ccccccccccccc}
& \Phi_1 & & \Phi_2 & & \Phi_3 & & \Phi_4 & & \Phi_5 & & \Phi_6 & & \Phi_7 & \\
1 & \rightarrow & 2 & \rightarrow & 3 & \rightarrow & 4 & \rightarrow & 5 & \rightarrow & 6 & \rightarrow & 7 & \rightarrow & 8 \\
& & p_2 & & p_3 & & p_4 & & p_5 & & p_6\, p_7 & & p_8 &
\end{array}
$$
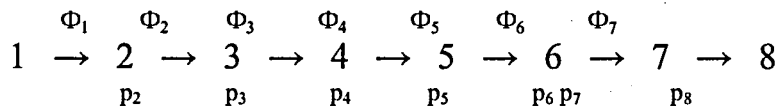
In order to use this approach the underlying assumptions are; (1) that all marked animals in the population at trapping period *t* have the same opportunity p_t of being recaptured; (2) all marked animals present in the population immediately after trapping period *t* have the same probability Φ_t of surviving until trapping period *t* + 1; (3) all animals have independent fates; (4) no tags are lost or misread; and (5) that temporary emigration, if present, is random (Pollock *et al.* 1990).

In this study model fitting and selection was performed using Program MARK version 4.2, introduced in (White and Burnham 1999) with information-theoretic model selection methods based on Akaike's information criterion (AIC) (Anderson and Burnham 1999; see Burnham and Anderson 2002 for a more thorough discussion). AIC uses Kullback-Leiber information or distance to determine an estimate of the expected, relative distance between the fitted model and the unknown true mechanism that actually generated the observed data (Anderson *et al.* 2001; Burnham and Anderson 2002). AIC selects the most parsimonious model from an a priori candidate set (also referred to as the 'K-L best model'). This model explains the highest proportion of variance in the data with the smallest number of parameters for adequate representation of that data (Burnham and Anderson 2002). Model selection methods also arrange candidate models in order of parsimony, allowing further conclusions on the relative importance of modelled effects and their interactions (Anderson *et al.* 2001).

A candidate model set was constructed as generalized linear models, following the format of Lebreton *et al.* (1992). The model set contained factors considered a priori to have an effect on survival and recapture probabilities. They included individual factors of sex and weight at first capture (representing a measure of age), environmental variables of rainfall and fragmentation, and temporal factors of seasonality and trend over the course of the study. All variables were included to form the global model, to be run for three of the four species (subscripts defined in Table 4.2):

Φ *f+s+w+r+se+tr* **P** *f+s+w+r+se+tr*

Table 4.2: The factors (and their symbols) used in the parameterization of survival and recapture probability models. Fragmentation and sex were considered as group variables. Weight was included as an individual covariate, while trend, rainfall, and season were considered as time covariates, with a linear effect on the logit scale.

Variable	Values	Notes
Fragmentation (*f*)	Group 1 = medium fragmentation Group 2 = low fragmentation Group 3 = continuous	Level of fragmentation (based on the amount of woodland within 4 km of the site
Sex (*s*)	Group 1 = Female Group 2 = Male	Gender
Trend (*tr*)	Capture intervals numbered 1-7	Linear trend (on the logit scale) over the course of the study
Rainfall (*r*)	Rainfall in each 3 month capture interval (0 – 3815mm)	Total rainfall recorded in the 3 months prior to each capture interval
Season (*se*)	1 = Dry season 2 = Wet season	Dry season (April – October) Wet season (November – March) Allows independent variation by season
Weight (*w*)	Weight at first capture	Weight in grams (g) of an animal at first capture
Month (*m*) (*quolls only*)	(Quolls only – replaced rainfall and Season in the global model)	Divides the year quarterly, into three month periods
Constant (.)	No variation	Uniform probability across all groups and time intervals

Factors associated with fire frequency and intensity at the study sites were also considered to potentially have an effect on survival and recapture probabilities, but could not be included as there was not adequate data for black-footed tree-rat and northern quoll. As 18 parameters were being investigated, it was impossible to investigate the global CSJ model of all effects, with all interactions. Such a model would be extremely over-parameterized and of no biological utility (Pardon *et al.* 2003). Unfortunately the small amount of data for northern quoll prevented the use of the global model, as it was over-parameterized (see n/K ratio for this species; Table 4.3), thus an abbreviated version of the global model was used for this species. Month (*m*) was used to replace variables season (*se*) and rainfall (*r*) (Table 4.2).

Φ f+s+w+m **P** f+s+w+m

AIC can perform badly if there is a large number of parameters in relation to sample size (Burnham and Anderson 2002). When the n/K ratio (where n is the number of captures and K is the number of parameters) is less than 40 a second-order bias-corrected form of AIC, AIC_c is recommended (Anderson and Burnham 1999; Burnham and Anderson 2002). Although the northern brown bandicoot and the brushtail possum had n/K ratios slightly greater than 40 for the global model (Table 4.3), AIC_c was still used as the second-order correction becomes negligible, if n is large with respect to K (Burnham and Anderson 2002) and thus there is no reason why AIC_c should not always be used. A two-stage model selection approach was used, following the recommendation of Lebreton et al. (1992).

Recapture probabilities were modelled first in combination with the global parameterization for survival. This retains as much power as possible for tests on survival parameters, which are of greater biological interest in this study (see Pardon et al. 2003). Once the most parsimonious recapture model has been identified, this parameterization of recapture was used on all candidate models for survival probability. AIC weights were calculated for each model set to provide a measure of the relative likelihood of each model, based on the data and the candidate set (Burnham and Anderson 2002).

Although goodness of fit (GOF) testing should ideally be carried out on the global model (Lebreton et al. 1992; Burnham and Anderson 2002), this was not possible as there is currently no analytical means to assess the fit of a model containing individual covariates (Cooch and White 2005). For this reason, GOF testing was carried out on the global model with the individual covariate (weight) removed from the model (called the modified global model or M-G model from here in). The parametric bootstrap approach was used to determine GOF (White et al. 2001) and was carried out in program MARK (White and Burnham 1999; White et al. 2001). This approach allows the deviance of the M-G model to be ranked against the deviance of 1000 bootstrapped simulations that are simulated from parameter estimates of the M-G model and the assumed model structure. For all four species the deviance of the M-G model was contained within the deviance range of the bootstrap simulations (Table 4.3), indicating that the observed deviance of the M-G model for each species was reasonably likely to be observed. This confirms that the M-G model for each species satisfied the CJS assumptions and is a valid basis for inference.

Table 4.3: Values calculated to determine the goodness-of-fit of the global model to the dataset of each species.

Species	no. of captures (n)	no. of parameters (K)	n/K ratio	P value	c-hat ($\hat{c}$)
N.B. Bandicoot	784	18	43.6	0.167	1.511
Brushtail possum	769	18	42.7	0.221	1.177
Black-footed tree-rat	174	18	9.7	0.195	1.179
Northern quoll	89	16	5.6	0.103	3.900

The level of overdispersion within the data was also estimated using the M-G model, because of the limitations mentioned above. Using the method described by White *et al.* (2001), the quasi-likelihood parameter $\hat{c}$ was estimated as the ratio of the M-G model deviance to the mean deviance of the bootstrapped simulations (values of $\hat{c}$ for each species are shown in Table 4.3). As a general rule of thumb, the estimated overdispersion parameter should be $1 \leq \hat{c} \leq 4$, with c = 1 when no overdispersion exists (Anderson *et al.* 1994; Burnham and Anderson 2002). As the data for each of the four species showed some level of overdispersion, quasi-likelihood adjustments ($QAIC_c$) were used.

In general, inferences should be based only on models that make up the top 90% of AIC or $QAIC_c$ weights (Burnham and Anderson 2002). When there is no one model that stands out as the best model, model averaging procedures should be carried out. Burnham and Anderson (2002) suggest that, where possible, inference should be based on all the models, via model averaging and model averaged adjustments, rather than selecting the best model and ignoring the rest. Model-averaging was carried out in MARK (White and Burnham 1999), and takes the estimates from the various models in the candidate set and weights them by the relative support for that model in the dataset, using the $QAIC_c$ weights (Burnham and Anderson 2002; Cooch and White 2005).

Estimating Population Size

Estimation of population size from mark-recapture data is reliant on the assumption that marked and non-marked individuals do not differ in the probability of survival and capture. Assuming that this assumption holds, the population size can be estimated at any time by the following equation:

$$n/p$$

where n is the number of individuals captured and p is the estimated capture probability. This method was used to estimate the populations of the four mammal species at all study sites.

Results

General Findings

Over the two years of the survey a total of 2823 captures of 955 individuals (of the four target species) from 6832 trap nights was recorded, with an overall trap success rate of 41%. The northern brown bandicoot was the most common species within the study area with 411 individuals captured during the study, closely followed by the northern brushtail possum with 358 individuals captured (Table 4.4). The black-footed tree-rat and northern quoll were captured less frequently with 98 and 62 individuals captured, respectively (Table 4.4). For all species, except the northern quoll, males were recorded at a slightly higher ratio than females (Table 4.4). Non-target species were rarely captured, and included the pale field rat *Rattus tunneyi* (41 captures), blue-tongue lizard *Tiliqua scincoides* (six captures), sand goanna *Varanus gouldii* (four captures), frillneck lizard *Chamydosaurus kingii* (three captures), grey-crowned babbler *Pomatostomus temporalis* (one capture), brown quail *Coturnix ypsilophora* (one capture), pheasant coucal *Centropus phasianinus* (one capture) and olive python *Liasis olivaceus* (one capture).

Table 4.4: Trapping characteristics for each of the four small mammal species over the two year study.

| Species | No. of individuals (n) | | | No. of captures | | Captures per 100 trap nights |
	Total	Males	Females	Total (within + btw sessions)	Between sessions only	Survey Period (2yrs)
N. B. bandicoot	411	211	200	1266	784	20.9
Brushtail possum	358	200	158	1200	769	19.8
B.-F. tree-rat	98	53	45	228	174	3.8
Northern quoll	62	21	41	129	89	2.1

Tipperary

As mentioned earlier, the Tipperary study area could not be included in the mark-recapture analysis. This was because limited data were obtained for all species except the northern brown bandicoot. The data were also collected for only one year, and data were collected at different times to the data collected in the Litchfield study area.

A total of 302 captures of 180 individuals occurred at Tipperary over one year of sampling. The northern brown bandicoot was the most abundant species at the study area, with 155 individuals captured during the study (Table 4.5). Capture rates for all four species were considerably lower than those recorded at the Litchfield study area (Tables 4.4 and 4.5). Males made up a larger

proportion of the population of northern brown bandicoots and black-footed tree-rats, constituting 61% and 65% of the captures respectively (Table 4.5).

In late November 2002, an intense late season fire swept through the paddock containing sites 62 and 66 (see Figure 4.2). Sampling one week after the fire resulted in the capture of two northern brown bandicoots at site 66. The previous sampling period (September 2002) had identified 46 individual northern brown bandicoots and three black-footed tree-rats present at the site. Another three sampling occasions were carried out at the site since the fire, in March 2003, July 2003 and September 2004. These surveys resulted in no captures of mammals at site 66. It appears that 21 months after the fire mammals have not yet recolonised the site.

Table 4.5: Trapping characteristics for each of the four small mammal species over one year at the Tipperary study area.

Species	No. of individuals (n)			No. of recaptures		Captures per 100 trap nights
	Total	Males	Females	Total	Between sessions	Survey Period
N.B. bandicoot	155	95	60	278	177	14.5
Brushtail possum	2	1	1	3	3	0.2
Black-footed tree-rat	17	11	6	22	22	1.1
Northern quoll	6	1	5	8	6	0.4

Survival and Recapture

Northern Brown Bandicoot

With the global parameterization used for the survival probability, the most parsimonious model for recapture probability was a combination of fragmentation, weight and sex, with a sex/fragmentation interaction ($p_{f+w+s(s*f)}$). As indicated by the $QAIC_c$ weight, this model had a 91% probability of being the best recapture model from the candidate set (Table 4.6). All other models were relatively unlikely in comparison, with the second best model having only a 2% probability of being the best model.

Recapture probability estimates from the best model vary with degrees of fragmentation. Recapture rates are highest in continuous areas and lowest in areas of low fragmentation (Figure 4.4). Recapture rates stay constant for the duration of the study, but vary between sexes and weight at first capture. Males show lower levels of recapture than females across all levels of fragmentation, with male recapture rates substantially lower in low and medium fragmentation sites (Figure 4.4). Recapture rates also decline with increasing body size (Figure 4.4).

Table 4.6: The Goodness-of-fit statistics of the top 5 recapture and top 6 survival models for Northern brown bandicoot. The QAICc estimate, the weight or likelihood of the model (QAICc weight), the number of parameters and the deviance of each model are given. See Table 4.2 for a list of parameter symbols.

Probability	Model	QAICc	QAICc Weight	No. Parameters	Deviance
Recapture	phi(full)p(f+w+s₊(s*f))	883.82	0.91	15	853.11
	phi(full)p(f+w₊(f*w))	891.17	0.02	14	862.55
	phi(full)p(f+w)	892.08	0.01	12	867.62
	phi(full)p(f+w+tr₊(f*w))	892.48	0.01	15	861.77
	phi(full)p(f+w+s₊(f*w))	892.75	0.01	15	862.04
Survival	phi(s+se+f₊(f*s))p("best")	878.88	0.17	14	850.26
	phi(s+se+f₊(s*se))p("best")	879.49	0.13	13	852.95
	phi(f)p("best")	879.50	0.13	10	859.17
	phi(s+se)p("best")	879.72	0.11	10	859.39
	phi(s)p("best")	880.29	0.08	9	862.03
	phi(s+se₊(s*se))p("best")	880.31	0.08	11	857.92

The best recapture model ($p_{f+w+s+(s*f)}$) was then adopted as the parameterization of recapture rate for the northern brown bandicoot and was used in all models for modelling the survival probability (referred to as the "best" model). The most parsimonious model for survival probability was a combination of sex, season, and fragmentation, with an interaction of fragmentation and sex ($\Phi_{s+se+f+(s*f)}$), and had only a 17% probability of being the best model from the candidate set (Table 4.6), with the second and third placed models having a 13% chance of being the best survival model. As no single model was clearly superior to some of the others in the candidate set, with little difference in the QAIC$_c$ weights, model-averaging procedures were required to adjust the survival estimates based on model uncertainty. Survival and recapture estimates for the best ranked model are shown in Figures 4.5 and 4.4 respectively.

Survival probability estimates show a pattern of seasonal variation with the northern brown bandicoot showing a slightly higher rate of survival during the dry season (May and August trapping sessions) (Figure 4.5). Survival rates of both sexes are also reduced with increasing levels of fragmentation, with females showing higher levels of survival than males (Figure 4.5).
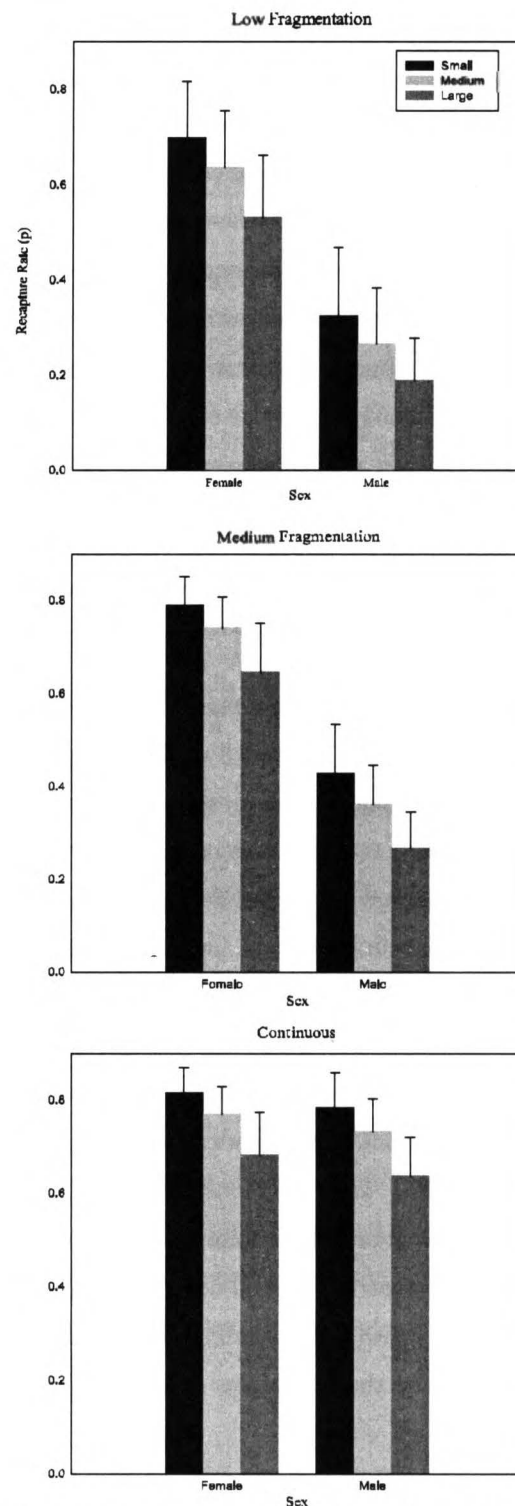
Figure 4:4: Recapture probability estimates for small (<700g), medium (700-1000g) and large (>1000g) indiviuals for female and male northern brown bandicoots, derived from the most parsimonious model ($p_{f+w+s+(s*f)}$) over the duration of the study (±SE).
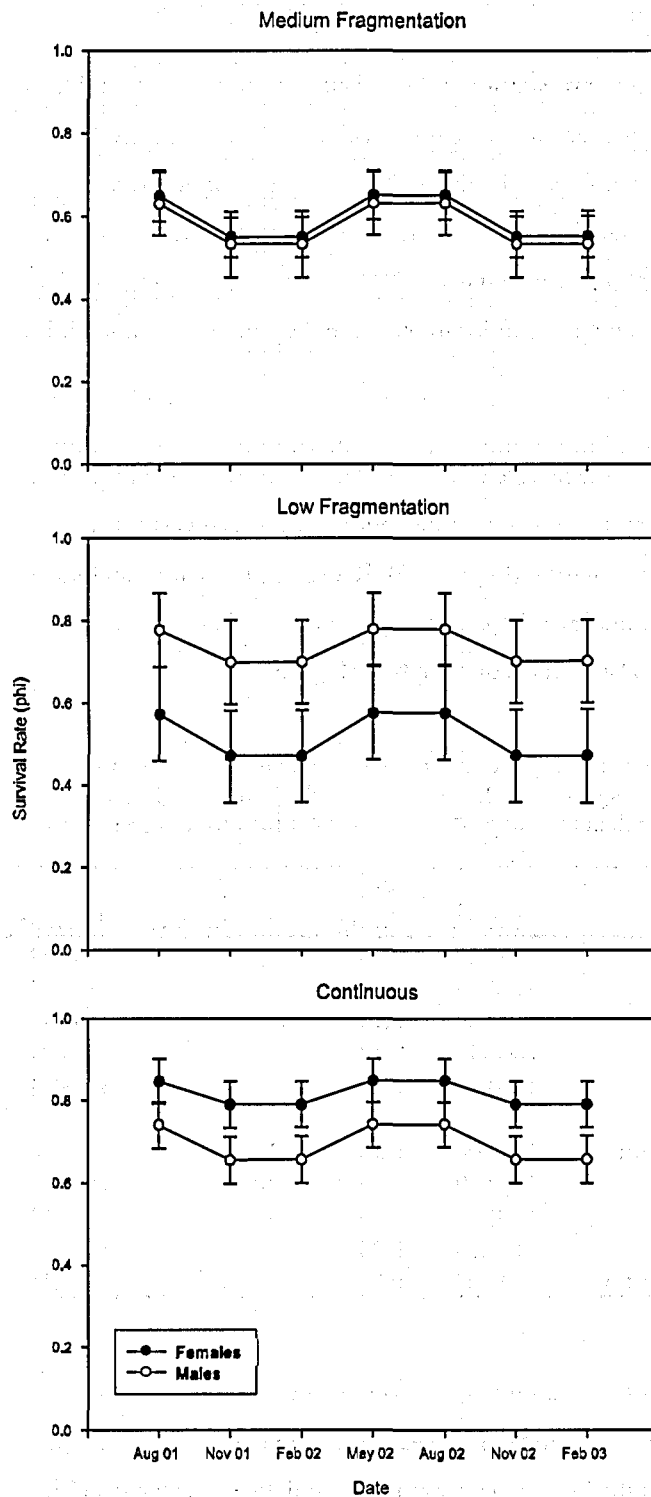
Figure 4:5: Survival probability estimates for northern brown bandicoot, derived from model-averaged estimates of survival based on weighted models, over the duration of the study (±SE).

Northern Brushtail Possum

The most parsimonious model for recapture probability of the brushtail possum was found to be the interaction of fragmentation and trend over time ($p_{f+tr+(tr*f)}$) (Table 4.7). As indicated by the $QAIC_c$ weight, this model had a 35% probability of being the best recapture model from the candidate set (Table 4.7). The next best model for recapture rate combined fragmentation and trend over time (p_{f+tr}) without the interaction term, and had a 24% probability of being the K-L best model (Table 4.7). As no single model was superior to others in the candidate set, model-averaging procedures were performed.

Recapture probabilities show an increase in recapture rates over the course of the study (Figure 4.6). Recapture rates vary with the different levels of fragmentation, with the lowest rates recorded in sites with a low level of fragmentation (Figure 4.6). Recapture rates are also higher for females in sites of both low and medium level fragmentation. However, this is reversed at the continuous site, with males showing higher rates of recapture (Figure4.6).

Table 4.7: Goodness-of-fit statistics of the top six recapture and five survival models for Northern brushtail possum. The $QAIC_c$ estimate, the weight or likelihood of the model ($QAIC_c$ weight), the number of parameters and the deviance of each model are given. See Table 4.2 for a list of parameter symbols.

Probability	Model	QAICc	QAICc Weight	No. Parameters	Deviance
Recapture	phi(full)p(f+tr+(tr*f))	1197.89	0.35	14	1169.22
	phi(full)p(f+tr)	1198.69	0.24	12	1174.20
	phi(full)p(s+f+tr+(tr*f))	1199.68	0.14	15	1168.91
	phi(full)p(s+f+tr)	1200.49	0.10	13	1173.91
	phi(full)p(f)	1200.75	0.08	11	1178.33
Survival	phi(f+w+se+tr+(se*tr))p("best")	1190.06	0.36	13	1163.48
	phi(f+se+tr+(se*tr))p("best")	1192.79	0.09	12	1168.30
	phi(f+w+r+tr)p("best")	1193.54	0.06	11	1171.12
	phi(f+w+r)p("best")	1193.56	0.06	10	1173.21
	phi(f+w+se+tr+(se*f))p("best")	1194.02	0.05	14	1165.35

The most parsimonious model for survival probability was a combination of fragmentation, weight, season, and trend over time, with an interaction of season and trend ($\Phi_{f+w+se+tr+(se*tr)}$), and had only a 36% probability of being the best model from the candidate set (Table 4.7) The next best model only had a 9% chance of being the best model, the level of support was not considered substantially higher, thus model-averaging was conducted. The individual covariate, weight (w) was considered to be an important parameter affecting survival of the brushtail possum, as it occurred in all of the highest rated models. There are three options available in MARK, to select what individual covariate values are used to compute the real parameter estimates. For all models the default option was used, which estimates parameters based on the

mean of the individual covariate. However, once an individual covariate is identified as being an important parameter in determining rates of survival or recapture, specified values of the individual covariate need to be used to determine how that variable (weight) is affecting survival. For this reason, models were re-run with three specified weights (small = 700g; medium = 1300g and large = 1900g).

Survival probability estimates for the brushtail possum followed a seasonal trend over the course of the study, with slightly higher rates of survival observed over the dry season (Figure 4.7). Weight at first capture was also an important factor influencing survival, with small animals having lower rates of survival than larger animals (Figure 4.7).
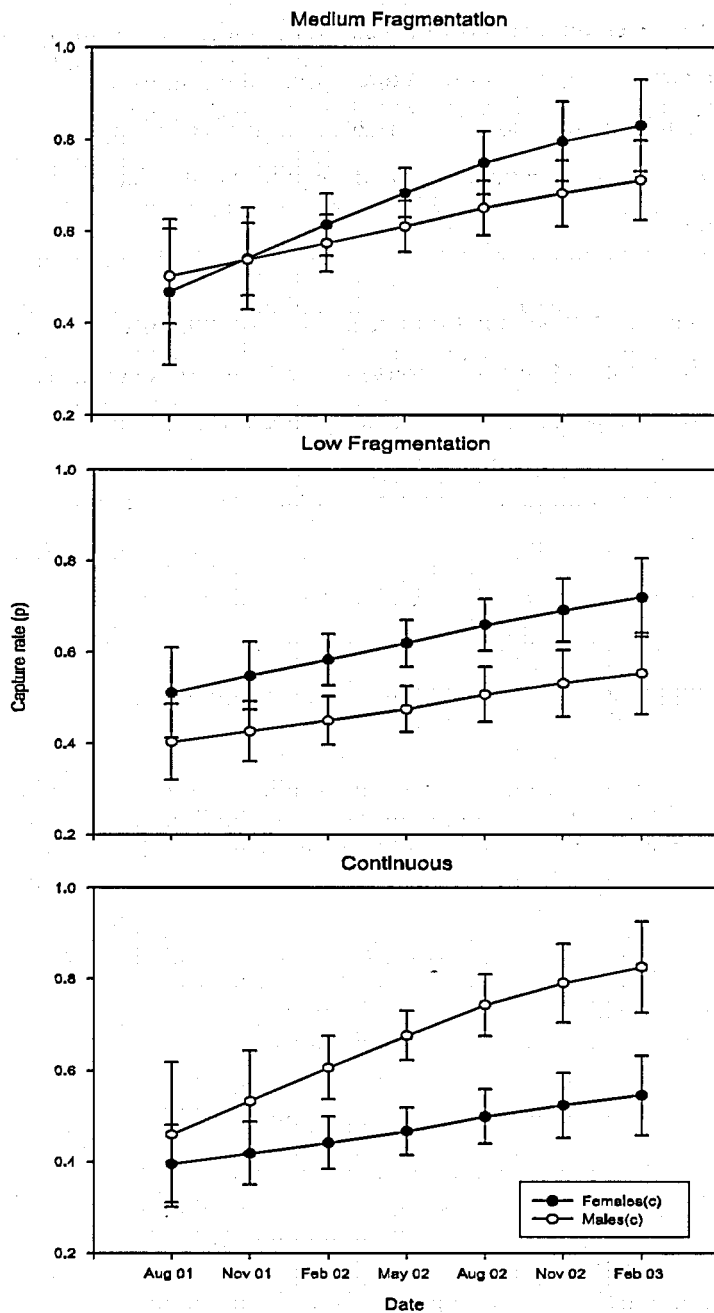
Figure 4:6: Recapture probability estimates for the brushtail possum, derived from model-averaged estimates of survival based on weighted models, over the duration of the study (±SE).
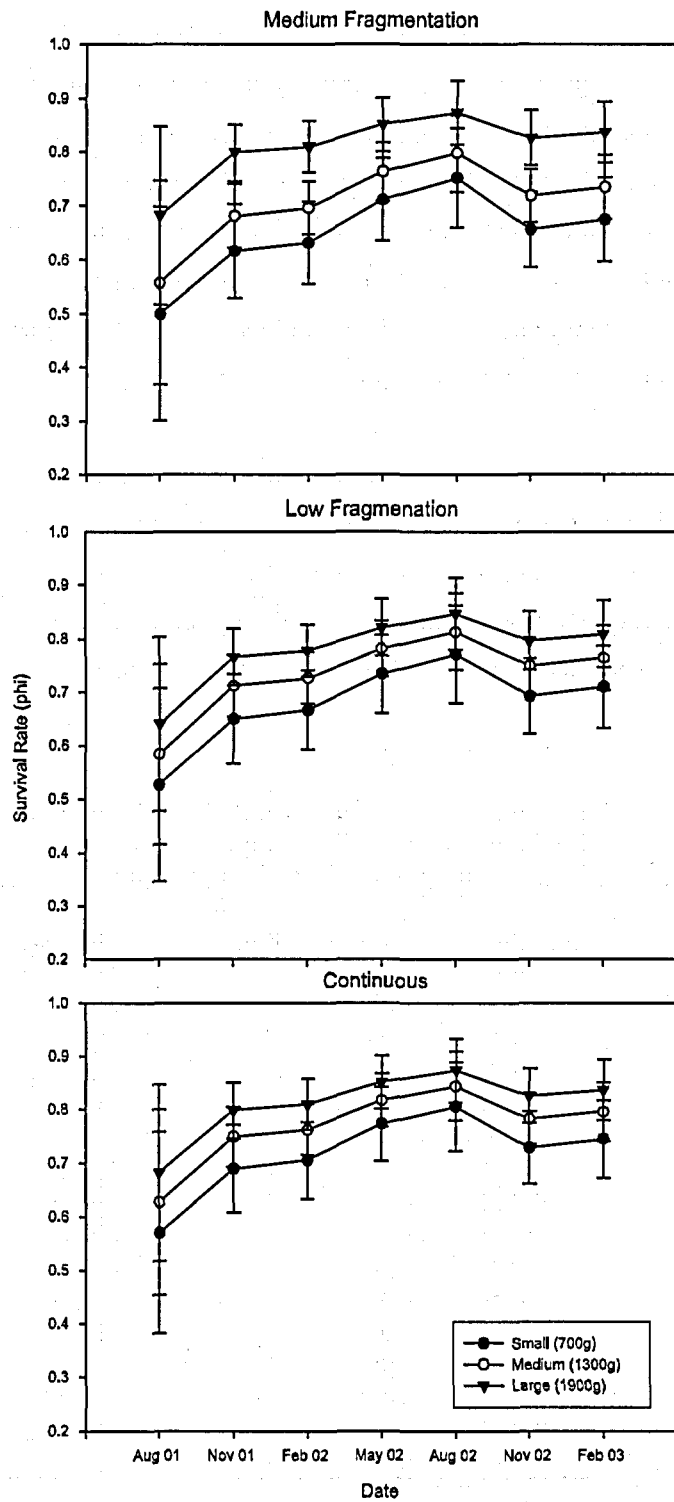
Figure 4:7: Survival probability estimates for the brushtail possum, derived from model-averaged estimates of survival based on weighted models for the duration of the study (±SE).

Black-footed tree-rat

The most parsimonious model for recapture probability of the black-footed tree-rat was found to include sex, fragmentation and the interaction of fragmentation and sex, with a trend over time $(p_{f+s+tr+(s*f)})$ (Table 4.8). As indicated by the QAIC$_c$ weight, this model had a 68% probability of being the best recapture model from the candidate set (Table 4.8). Although this model had substantially greater support than all other models in the candidate set, with the next best model only having 6% chance of being the best model, the general rule that inferences should be based on the top 90% of QAIC$_c$ weights is not met, thus model-averaging was conducted.

Estimates of recapture rates for the black-footed tree-rat showed a steady decrease over the duration of the study for all levels of fragmentation (Figure 4.8). Recapture rates were highest in sites of low level fragmentation and lowest in sites of medium fragmentation (Figure 4.8). Males and females had the same rates of recapture in continuous and low fragmentation sites. However, in sites with medium level fragmentation males had higher recapture rates than females (Figure 4.8).

Table 4.8: Goodness-of-fit statistics of the top five recapture and ten survival models for the black-footed tree-rat. The QAICc estimate, the weight or likelihood of the model (QAICc weight), the number of parameters and the deviance of each model are given. See Table 4.2 for a list of parameter symbols.

Probability	Model	QAICc	QAICc Weight	No. Parameters	Deviance
Recapture	phi(full)p(s+f+tr$_+$(s*f)) -	265.92	0.68	15	232.61
	phi(full)p(s+f+tr)	270.78	0.06	13	242.30
	phi(full)p(s+tr)	271.19	0.05	11	247.42
	phi(full)p(s+r+tr)	271.27	0.05	12	245.16
	phi(full)p(s+f$_+$(s*f))	271.35	0.04	12	245.24
Survival	phi(r+tr)p("best")	263.29	0.11	10	241.82
	phi(r+tr+w$_+$(r*tr))p("best")	263.36	0.10	12	237.26
	phi(r+tr+w)p("best")	263.38	0.10	11	239.61
	phi(r+tr+s)p("best")	263.39	0.10	11	239.61
	phi(s+f+tr+r+w)p("best")	263.56	0.09	14	232.68
	phi(f+r+tr)p("best")	263.73	0.09	12	237.63
	phi(r+tr+f)p("best")	263.73	0.09	12	237.63
	phi(r+tr$_+$(tr*r))p("best")	264.23	0.07	11	240.46
	phi(r+tr$_+$(r*tr))p("best")	264.23	0.07	11	240.46
	phi(s+r+tr+w$_+$(r*tr))p("best")	264.46	0.06	13	235.99

The most parsimonious model for survival probability was a combination of rainfall and trend over time (Φ_{r+tr}), but had only an 11% probability of being the best model from the candidate set (Table 4.8), while the second, third and fourth placed models had a 10% chance of being the best survival model. As no single model was clearly superior to some of the others in the

candidate set, with little difference in the $QAIC_c$ weights, model-averaging procedures were required to adjust the survival estimates to allow for model uncertainty.

Survival probability estimates followed a seasonal trend in rainfall. Females had a slightly higher rate of survival than males in the first year and equal survival in the second year (Figure 4.9). There was also an overall increase in black-footed tree-rat survival over the duration of the study (Figure 4.9).
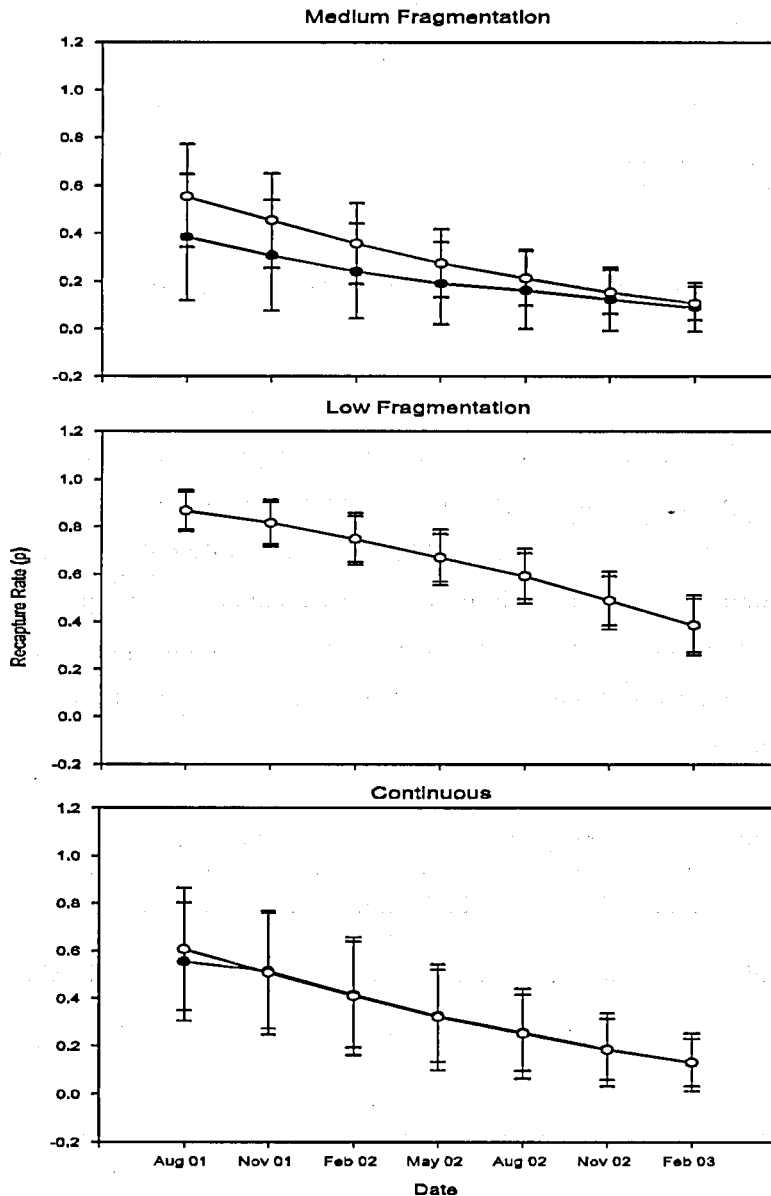
Figure 4:8: Recapture probability estimates for the black-footed tree-rat, derived from model-averaged estimates of recapture based on weighted models, over the duration of the study (±SE).
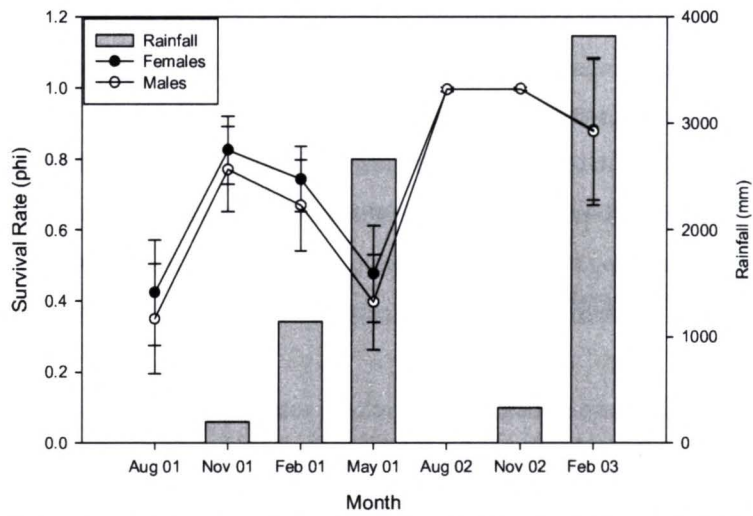
Figure 4:9: Survival probability estimates of female and male black-footed tree-rats, derived from the most parsimonious model (Φr+tr) over the duration of the study (±SE), and rainfall in (mm) for the 3 month period prior to trapping.

Northern quoll

The most parsimonious model for recapture probability was constant recapture over the study (p.), and had a 35% probability of being the best model from the candidate set (Table 4.9). The model for survival probability included only sex (Φ_s), and had only a 26% probability of being the best model from the candidate set (Table 4.9). The next best survival model was weight (Φ_w), and had a 19% probability of being the best model. As no single model for recapture and survival had substantially more support than some of the others in the candidate set, model-averaging procedures were carried out.

Table 4.9: Goodness-of-fit statistics of the top 5 recapture and 6 survival models for the northern quoll. The QAICc estimate, the weight or likelihood of the model (QAICc weight), the number of parameters and the deviance of each model are given. See Table 4.2 for a list of parameter symbols.

Probability	Model	QAICc	QAICc Weight	No. Parameters	Deviance
Recapture	phi(full)p(.)	46.40	0.35	6	33.11
	phi(full)p(f)	48.46	0.12	7	32.71
	phi(full)p(w)	48.80	0.10	7	33.05
	phi(full)p(m)	48.83	0.10	7	33.08
	phi(full)p(s)	48.85	0.10	7	33.10
	phi(full)p(s+f)	50.95	0.04	8	32.67
Survival	phi(s)p("best")	41.29	0.26	3	34.94
	phi(w)p("best")	41.94	0.19	3	35.58
	phi(s+w)p("best")	42.72	0.13	4	34.12
	phi(s+f)p("best")	42.94	0.11	4	34.34
	phi(f)p("best")	43.05	0.11	3	36.70

Recapture rates were constant across all levels of fragmentation and throughout the course of the study, however females showed slightly higher rates of recapture than males (Figure 4.10). Estimates of survival remained relatively constant over the study with females showing slightly higher survival rates than males (Figure 4.11). Survival rates of animals in sites of low level fragmentation were lower than those of animals in continuous sites.
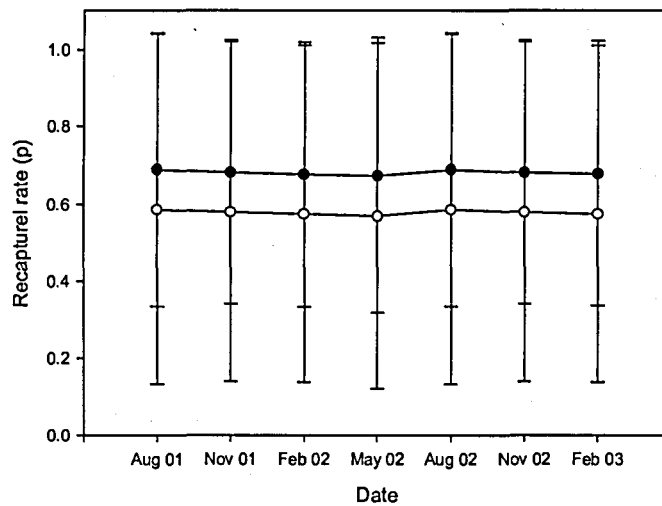
Figure 4:10: Recapture probability estimates for the northern quoll, derived from model-averaged estimates of recapture based on weighted models, (p.) over the duration of the study (females closed dots; males open dots) (±SE).
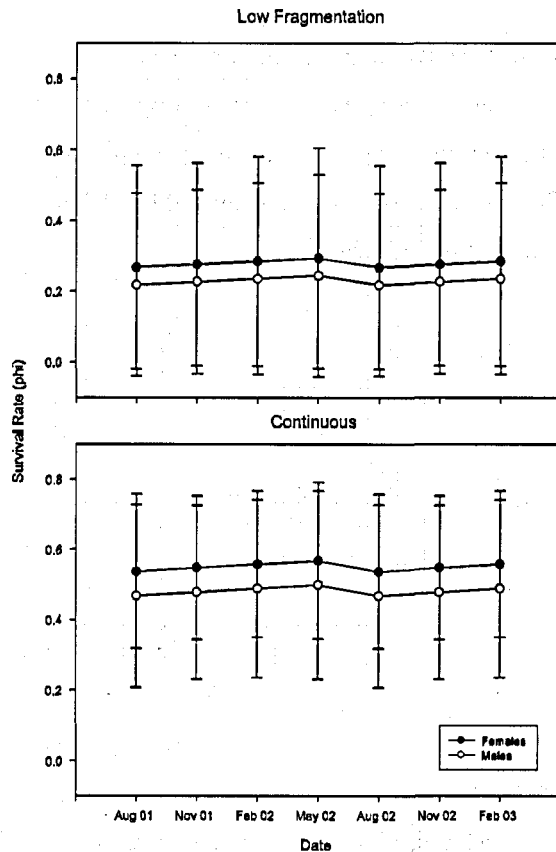
Figure 4:11: Survival probability estimates for the northern quoll, derived from model-averaged estimates of survival based on weighted models, over the duration of the study (±SE).

Population Estimates

The number of individuals of each species captured during each sampling period at a site (i.e. all quadrats for a site were pooled) was used to determine a population estimate for that species at each site. The average population estimates of the four species varied greatly between sites (Table 4.10) and between sampling periods (Appendix 4.1).

Table 4.10: Average population estimates for each of the four species at each site. Note: The population estimate has not been converted into a density.

| Site	Area (ha)	No. of quadrats (used for mark-recapture study)	Level of Fragmentation	N.B. bandicoot	Brushtail possum	B-f tree-rat	N. quoll
1	6.0	1	medium	7.0	13.8	6.3	0.0
2	49.7	4	medium	68.9	33.9	3.5	0.0
5	13.2	2	medium	37.6	9.8	5.8	0.0
35	2304.0	6	continuous	58.5	49.8	13.2	14.0
36	1.3	1	low	3.8	12.8	1.4	0.7
37	8.3	1	low	4.0	19.3	5.0	0.5
39	7.9	1	low	9.5	13.7	4.8	1.0
40	29.7	2	low	9.2	31.1	12.2	2.5

Species Population Estimate heading spans the last four columns (N.B. bandicoot, Brushtail possum, B-f tree-rat, N. quoll).

Discussion

Of the parameters investigated in this study, the primary determinants of survival and recapture varied across the species. For this reason each species will be discussed separately with broad conclusions at the end.

Northern brown bandicoot

Survival of northern brown bandicoots increased slightly from May to August. This may reflect recruitment of subadults into the trappable population from the previous breeding season, and supports the findings of a study conducted in suburban Darwin by Smith (1980). Subadults may remain in the population until the start of the breeding season, when they disperse in search of mates, thus resulting in a decrease in both true survival and apparent survival during the breeding season. Females were also found to have higher rates of survival and recapture than males. Males may often exhibit lower survivorship because of the costs associated with competition for mates, dispersal and increased food demands (Owen-Smith 1993). Males may also cover greater distances and be more transient in nature than females, thereby decreasing their apparent survival. Seasonal cycles in activity levels, methods of foraging and breeding behaviours may contribute to variation in survival and recapture rates (Friend 1990).

Northern brushtail possum

The brushtail possum showed a steady increase in survival over the course of the study. Small animals showed lower rates of survival than large animals, suggesting low recruitment into the population, as small, young animals may have a higher rate of migrating or true survival. A study of the brushtail possum in Kakadu National Park by Kerle (1998) found that only 40% of juveniles were recruited into the population with most disappearing from the study area. Recapture rates for males were greater than for females in continuous sites. This also supports the findings of Kerle (1998), who found that males were more readily trappable than females. In fragmented sites females were found to have higher rates of capture than males, suggesting that in fragmented environments males may be more transient because of competition for resources and access to mates.

Black-footed tree-rat

Rainfall was the primary factor influencing survival of the black-footed tree-rat. Rainfall may reflect changes in food availability at the sites, because of a shortage in fruiting at the end of the wet season (Feb – May) (Woinarski et al. 2005), with the black-footed tree-rat being

predominantly frugivorous and having large home ranges (chapter 5), and so animals may travel large distances in search of preferred food resources.

Recapture rates for the black-footed tree-rat were lowest in medium level fragmentation. As shown in chapter 5, black-footed tree-rats have a relatively large home range, are capable of moving long distances and will often utilize more than one fragment. Hence, animals in fragmented environments may be more transient, moving between fragments, and thus having a lower likelihood of being recaptured. This supports the findings from Chapter 3 for this species, showing a sensitivity to habitat fragmentation.

Northern quoll

The best survival and recapture models for the northern quoll are dubious and relatively unrealistic. This is due to a lack of adequate data for the species, with only 89 captures recorded during the study. The extremely large error bars (Figures 4.10 and 4.11) demonstrate the large amount of variability in the data. The over-dispersion adjustment, c-hat ($\hat{c}$) is at the higher end of the acceptable range, suggesting there is some lack-of-fit of the data, with the fitted model not accounting for an acceptable amount of variation in the data (Burnham and Anderson 2002). As the size of $\hat{c}$ increases, the penalty for a given number of parameters will increase, hence, the $QAIC_c$ tends to increasingly favour models with fewer parameters (Cooch and White 2005). This can be seen in the results for the northern quoll (Table 4.9), with all the top models favouring the smallest number of parameters. We know, based on the mating system of the northern quoll, that survival would not remain relatively constant for the duration of the study, as males suffer from complete post-mating mortality, with most males dying within a few weeks of mating (Dickman and Braithwaite 1992; Oakwood 2000; Oakwood et al. 2001). We should therefore see a drop in male survival in the August trapping session.

Although not included as an important parameter (most likely because of the reason discussed above), the level of fragmentation maybe having an effect on the survival of the northern quoll. Throughout the study, despite intensive trapping at the sites this species was never recorded over the 2-years of the mark-recapture at sites with a medium level of fragmentation. This supports the findings from chapter 3, that northern quolls were not present at sites with less than 65% vegetation retained within a 4 km radius of the site. Survival rates were also lower in sites with a low level of fragmentation (Figure 4.11).

Impacts of Fragmentation

The main objective of this study was to investigate the effects of habitat fragmentation on the survival of four small mammal species. Fragmentation was considered to have an influence on the survival of the northern brown bandicoot and brushtail possum, occurring in the final models. In each case survival was lower in the fragmented sites than in the continuous site, although, in general these survival rates were not significantly lower, they do highlight the fact that habitat fragmentation is having an effect on the survival of small mammals in this study. Inevitably, studies conducted within a few years of clearing events (such as this study) may portray a better picture than is likely to occur in the longer term. Many species will be doomed to local extinction long before the actual event. As land clearing and habitat fragmentation is only a recent phenomenon in the area, one theory is that these fragments may still be experiencing temporarily increased population densities and over crowding, especially for the brushtail possum and northern brown bandicoot. Variation in the amount of time required for species relaxation to occur makes it hard to determine the full effects of fragmentation. However, the speed with which species re-adjust will depend on generation time (Brook *et al.* 2003), so small rodents and dasyurid marsupials will adjust quickly while longer-lived species may take several decades to adjust. This appears to be the case in this study with the northern quoll having already disappeared from sites with a medium level of habitat fragmentation and showing reduced survival at fragmented sites with low fragmentation levels. Soulé *et al.*(1988) found that the time since a fragment was isolated had a negative influence on the survival probabilities of species within the patch. As a consequence, these results may well represent an optimistic assessment of the impact of fragmentation because time since isolation is yet to have its full impact. The implication of this conclusion is that the survival of the small mammal fauna of the open forest and woodland fragments in the Northern Territory will continue to decline.

Another explanation may be that individuals are more transient in fragmented environments. Although recapture rates account for temporary emigration, permanent emigration cannot be differentiated from survival probability. Hence, in this context, survival really refers to local persistence at the study site (Pardon *et al.* 2003). Animals dispersing from the fragment would be recorded as absent and thus contribute to lower levels of survival. The radio-tracking of black-footed tree-rats (see Chapter 5) showed that animals were able to move between fragments. The three other species studied in this chapter are of similar size and may also be able to move between sites

Appendix 4.1: Population estimates for the four mammal species at each site over the duration of the study

Species	Fragmentation Level	Study Site	Aug-01	Nov-01	Feb-02	May-02	Aug-02	Nov-02	Feb-03	Mean
Northern brown bandicoot	Medium	1	9.7	11.2	4.2	5.6	7.1	5.7	5.7	7.0
		5	41.8	46.3	43.5	44.8	37.8	29.5	19.6	37.6
		2	84.0	79.5	59.0	60.5	78.8	85.9	34.9	68.9
	Low	36	7.7	3.9	1.6	3.9	1.6	0.0	7.7	3.8
		39	17.3	19.6	10.9	6.4	8.7	1.6	1.6	9.5
		40	24.7	5.5	14.8	1.6	5.5	9.3	3.2	9.2
		37	5.5	3.9	3.9	3.9	7.1	3.9	0.0	4.0
	Continuous	35	54.6	60.1	61.3	60.1	63.8	48.8	60.8	58.5
Brushtail possum	Medium	1	18.7	11.1	13.5	12.2	14.3	13.6	13.2	13.8
		5	12.2	11.1	7.0	7.8	10.3	10.7	9.2	9.8
		2	62.1	35.2	23.7	33.7	34.8	29.5	18.5	33.9
	Low	36	27.6	13.8	11.3	11.6	3.5	6.6	15.0	12.8
		39	22.2	4.2	13.0	9.0	11.4	18.1	18.2	13.7
		40	32.5	38.0	22.6	19.2	36.4	40.5	28.9	31.1
		37	28.6	24.2	10.8	17.0	18.5	19.9	16.4	19.3
	Continuous	35	60.5	66.0	28.4	34.9	53.0	51.4	54.2	49.8
Black-footed tree-rat	Medium	1	2.6	2.2	6.9	5.2	6.1	20.9	0.0	6.3
		5	1.8	0.0	0.0	14.1	4.7	14.5	0.0	5.0
		2	0.0	0.0	0.0	7.3	16.9	0.0	0.0	3.5
	Low	36	0.0	0.0	5.3	0.0	0.0	2.0	2.6	1.4
		39	6.9	6.1	6.7	3.0	8.4	0.0	2.6	4.8
		40	8.1	9.8	10.7	6.0	10.1	22.4	18.1	12.2
		37	4.6	6.1	4.0	3.0	1.7	10.2	5.2	5.0
	Continuous	35	6.7	13.7	7.3	3.1	11.9	26.8	22.7	13.2
Northern Quoll	Medium	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Low	36	1.4	0.0	3.2	0.0	0.0	0.0	0.0	0.7
		39	0.0	0.0	0.0	1.8	0.0	0.0	4.9	1.0
		40	1.4	0.0	6.4	1.5	0.0	1.5	6.7	2.5
		37	0.0	0.0	1.7	0.0	0.0	0.0	1.5	0.5
	Continuous	35	20.5	10.2	14.1	20.6	13.3	5.9	13.5	14.0
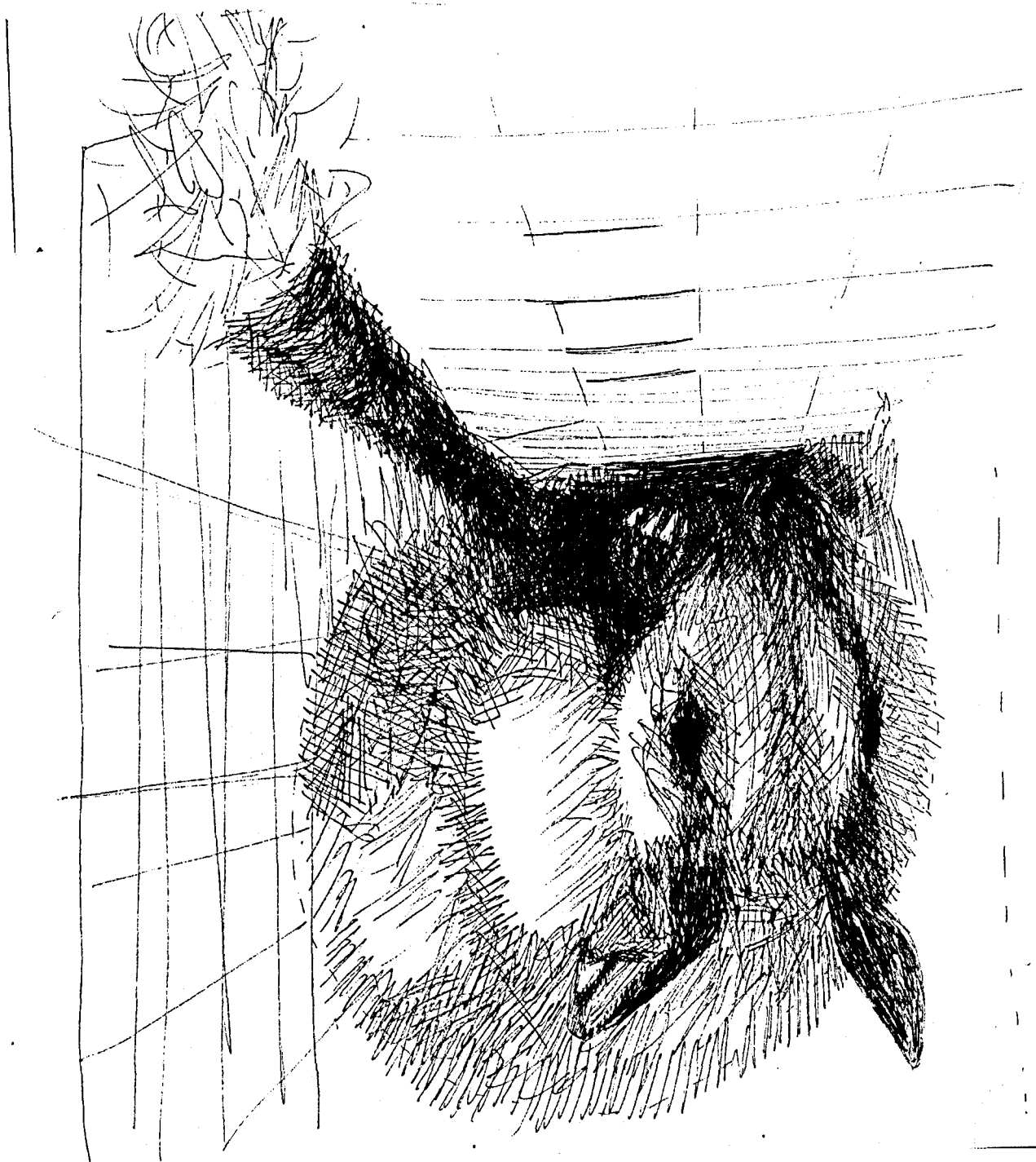
CHAPTER 5

Effects of Habitat Fragmentation on the Movement and Home Range of Black-footed tree-rats Mesembriomys gouldii

Introduction

The transformation of once continuous expanses of native vegetation into fragmented remnants has a wide range of impacts on the population dynamics of individual species that are able to persist in remaining fragments. Many demographic changes have been reported in fragmented populations, including increased variations in population size (Lande and Barrowclough 1987; Diffendorfer et al. 1995; Collins and Barrett 1997; Dooley and Bowers 1998), recruitment (Brooker and Brooker 2002), reproductive output and sex ratios (Collins and Barrett 1997) and rate of emigration (Johannesen and Ims 1996). Yet altered behaviour of individuals of particular species as a consequence of habitat fragmentation is largely unstudied for most Australian mammals (Pope et al. 2004). However, the consequences of behavioural changes on populations may affect growth rates, rates of dispersal, mating systems and social organisation (Ims et al. 1993; Wauters et al. 1994; Collins and Barrett 1997; Andreassen et al. 1998; Andreassen and Ims 1998; Bjørnstad et al. 1998).

Many studies have described changes in the movements, home range and overlap in area as a consequence of fragmentation (Barbour and Litvaitis 1993; Ims et al. 1993; Wauters et al. 1994; Collins and Barrett 1997; Pope et al. 2004). How species are affected by fragmentation will depend on specific characteristics of their autecology. Species with small home ranges or low dispersal propensity, which can be contained within remaining fragments, may show little or no ecological response to fragmentation. Conversely, species with large home ranges that equal or exceed the size of the fragment will inevitably be affected, potentially leading to changes in the characteristics of spatial use by individuals (Ims et al. 1993).

The black-footed tree-rat Mesembriomys gouldii is a large (ca. 500g), nocturnal, murid rodent, restricted to open forests and woodlands of northern Australia (Strahan 1995; Rankmore 2003). It is one of a number of mammal species in the tropical savannas that has declined in distribution since European settlement. Previous studies on this species have focused on population dynamics (Friend 1987), reproduction (Crichton 1969) and, to a lesser extent, activity area and den tree preferences (Griffiths et al. 2002) and diet (Morton 1992). This study aims to determine the effects of habitat fragmentation on movement and home range sizes of

black-footed tree-rats at three areas within the Darwin region, with varying degrees of habitat fragmentation, and to compare changes with season for each sex.

Methods

Study sites

Radio-tracking of black-footed tree-rats was conducted at the mark-recapture study sites (see Chapter 4 for details and maps). For the purposes of investigating the effects of habitat fragmentation on home range size and movement, data from fragments within particular areas were combined to create four sites (Table 5.1). The three fragmented sites (Lambell's Lagoon, Humpty Doo, and Tipperary) varied in the extent of clearing and fragmentation that has occurred in the area (Table 5.1). Intensive radio-tracking via telemetry towers was not conducted at all sites due to time constraints (see radio-tracking methods for details). All fragmented sites were grouped together to compare fragmented and un-fragmented home range size.

Table 5.1: Grouping of study sites into areas with different levels of habitat fragmentation. Note there is only one control site (un-fragmented). Columns give the number of fragments surveyed at that location; the number of fragments included in the intensive radio-tracking and a relative density estimate at each location (captures per 100 trap nights).

Location	Fragmentation level	Total no. fragments	No. of study fragments (Tower)	Captures per 100 Trap nights
Continuous	not fragmented	1	1	1.35
Humpty Doo	medium	3	2	1.41
Lambells	low	4	0	8.59
Tipperary	high	4	1	1.15

Trapping and collar attachment

Radio-tracking of black-footed tree-rats was conducted on animals trapped during the mark-recapture sessions (Chapter 4). Black-footed tree-rats were captured in large cage traps (56 x 20 x 20 cm) placed on the perimeter of one hectare quadrats. Each quadrat consisted of 16 traps baited with a mixture of peanut butter, rolled oats and honey. Within fragments, quadrats were positioned to cover most of the fragment, with the assumption that a quadrat could permit capture of all animals within a 100m radius of the quadrat. Therefore, trapping effort per site increased with increasing patch size. Trapping was conducted every three months from May 2001 to February 2003 at Humpty Doo and from June 2002 to March 2003 at Tipperary (Chapter 4).

In order to be selected for radio-tracking black-footed tree-rats had to be categorised as adults, weighing over 500g. Adult animals are more likely to have already established territories and remain at the site. Originally it was planned to stratify collars across genders and study sites however the short persistence of collars and the low capture rates of individuals at some sites meant that most animals that were considered to be adults and in good condition where collared.

Black-footed tree-rats selected for radio-tracking were weighed, measured and fitted with two-stage radio-transmitters weighing 25-28g, which were 2-3% of the animals body weight. This procedure took approximately 15 minutes per individual and animals were then released at their point of capture (Figure 5.1). Three types of collar were used: a whip aerial with cable tie (20% of individuals) (Sirtrack, New Zealand), modified bird transmitters with a whip aerial and leather and wool collar (25%) manufactured by the author; and a whip aerial with leather and wool collar (55%) (Sirtrack, New Zealand). All collars consisted of a two-stage transmitter with a 22 cm whip antenna, with a life expectancy of four months and a range of 1-2 km. The wool-lined leather collar that was accepted after commencement of radio tracking, added to the weight of the transmitter, thus reducing the potential battery life expectancy available. However, as collars were to be worn for 3 months this style of collar was selected to reduce the likelihood of abrasions and ulcerations. Being a natural fibre, wool allows the skin to breathe in the humid climatic conditions. Severe ulcerations caused by lighter PVC collars were observed in a study of Northern Quolls *Dasyurus hallucatus* (M. Oakwood pers. comm). Recaptured tree-rats were inspected for potential abrasion from the collars. Most showed no adverse signs from the collar while others lost a ring of fur from under the collar.

Radio-tracking

Two types of radio-tracking data were collected which I define as "intensive" and "long-term," and describe in detail below. The aim of intensive tracking sessions was to collect data on foraging activity and movement data that could be compared between sites with different levels of habitat fragmentation. Long-term radio-tracking data were collected as diurnal fixes of nesting locations to determine seasonal changes in home-range size, to detect possible dispersal movements and identify den tree preferences (chapter 6). These data were used to determine activity areas for black-footed tree-rats, and both the long-term and intensive data was used to estimate home range.

Longer-term Radio-tracking

Diurnal radio-tracking to locate nesting sites was conducted on foot using a collapsible 3-element Yagi antenna (Sirtrack, New Zealand) and an Icom IC-R10 receiver. Animals were tracked to their den sites once a day, for as many days as possible during a 3 month period. Once a den tree had been identified, information on den tree characteristics were collected and the tree was given an individual tag for future identification (see chapter 6).

Intensive Radio-tracking sessions

Initially, intensive radio-tracking sessions were to be conducted on foot for a few nights each month. However this method proved unsuccessful, with the animals detecting our presence and fleeing long before we were able to obtain an accurate fix. This left the option of remote radio-telemetry using stationary towers. Once the towers were obtained there was a limited time frame in which data could be collected as the telemetry towers could not be used during the wet season, because of the regularity of electrical thunder storms. For this reason only three intensive radio-tracking sessions were conducted between July and November, one session at three different sites. Tracking sessions were conducted over four continuous nights at each location. Fixes were obtained using four permanent radio-telemetry towers to triangulate positions of radio-collared black-footed tree-rats at defined intervals. Each tower consisted of a 9m radio-telemetry mast fitted with twin four element Yagi antennas (Faunatech, Australia), a null peak box (Sirtrack, New Zealand) and an ATS (Model 2100, Advanced Telemetry Systems Inc., USA) or Telonics (Model TR2, Telonics Inc, USA) receiver (Figure 5.2). Towers were positioned to encompass all known nesting locations (collected from diurnal fixes) of individuals to be tracked. The positions of each tower and of two dummy radio-transmitters placed within the study site for calibration were obtained using a GPS with 5 m accuracy. The towers were aligned to north by taking a fix on a transmitter that was positioned with a GPS 200-500 m away directly north of the tower.

Tower observers were trained for approximately half a day before the commencement of each session. At the start of each night, observers synchronized their watches, and an ordered list of all frequencies (collared animals and dummy transmitters) was supplied. Observers were given a five-minute interval in which to determine a bearing for each frequency. Observers recorded the range of the null signal for each bearing with the midpoint of this range subsequently used for triangulation. Notes were also collected on signal strength, quality and ease of detection. Locations were recorded for each tagged tree-rat at 30 ± 10 minute intervals between 1900 and 0600 hours. One to two breaks were taken during the night to allow observers to stretch and discuss problematic signals. The number of black-footed tree-rats tracked per session varied

from two to six. Bearings to dummy transmitters were taken at the same interval as that of tagged tree-rats. This provided a useful check of system accuracy as observers were not informed of which radio-tracking frequencies belonged to tree-rat tags and which to dummy tags. Observers were required to rotate between towers each night. Systematic errors (consistent difference in direction between the true bearing and the bearing determined by radio-location from each station) were corrected for by calculating the error in the bearings to the dummy transmitters.

Figure 5:1: Black-footed tree-rat being released with radio-collar attached.

Figure 5:2: An erected radio-telemetry tower at the edge of a fragment at Tipperary station.

Calculation of radio-tracking locations

Triangulation of bearings was carried out using LOCATE II (Nams 1990). This program uses a maximum-likelihood estimator (MLE) to compute the most likely transmitter location from three or more compass bearings, by weighting bearings nearer to the approximated position of that individual higher than those more distant (Nams 1990). The MLE calculates the deviation

of each bearing from the estimated location to get an error angle from which an error ellipse with a 95% confidence was determined (Nams 1990). Bearings from individual stations were manually rejected if they did not fit the triangulation combination of all other stations. All positions resulting from fewer than three stations were excluded from further analysis, as an error ellipse could not be calculated. All triangulation calculations with an error ellipse > 1 ha were also eliminated from further analysis. The locations of trapped black-footed tree-rats were also used as nocturnal fixes.

Animals often move in an apparently non-random fashion, and this has particular implications for radio-tracking studies. Ecologists using radio-telemetry to collect frequent location data are faced with strongly autocorrelated data sets (De Solla et al. 1999). Autocorrelation of location data can be defined, whereby the location of an animal at time $t + \Delta t$ is not independent of its position at time t, therefore allowing one to predict an animal's position based on its last position (Rooney et al. 1998). In the past, consideration of autocorrelation of locations has been ignored, because the lack of independence between locational fixes leads to an underestimate of home range size (Swihart and Slade 1985; Harris et al. 1990; White and Garrott 1990). More recently, it has been argued that autocorrelated observations are not only acceptable, but also De Solla et al. (1999) argued that eliminating autocorrelated observations reduces sample size, reduces the accuracy of home-range analyses and discards biologically relevant information. If sampling is representative and time intervals between locations relatively constant, as is the case for these intensive tracking data sets, autocorrelated locations can better represent home-range size and time partitioning of animals within home-ranges (De Solla et al. 1999). For this study, location data were gathered throughout the night and sample sizes for individuals were similar each night.

Home-range estimation and statistical analysis

Throughout the literature there are many techniques for describing and calculating home-range (Harris et al. 1990; Millspaugh and Marzluff 2001). In this study, two methods were used to determine home range size using the RANGES 6 computer program (Kenward et al. 2003). The two methods were used because a review of home range studies by Harris et al. (1990) recommended a combination of techniques to allow for comparison between studies that only used one method of estimation. The minimum convex polygon method (MCP - Mohr 1947) involves fitting the smallest possible polygon that encompasses all locational fixes (Harris et al. 1990). This is the simplest method of calculating home range, and has been widely used in the past (Goldingay and Kavanagh 1993; Jackson 2000; Meek and Saunders 2000; Mallick et al. 2000; Oakwood 2002; Puckey et al. 2004), thus allowing for comparison with these and other

studies. MCP is also considered to be more robust than other techniques when the number of fixes is low. However the area and shape of the home range estimated by this method is heavily biased by outlying fixes (Harris et al. 1990).

The kernel method (Worton 1989) is a nonparametric method that estimates fix density indices for locations at intersections of an arbitrary matrix set across an animal's range, and then interpolates contours between the values of that matrix (Kenward et al. 2003). The kernel estimator was used as the second method of home range estimation in preference to the harmonic mean, as the kernel method is mathematically more robust and produces more consistent results than harmonic mean contouring (Kenward et al. 2003). Contours were fitted to actual fixes and the grid size was left at the Ranges6 default setting of 40 x 40 m. The default smoothing factor of the standard deviation divided by the number of fixes was used (Kenward et al. 2003).

It has been reported that these commonly used techniques are not ideal for use in fragmented or linear environments because the "ballooning isopleths" include areas of unused cleared land within the home range estimates (Andreassen et al. 1998; van der Ree et al. 2001). Although there are other methods that can be used to describe spatial organisation under these conditions (see Kenward 1987; White and Garrott 1990), it is hard to compare these estimates with those commonly used in other studies. For this reason I chose to estimate home range and activity area using the methods discussed above. As expected, large areas of cleared land were included in some of the home range estimates (Figure 5.11). Within the fragmented areas, home ranges and activity areas were transposed over GIS imagery of the study areas (see Chapter 3 for imagery details) to investigate the occurrence of fixes within cleared areas. Once it had been confirmed that no fixes were recorded in cleared areas the home range and activity area polygons were transformed into Arcview shapefiles and split into polygons of cleared and vegetated land. The area of these two categories was then calculated and the area covered by native vegetation given as the home range or activity area estimate.

Incremental area plots (Kenward et al. 2003) were conducted to calculate the number of fixes needed to accurately define a home range for each of the estimation techniques. Incremental area plots are created by drawing an outline around the first three fixes, then adding successive fixes and drawing the outline again. This is repeated until all fixes have been added (Kenward et al. 2003). When individual ranges were broken up, such as activity area (den trees only) and seasonal differences, the number of fixes attained were greatly reduced. As a consequence, individual ranges with 15 or more fixes were used to compare activity and seasonal ranges.

A utilisation plot was used to identify the percentile contour line defining the core home range of black-footed tree-rats. This method plots contours around the fixes at 5% intervals, ranging from the 100 percentile contour down to the 20 percentile contour (Kenward *et al.* 2003). When the home range area of the contours is plotted a plateau is reached and this determines the core home range of a species (Kenward *et al.* 2003).

Within this study the 100 percentile contour line was used for the MCP estimation of home range, while the 95 percentile contour was used as the overall estimate of home range for the kernel method. Analyses were conducted on two different datasets; activity area (diurnal fixes only) and home range (diurnal and nocturnal fixes). Recognising that home range estimates are affected by the length of time spent collecting data, the areas presented here are 3 month home-range estimates and probably underestimate the annual or lifetime home range area of black-footed tree-rats.

The accuracy and precision of data collected during radio-tracking studies is often not determined or reported (White and Garrott 1990; Saltz 1994; Withey *et al.* 2001b). The way in which the data are collected will influence the accuracy of the data. Direct observation of radio-tagged animals will be as accurate as the researcher's GPS unit, while remote forms of obtaining fixes (such as triangulation) can have large inaccuracies (White and Garrott 1990; Garton *et al.* 2001; Withey *et al.* 2001b). In this study, the accuracy of the data varied, depending on the procedure by which it was collected. Locations obtained from trap locations and diurnal fixes of den trees had a high level of precision. Fixes collected during the intensive tracking sessions were less accurate, a factor that needed to be taken into account when calculating estimates of home range. In order to gauge the accuracy of fixes obtained from the telemetry towers, I used 95% confidence distance as suggested by Kenward *et al.* 2003). The area of all error ellipses less than 1 ha (i.e. all points to be included within the analyses) was averaged to provide a mean ellipse size for each site. It was assumed that all error ellipses were circular in shape around the fix location, and the radius of the circle was calculated. The 95% confidence distance was calculated as being two times the radius and varied from 53 – 65 m in length. The Ranges 6 computer program provides the option to adjust home range estimates based on the accuracy of the data, by adjusting the tracking resolution (Kenward *et al.* 2003). The tracking resolution is used to establish the width of a boundary strip that is included in the edges and areas of the polygon, with the boundary strip being half the value of the nominated tracking resolution (Kenward *et al.* 2003). All analyses were conducted using the default tracking resolution of 1 m to allow for comparison with studies that have not taken data accuracy into account, as well as a site-based 95% confidence distance tracking resolution, to provide a more accurate estimate of home range size.

Parametric statistical tests used for other comparisons include one-way ANOVA, nested ANOVA, and linear regression using Statistica ver.6 (StatSoft 2000). The relative population densities (presented as captures per 100 trap nights) at each site used in the linear regression was taken from Chapter 4. Data not conforming to the assumptions of these tests were log transformed. Results are shown as mean ± standard error.

Results

Between August 2001 and February 2003, 752 discontinuous fix locations were taken of 51 individual black-footed tree-rats (31 males and 20 females). These individuals averaged only 26.2 days with a functioning radio transmitter during which an average of 14.7 fixes were taken. Of these, 21 animals had ten or fewer fixes, with seven animals yielding no fixes. A large number (47%) of collars ended before their expected lifespan. Three collars were dropped by animals soon after attachment.

Incremental area plots showed approximately 20 fixes were needed to estimate within 10% of the final home range size for the MCP method, while 34 fixes were required for the kernel estimator (Figure 5.3). Visualisation of the utilisation plots indicated that the 25 percentile home range was an appropriate estimate of the core area used by each animal (Figure 5.4). Estimations of 50 percentile core areas were also calculated for comparison with other studies.

a. Minimum Convex Polygon
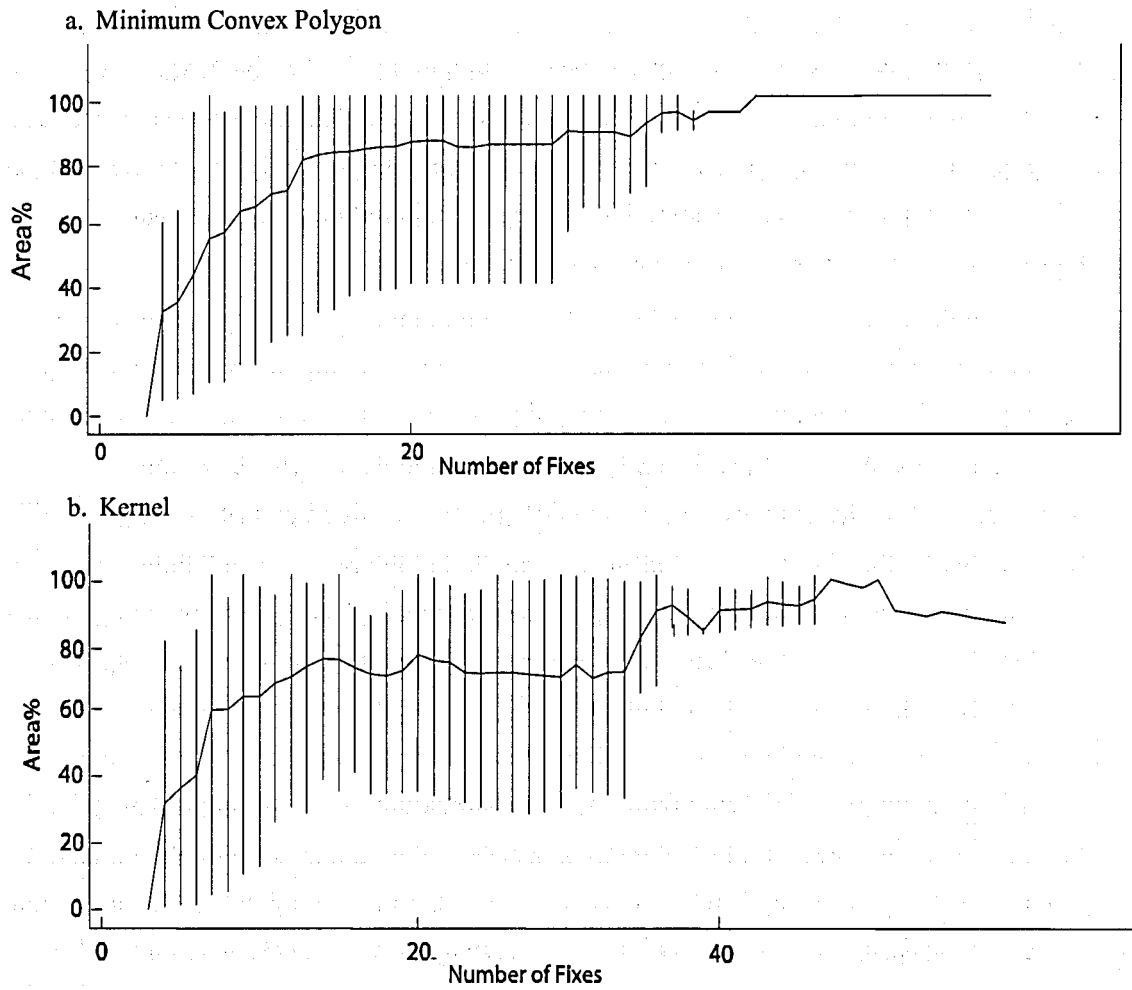
b. Kernel

Figure 5:3: Incremental area plots of all animals' home ranges according to (a) MCP and (b) kernel methods. The area (%) of the y-axis refers to the percentage of the total home range made up by a contour fitted using the number of fixes of the x-axis.
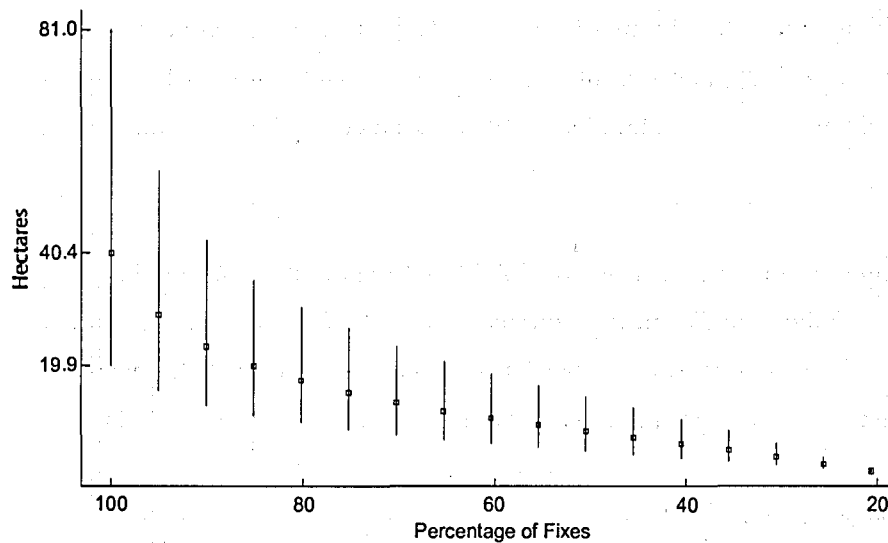
Figure 5:4: Utilisation plot of all home ranges determined by the kernel estimator. Smaller error bars and the plateau in the decline in home range size at 25% indicates that this is the percentage of location fixes that should be conservatively used to estimate the core range of black-footed tree-rats.

Home Range

The estimates of home range sizes by the two methods are shown for the nine individuals with the most records in Table 5.2. More responsive to outliers (Harris *et al.* 1990), the MCP method generally gave the larger estimate of home range size (Table 5.2). Home ranges based on the MCP method ranged from 9.1 to 88.2 ha with a mean of 40.5 ha over all individuals (Table 5.2). The mean home range for black-footed tree-rats in un-fragmented open forests was 67.3 ± 10.4 hectares, with a mean core range size of 16.7 ± 4.0 hectares (Table 5.3). Home range size was not strongly correlated with the number of fixes obtained (Exact test of Spearman's correlation coefficient, $r_s = 0.41$, $P = 0.28$, $n = 9$).

Home range using the 95% kernel estimate produced a mean home range size for all individuals with more than 34 fixes (n = 5) of 46.1 ha, and ranged from 23.7 to 80.9 ha (Table 5.3). Core areas (50% and 25% kernel) ranged from 6.2 to 24.2 ha with a mean of 13.1 ha for the 50% core area and 1.8 to 3.0 ha with a mean of 2.6 ha for the 25% core (Table 5.3). Note that distributions using this method were often multimodal, resulting in home ranges (95th isopleth) that were made up of disjointed areas (Figure 5.5).

Although the kernel estimator provided a larger home range estimate than the MCP method, it did not appear robust enough to exclude areas that by appearance were unlikely to be utilised during the animal's movements (Figure 5.5 and Figure 5.7). Based on my observations of the movements of collared black-footed tree rats, the minimum convex polygon method was

considered to be the most realistic (Figure 5.5 and Figure 5.7). Therefore, it has been used in further statistical tests. For further analysis of core areas, the 50% core was used, because the 25% core focused almost solely on the location of the dominant den trees used by the individual.

Mean maximum range length for all animals was 1077 ± 104.8 m (Table 5.3). Average maximum range length did not differ greatly between males (1164 ± 134.2 m) and females (1087.5 ± 180.8 m) (Table 5.3). Maximum range length was not correlated with the number of fixes obtained (Exact test of Spearman's correlation coefficient, $r_s = 0.1$, $P = 0.8$, $n = 9$).

Differences between the sexes

The largest three home ranges were those of males, with the mean home range of males (51.0 ± 13.2 ha) being almost twice as large as that of females (27.4 ± 10.4 ha) (Table 5.3). However, possibly partly due to small sample size, this difference was not significant (Table 5.4). Core ranges for males (16.2 ± 4.4 ha) were also twice as large as those of females (8.4 ± 2.2 ha), but were not analysed statistically because of small sample size (Table 5.3).

Table 5.2: Home range estimates for individual radio-tracked Black-footed tree-rats. Individuals with 20 or more fixes (MCP) and 34 or more fixes (kernel) were used.

Animal i.d.	Sex	Site	No. of fixes	Max range length (m)	MCP (ha)	95% Kernel (ha)	50% Kernel (ha)	25% Kernel (ha)
C36	Male	Unfragmented	35	1110.00	57.35	48.81	15.41	2.98
C28	Female	Unfragmented	34	1070.00	56.41	41.80	10.62	2.58
C5	Male	Unfragmented	37	1558.00	88.16	80.87	24.21	2.84
HD66	Male	Humpty Doo	30	988.00	36.57			
HD18	Female	Humpty Doo	33	1604.00	16.58			
HD58	Female	Humpty Doo	22	856.00	9.11			
HD34	Male	Humpty Doo	20	687.00	9.69			
T46	Female	Tipperary	45	820.00	27.50	23.7	6.20	2.76
T44	Male	Tipperary	57	1000.00	63.19	35.10	9.00	1.75
Mean			34 ± 4	1077 ± 104.82	40.51 ± 9.14	46.05 ± 9.64	13.09 ± 3.16	2.58 ± 0.22

Table 5.3: Mean overall and core home range sizes (ha) derived by each of the two methods by sex, landscape position and site (±SE). Individuals with 20 or more fixes (MCP) and 34 or more fixes (kernel) were used. Nocturnal fixes were not collected at the Lambells site.

	Mean	Maximum range length (m)	Minimum Convex Polygons ± S.E. (n)	Kernel ± S.E. (n)		
			Overall	Overall	50% Core	25% Core
Sex	Female	1087.5 ± 180.79 (4)	27.4 ± 10.4 (4)	32.7 ± 9.0 (2)	8.4 ± 2.2 (2)	2.7 ± 0.1 (2)
	Male	1164 ± 134.17 (5)	51.0 ± 13.2 (5)	54.9 ± 13.6 (3)	16.2 ± 4.4 (3)	2.5 ± 0.4 (3)
Landscape position	Unfragmented	1246 ± 135.47 (3)	67.3 ± 10.4 (3)	57.2 ± 12.0 (3)	16.7 ± 4.0 (3)	2.8 ± 0.1 (3)
	Fragmented	1053.6 ± 158.85 (6)	27.1 ± 8.4 (6)	29.4 ± 5.7 (2)	7.6 ± 1.4 (2)	2.3 ± 0.5 (2)
Sites	Unfragmented Lambells	See above				
	Humpty Doo	1149.33 ± 230.50 (4)	18.0 ± 5.7 (4)			
	Tipperary	910 ± 90 (2)	45.3 ± 17.8 (2)	29.4 ± 5.7 (2)	7.6 ± 1.4 (2)	2.3 ± 0.5 (2)

Differences between the sites

There were significant differences in home range size between the sites (Table 5.3 and Table 5.4) with animals at Humpty Doo having significantly smaller ranges than at the Unfragmented, but not the Tipperary site, (Tukey's test for Unfragmented $P = 0.02$ and for Tipperary $P = 0.4$).

Differences between fragmented and un-fragmented sites

There was a significant difference detected in overall home range size between fragmented (27.1 ± 8.4 ha) and un-fragmented sites (67.3 ± 10.4 ha) (Tables 5.3 and 5.4).

Table 5.4: Statistical test results on home ranges estimated by the MCP method. Significant results ($p<0.05$) are denoted with an asterisk (*).

Comparison	Test	Test Statistic	Probability
Overall Home Range			
Males versus Females	One-way ANOVA	$F_{1,7} = 1.81$	0.220
Un-fragmented versus Fragmented	One-way ANOVA	$F_{1,7} = 8.137$	0.024*
Sites	One-way ANOVA	$F_{2,6} = 7.111$	0.026*
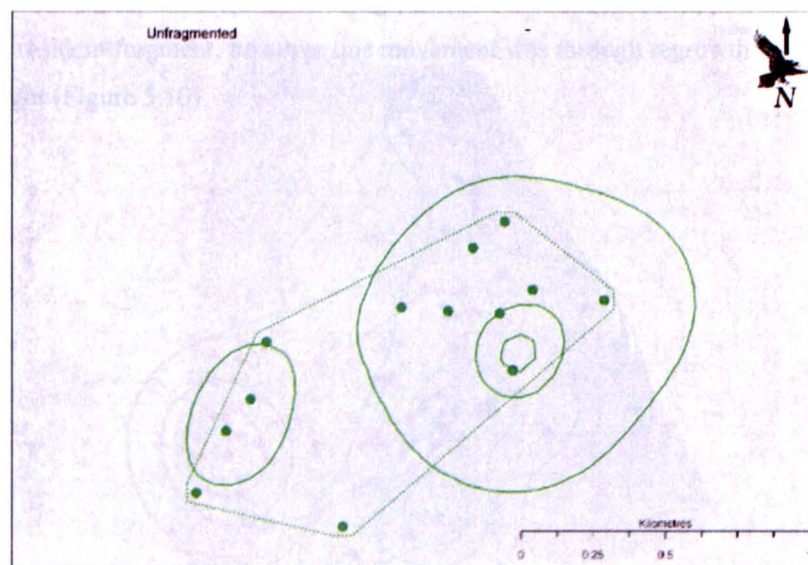
Figure 5:5: A comparison of the two estimation methods for a male black-footed tree-rat (C5) from the un-fragmented site. Hashed line is the MCP estimate and continuous line the kernel method (95%, 50% and 25%). Individual location fixes are shown with a dot. The circle in the bottom left corner is caused by a discontinuous 95% contour. These discontinuities can indicate multiple range centres or dispersal when larger numbers of fixes are involved. Note: the number of individual fixes does not equate to the number of fixes collected (Table 3), as many fixes were repeated den trees.
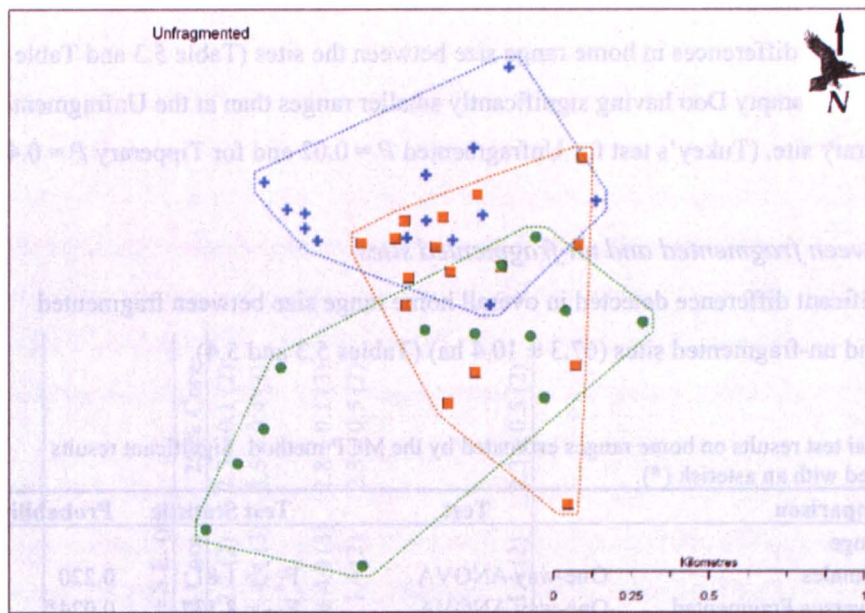
Figure 5:6: The overlap of home range (MCP estimate) for animals at the un-fragmented site. Individual fixes are shown by green dots (C5 – male), orange squares (C28 – female) and blue crosses (C36 – male).
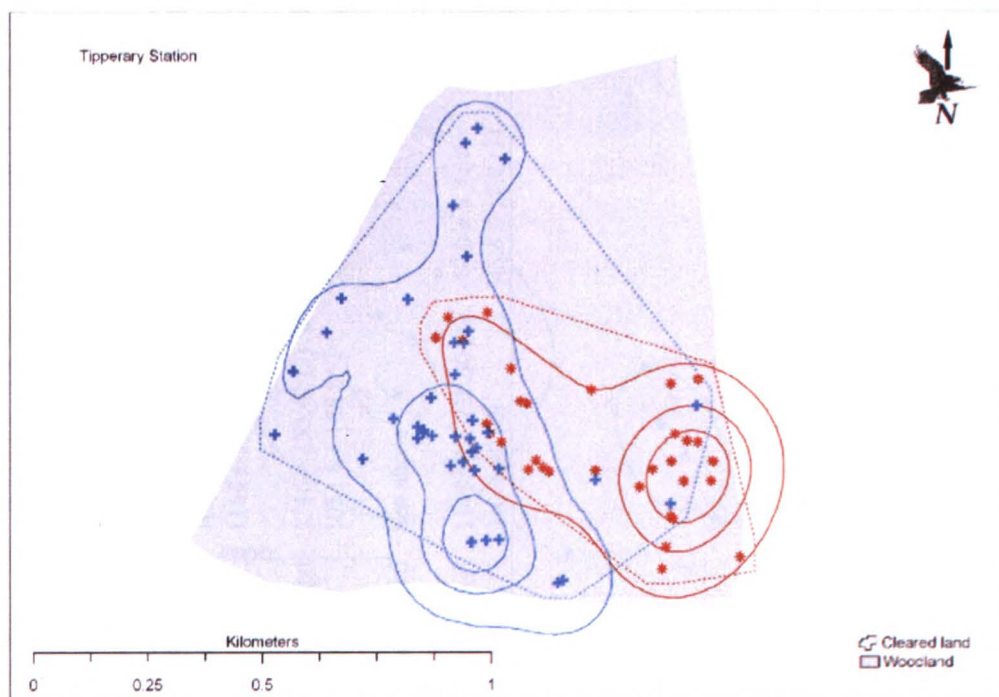
Figure 5:7: A comparison of the two home range estimates for a male black-footed tree-rat (T44 - blue) and female (T46 - red) from the Tipperary study site. Hashed line is the MCP estimate and continuous line the kernel method (95%, 50% and 25%). Individual location fixes are shown with red asterisk (T46) and blue crosses (T44). The fragment boundary is shaded. Note: the kernel method estimates areas outside the fragment as being within the home range.

Activity Area

For the purpose of this study 'activity area' is defined as the area occupied by the den tree locations of animals. Many radio-tracking studies of mammals in northern Australia have only collected diurnal fixes of a species denning location and have not obtained information on nocturnal foraging activity. This provides a comparison with other studies of mammals from this region. As only a small subset of animals was able to be included in the home range estimation (see discussion) it allows for a larger set of data to be used. MCP was the only method used to investigate activity area. The mean activity area of all individuals was 10.5 ± 1.9ha (Table 5.5). The mean activity area for black-footed tree rats in un-fragmented areas was 16.9 ± 4.3 hectares (Table 5.6).

Individuals at fragmented sites were found to move between fragments within that site. Black-footed tree-rats were found denning in the roofs of houses and in the non-native vegetation surrounding them (Figure 5.9). The largest movement across a cleared area (the "matrix") was 700 m at the Tipperary study site, by female (T28) (Figure 5.10). This movement was only detected once during the three month tracking period. Male (T1) at the Tipperary site moved 1.2 km from his resident fragment, however this movement was through regrowth of approximately 3-4 m in height (Figure 5.10).

Table 5.5: Activity area estimates (MCP) for individual radio-tracked black-footed tree-rats. Individuals with 10 or more fixes only.

Animal I.d.	Sex	Site	No. of fixes	MCP (ha)	Weight at first capture (g)
HD76	Male	Humpty Doo	12	2.5	520
HD74	Male	Humpty Doo	11	3.7	640
L9	Male	Lambells	17	3.8	727
L44	Male	Lambells	10	4.6	600
L80	Male	Lambells	19	6.1	680
HD12	Male	Humpty Doo	45	6.9	659
C4	Male	Unfragmented	31	9.7	639
C140	Male	Unfragmented	28	10.8	718
C5	Male	Unfragmented	28	11.8	620
T1	Male	Tipperary	23	13.6	755
C14	Male	Unfragmented	22	15.3	690
C12	Male	Unfragmented	19	22.9	730
T44	Male	Tipperary	23	26.4	685
C36	Male	Unfragmented	32	40.4	639
L16	Female	Lambells	44	1.4	587
L718	Female	Lambells	30	1.9	658
L476	Female	Lambells	24	2.2	528
HD18	Female	Humpty Doo	18	2.4	660
HD58	Female	Humpty Doo	16	3.5	535
L8	Female	Lambells	11	4.7	615
L6	Female	Lambells	26	5.8	717
C28	Female	Unfragmented	26	7.7	650
T46	Female	Tipperary	22	14.9	556
T28	Female	Tipperary	21	22.0	555
Mean			23.9 ± 1.7	10.5 ± 1.9	

Table 5.6: Mean activity area sizes (ha) derived by the MCP estimation method.

Mean	Minimum Convex Polygons ± S.E. (n)
Female	4.9 ± 1.3 (10)
Male	12.4 ± 2.7 (15)
Unfragmented	16.9 ± 4.3 (7)
Fragmented	6.5 ± 1.5 (18)
Continuous	16.9 ± 6.4 (7)
Lambells	3.7 ± 0.6 (8)
Humpty Doo	5.9 ± 2.4 (6)
Tipperary	12.9 ± 5 (4)

Differences between the sexes

The activity area of males (12.4 ± 2.7 ha) was twice as large as that of females (4.9 ± 1.3 ha) (Table 5.6). Males also had the four largest home ranges (Table 5.5), though due to the small sample size this difference was not significant.

Differences between the sites

There were highly significant differences in activity area size between the sites (Table 5.6) with animals at Lambells (low fragmentation) having significantly smaller ranges than those at the Un-fragmented and Tipperary (high fragmentation) sites, but not significantly different from Humpty Doo (medium fragmentation) (Tukey's test for Un-fragmented $P = 0.01$; for Tipperary $P = 0.01$; and $P = 0.96$ for Humpty Doo). Animals at Humpty Doo also had significantly smaller activity areas than animals at Tipperary; and Un-fragmented, although this was not significant (Tukey's test for Tipperary $P = 0.05$; Un-fragmented $P = 0.06$).

The trend in differences between sites for home range, activity areas and movement (see below) is potentially due to the density of black-footed tree-rats at the sites (Figure 5.8). However this could not be tested for significance because of the small number of sites (n = 4). Figure 5.12 shows the trend with psudoreplication of density for each individual at each site. The Lambells site has significantly smaller activity areas and average movement than the other sites, but substantially higher densities (Figure 5.8).

Differences between fragmented and un-fragmented sites

The mean activity area in the unfragmented site was three times as large as that of the fragmented sites, with a significant difference between fragmented (6.5 ± 1.5 ha) and unfragmented sites (16.9 ± 4.3 ha) (Table 5.7).

Table 5.7: Statistical test results on activity area estimated by the MCP method. Significant results are denoted with an asterisk (*).

Comparison	Test	Test Statistic	Probability
Activity Area			
Males versus Females	One Way ANOVA	$F_{1,23} = 2.77$	0.109
Un-fragmented versus Fragmented	One Way ANOVA	$F_{1,23} = 5.20$	0.032*
Sites	One Way ANOVA	$F_{3,21} = 6.69$	0.002**

NB: A two-way ANOVA of fragmented and un-fragmented sites with a site interaction could not be conducted as the un-fragmented sample only consisted of one site.
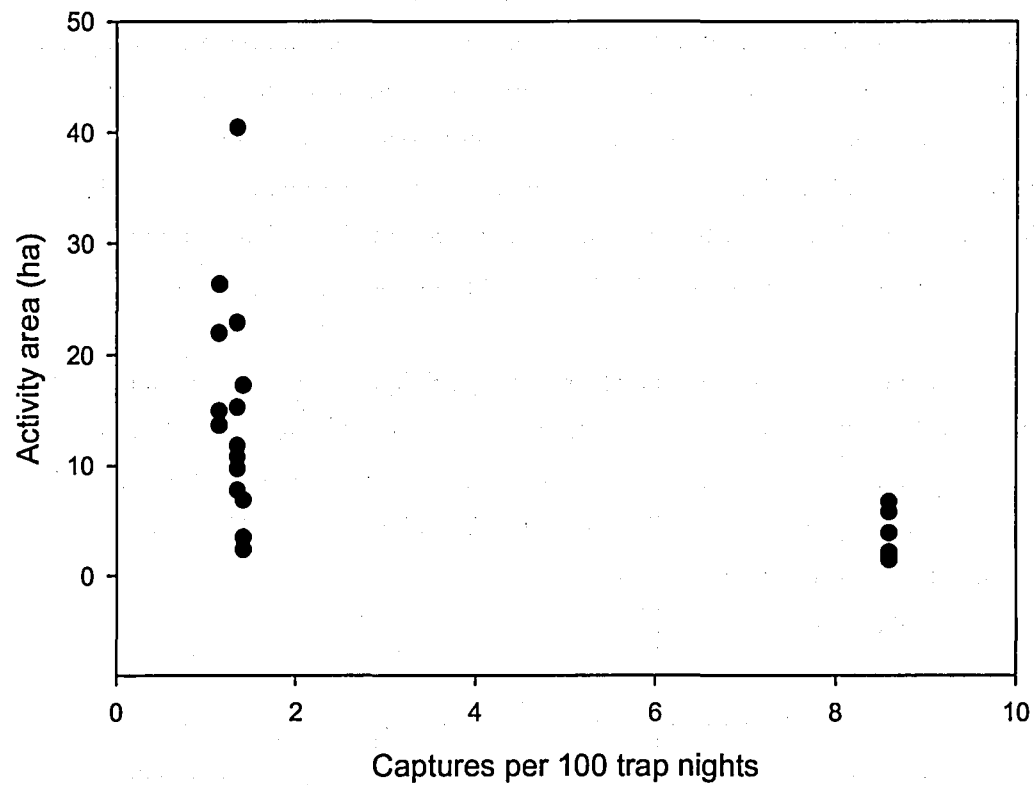
Figure 5:8: Activity area of black-footed tree-rats plotted in relation to a relative density estimate of black-footed tree-rats for each site (captures per 100 trap nights).
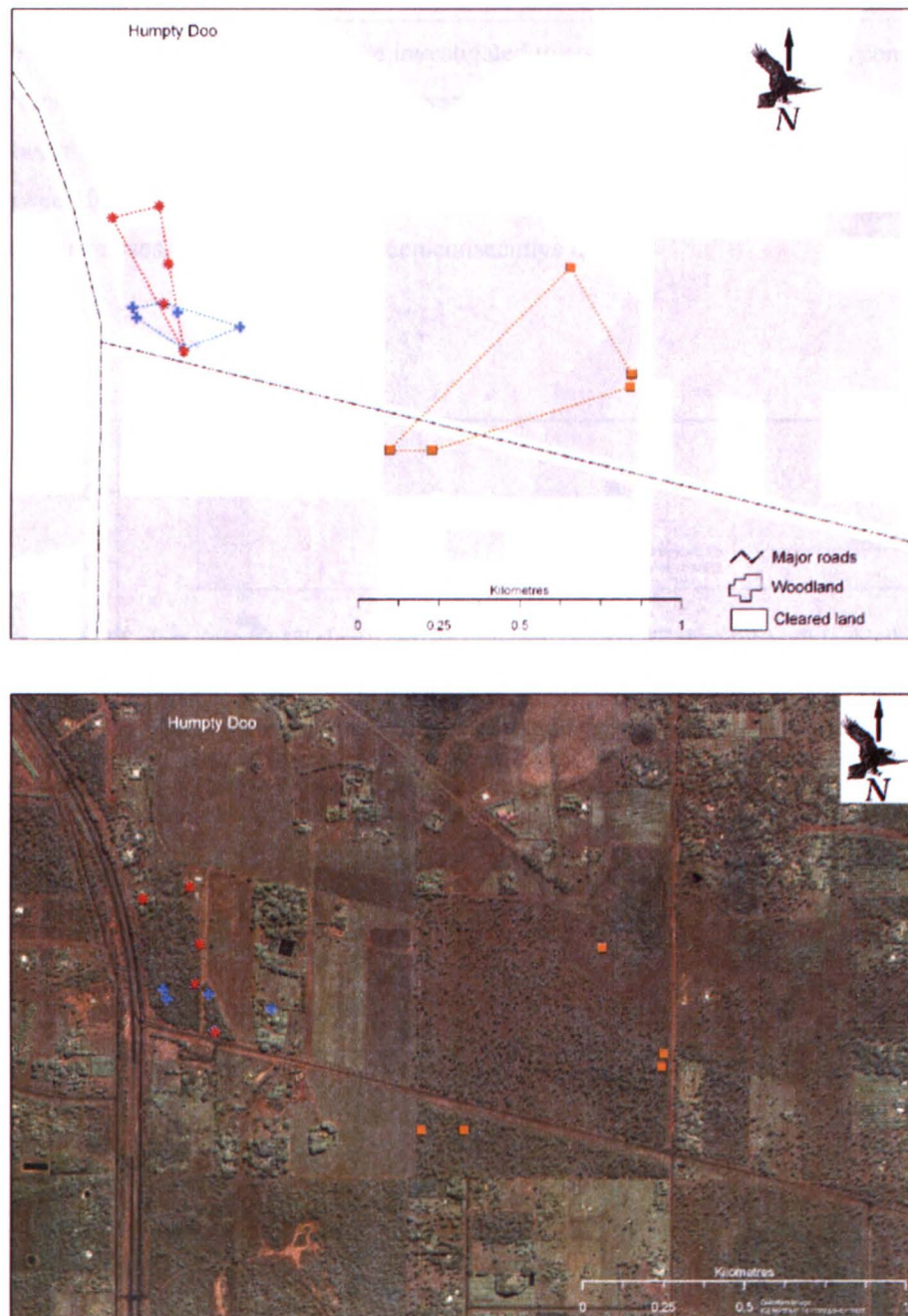
Figure 5:9: a) Location of MCP activity area estimates for female HD18 (blue), female HD58 (red) and male HD66 (orange) at the Humpty Doo study site. Native vegetation is shaded with cleared areas white, animals are shown to use locations within cleared areas. b) Quickbird satellite imagery in the background shows they were actually located in areas of low density trees or in non-native vegetation surrounding human dwellings.
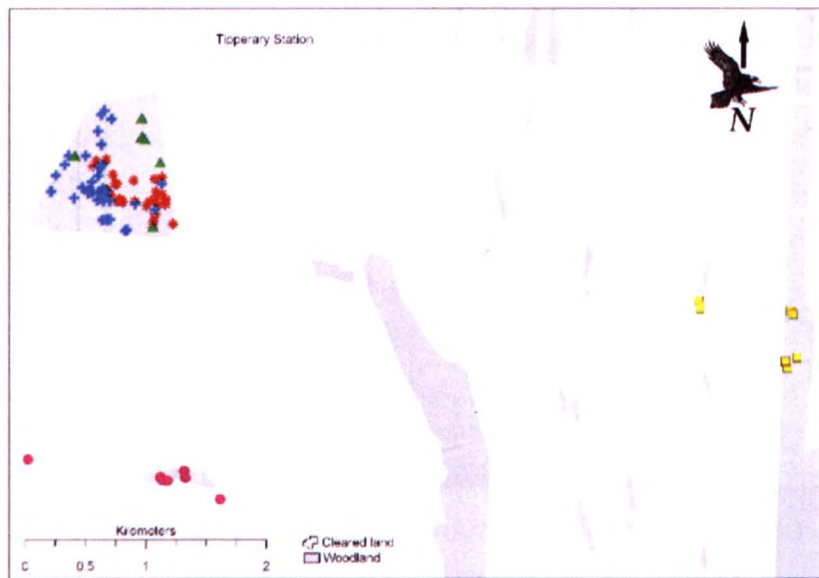
Figure 5:10: Individual fixes for male T44 (blue), female T46 (red), male T3 (green), male T1 (pink) and female T28 (yellow) at the Tipperary study site. Fragments are shaded. Animals within the largest fragment were not found outside the fragment. However animals within smaller patches moved across expanses of cleared land to reach other fragments. The cleared area transversed by female T28 was cleared pasture with scattered regrowth to 1.5 - 2 m. The cleared area covered by male T1 was regrowth to 4 - 4.5 m. This individual moved to a pandanus within the regrowth approximately 1.2 km from its last den, where it remained for 1 night and returned to its previous den location in the fragment.
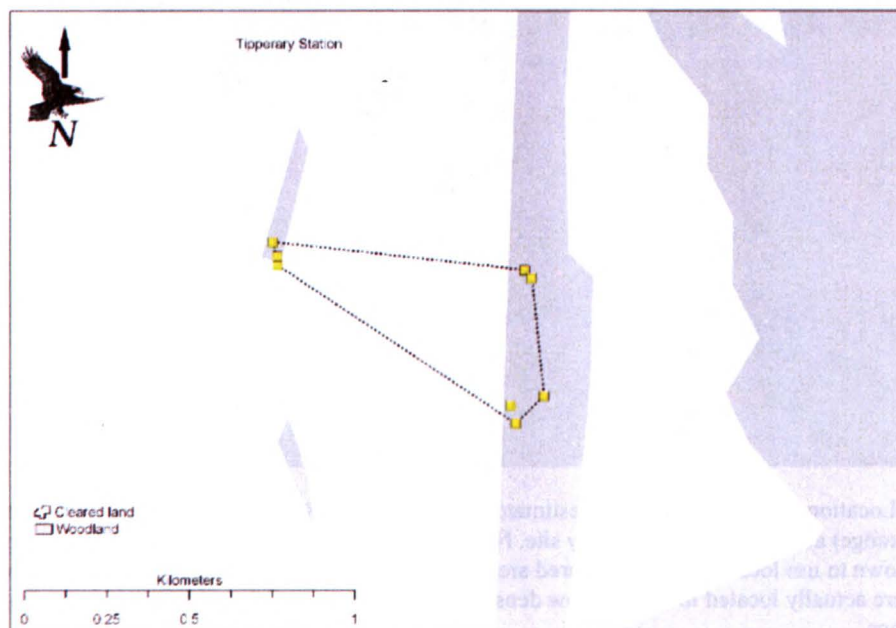
Figure 5:11: The MCP activity area for female T28 at the Tipperary study site (finer scale of part of Figure 5.10). Individual fixes are denoted by yellow squares. This figure highlights the inclusion within calculated MCP's of large areas of cleared land that was not actually used. Activity areas were adjusted for this by calculating the area of native vegetation within the activity area estimate using GIS software.

Movements

Movements between den trees were investigated to compare with past studies conducted on mammals within Australia's tropical savannas. The distances moved by black-footed tree-rats between den trees was not significantly correlated with the length of time (time interval) between fixes ($F_{1,168}$ = 3.15, P = 0.09) (Figure 5.12), thus all movements were included in further analyses, not just those between consecutive dens.
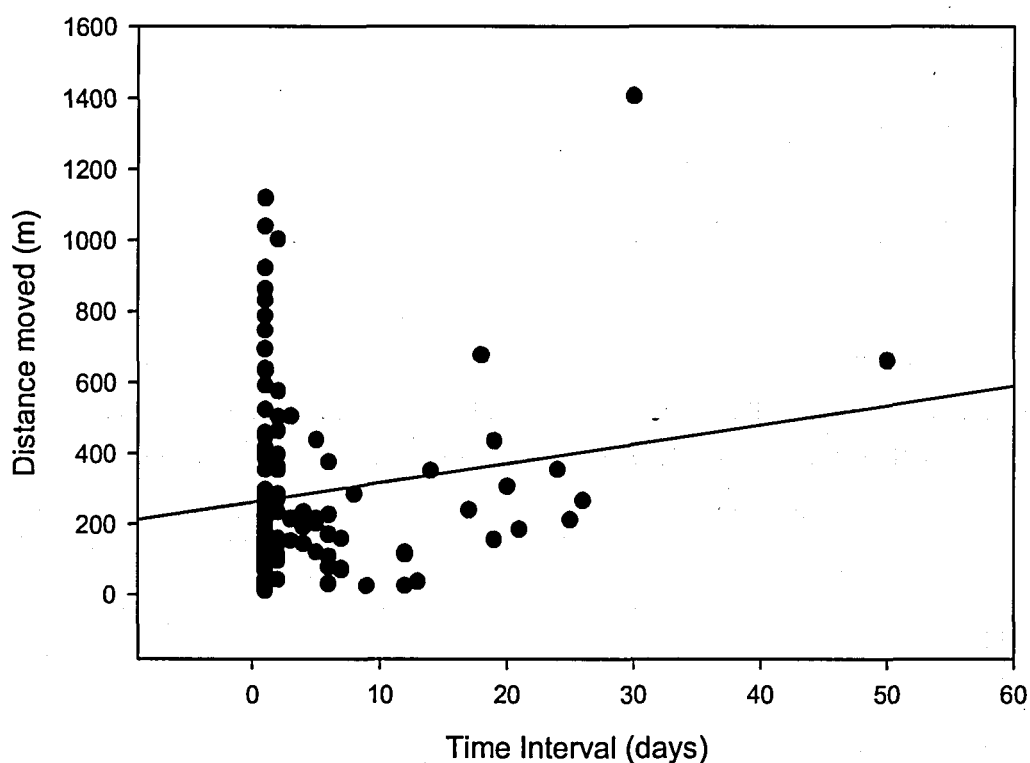
Figure 5:12: Regression plot of the distance moved by black-footed tree-rats between den locations against the time interval in days between the fixes.

Differences between the sites

Distances moved between den trees varied very significantly between sites (ANOVA $F_{3,166}$ = 12.3, P = <0.001) following the same pattern as activity areas (Figure 5.13). Animals at Lambells had significantly smaller movements than those at the Unfragmented and Tipperary sites, but not significantly different from Humpty Doo (Tukey's test for Unfragmented P = <0.001; for Tipperary P = 0.001; and P = 0.6 for Humpty Doo). Individuals at Humpty Doo also had significantly smaller activity areas than individuals at Tipperary; and Unfragmented (Tukey's test for Tipperary P <0.002; Unfragmented P <0.001).
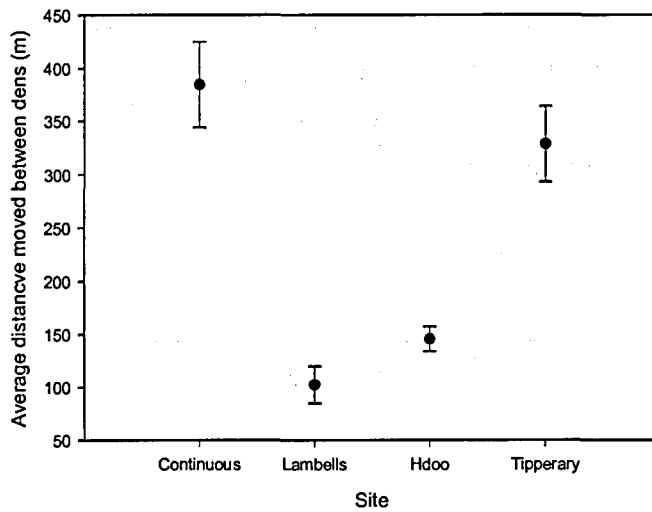
Figure 5:13: Average distance moved between den trees at the four study areas (±SE).

Differences between the sexes

Males moved further between den trees than did females (327 ± 28 m) and (199 ± 20 m) respectively (ANOVA, $F_{1,168}$ = 10.128, P = 0.002) (Figure 5.14).
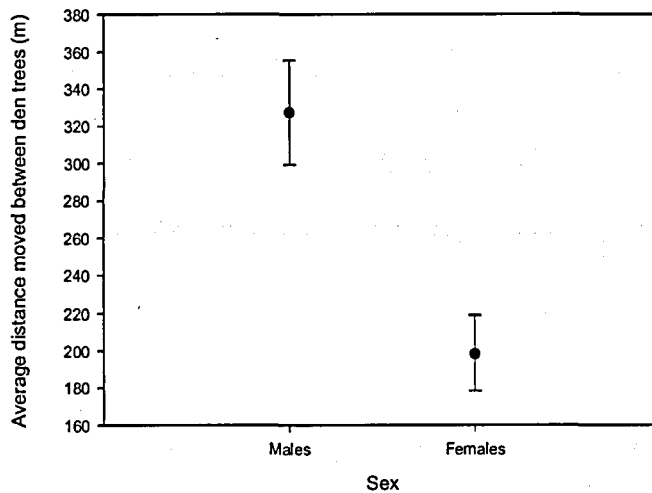
Figure 5:14: Average distance moved between den trees for females and males, over all sites, standard error bars shown.

Differences between fragmented and un-fragmented sites

Black-footed tree-rats moved further between den trees in un-fragmented (385 ± 40 m) than in fragmented sites (228 ± 20 m) (ANOVA, $F_{1,168}$ = 15.1, P = <0.001) (Figure 5.15).
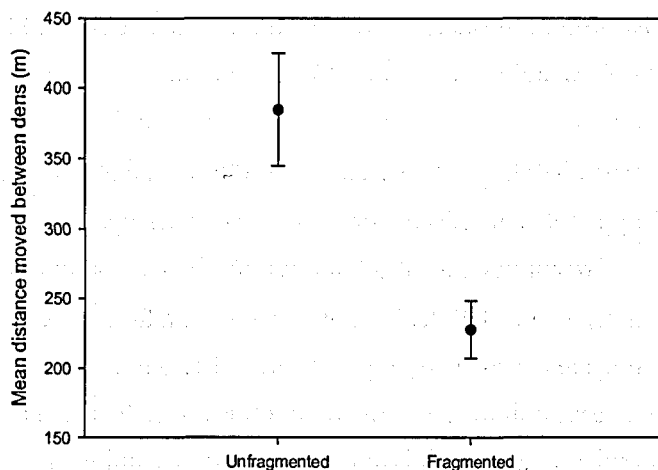
Figure 5:15: Average distance moved between den trees in un-fragmented and fragmented sites, standard error bars shown.

Discussion

Home Ranges, Activity Areas and Movements in unfragmented woodland

The number of autecological studies of mammals in the Northern Territory is relatively few (Woinarski 2004). Relatively little is known about even the most common mammal species when compared with the knowledge of mammals of southern Australia. This is the first substantial study to estimate home range size for black-footed tree rats. A previous study by Griffiths et al. (2002) investigated the activity area of three black-footed tree-rats in remnant vegetation near Darwin, recording activity areas of 7.3 to 18.2 ha over a 3 month period. These activity areas are comparable with this study which recorded activity area over a 3-4 month period.

Most studies of small/medium mammals in the tropical savannas of the Northern Territory have relied on trapping-grids to provide estimates of movement. This limits the ability to compare findings, as estimates from the trapping grids are inhibited by the grid's size and location (Griffiths *et al.* 2002). Pavey *et al.* (2003) found home range size based on trapping grids substantially underestimated overall home range, with radio-tracking producing estimates that were greater by a factor of 24.5 for males and 15.5 for females. For this reason, to allow comparison with previous studies of sympatric species in this area, home range, activity area and distances moved between dens were investigated during this study. One grid-based study (Friend 1987) looked at the distances moved between consecutive nights for black-footed tree-rats on a trapping grid, reporting an average movement of 66 m for males and 102 m for females. Consistent with the results of Pavey *et al.* (2003), that grid-based analyses under-

estimate movement patterns, my radio-tracking results suggest substantially larger movements than those reported by Friend (1987). The average distances moved by individual black-footed tree-rats in this study were, (327 ± 28 m) for males and (199 ± 20 m) for females.

This study, along with the results from Griffiths *et al.* (2002), suggests that the area required by black-footed tree-rats is substantially larger than that of most other sympatric small mammal species in the Kakadu National Park area. For example, the brushtail possum *Trichosurus vulpecula* was found to have a mean activity area of 1.12 ha for males and 0.89 ha for females using a large 20 ha grid (Kerle 1998), compared to an average activity area of 16.3 ± 3.1 for males and 6.8 ± 2.1 for female black-footed tree-rats. A study of the northern brown bandicoot *Isoodon macrourus* at Mitchell Plateau in Western Australia recorded an average activity area of 0.71 ± 0.35 ha based on the grid area utilized (GAU) after five captures (Kemper *et al.* 1990). However, another sympatric species, the northern quoll *Dasyurus hallucatus* which is of similar size to black-footed tree-rats, has a higher average den home range estimate (using MCP) of 35 ha for females and approx 84 ha for males (Oakwood 2002). However this estimate was derived in what was considered to be low quality habitat.

The size of home range estimates for black-footed tree-rats in the unfragmented environment suggests that they require large areas (67.3 ± 10.4 ha) when compared to other mammal species of Australia's tropical savannas. These estimates should only be considered as a guide as there is likely to be large variability, for a number of reasons. Firstly, the small sample size (n = 3) used to calculate the estimate creates its own problems. The areas presented here are three month home-range estimates only and probably underestimate the lifetime home range area of black-footed tree-rats. The small number of individuals with enough fixes to estimate home range limited investigating seasonal effects. Finally, the high seasonality of the wet-dry tropics leads to high variability in habitat and food resources, suggesting that home range and activity areas of black-footed tree-rats may expand and contract at different times of the year (Griffiths *et al.* 2002).

Factors affecting home range

The space used by a species provides important information about factors that limit the species. Larger animals tend to have larger home ranges, because of body mass (Harestad and Bunnell 1979) and energetic requirements (McNab 1963). However, the relationship between body size and energetics cannot explain all variation in the home range size of mammals (Fisher and Owens 2000). This variation can be accredited to differences in climate, diet, interspecific competition and predation risk (Harestad and Bunnell 1979; Damuth 1981; Gompper and

Gittleman 1991; Fisher and Owens 2000). Mammals that live in habitats that are low in productivity (e.g. desert) or that eat patchily dispersed food (e.g. fruit or meat) are predicted to have larger home ranges for their body size than species living in productive environments (e.g. rainforest) or those that eat more evenly dispersed food items, such as grass or leaves (Harestad and Bunnell 1979; Damuth 1981; Fisher and Owens 2000). The home range of black-footed tree-rats is larger than expected based on body size, however the patchy distribution of the fruits that dominate its diet may require it to move further in search of food (Strahan 1995; Rankmore 2003).

Population density has also been found to influence the size of a home range, being significantly larger in low density populations (Hayward et al. 2004; Pope et al. 2004). Damuth (1981) suggested that population density affects home range size in mammals because the energy availability for individuals is negatively related to the number of animals sharing an area. Although not analysed statistically in this study due to small sample size, the density of black-footed tree-rats at the Lambells study site was substantially higher than the other three study sites (Table 5.1) and had the smallest estimates of home range, activity area and movements between den trees. In general, habitats that are able to sustain higher population densities are likely to have high levels of productivity. Chapter 6 investigates this aspect further, investigating the relationship between habitat quality and density of black-footed tree-rats at the sites.

Although not statistically significant for home range and activity area, the differences in home range size between the sexes observed in this study are probably related to social organization and mating systems. In mammalian herbivores, the distribution and availability of food resources govern female home range (Clutton-Brock and Harvey 1978), and it is the factors that influence space use in females that ultimately determine social organization (Fisher and Owens 2000). Male spatial organization is in turn affected by space use by females, because male reproductive success is dependent on the number of mates he is able to find and defend (Clutton-Brock 1989). The black-footed tree-rat is considered to be solitary, suggesting that male home ranges should be larger than those of females, as males benefit from searching widely for mates (Fisher and Owens 2000). However, in areas of high quality habitat, a high degree of overlap in home range (as found in black-footed tree-rats - Figure 5.6) between individuals may reduce the area males need to cover to find mates thus reducing the difference between male and female home range size.

Fragmentation effects on home range

The size of home range and activity areas of black-footed tree-rats was not shown to be impacted by habitat fragmentation. The large home ranges observed at the highly fragmented study site (Tipperary) compared to the medium and low fragmented sites (Humpty Doo and Lambells respectively) are likely to be an artefact interacting factors, such as patch size, the level of fragmentation and differing study areas. The relative effects of these factors could not be detangles with the data available. Home range at Tipperary was determined based on two individuals located in a fragment, 100 hectares in size. As this fragment is substantially larger in size than black-footed tree-rats home range in continuous environments, it may be that this patch is capable of supporting a population with a similar spatial pattern to that experienced in continuous situations, as found by Pope *et al.* 2004) in a study of greater gliders *Petauroides volans*.

At fragmented locations, animals residing within small fragments were found to move between fragments across large open areas, but this did not occur with animals based in larger fragments (Figures 5.10 and 5.11). This suggests that the area of a fragment may be an important factor limiting the home range size of black-footed tree-rats. This supports the findings from the initial survey (Chapter 3) of a positive relationship with the area of a fragment (i.e. black-footed tree-rats prefer larger fragments). Unfortunately the limited data obtained on animals that moved between one or more patches prevented analysis from being conducted. Ultimately, it is likely that black-footed tree-rats depend on a certain amount of woodland to maintain a population, and this may be achieved either in a single large patch, or via several small patches.

Home Range Estimation Techniques

Neither of the two methods used in this study (MCP and Kernel) are ideal for estimating home range in fragmented areas. Both methods included within the estimates large areas of cleared vegetation, known not to be used by black-footed tree-rats. This was also shown by the lack of any locational fixes being obtained from cleared areas. It has been reported that these commonly used techniques are not ideal for use in fragmented or linear environments because the "ballooning isopleths" include areas of unused cleared land within the home range estimates (Andreassen *et al.* 1998; this study).

In some cases the kernel estimator produced mapped home ranges that appear to accurately depict the area used. At other times this method appeared to place excessive weight on the core areas resulting in large circles around them that encompassed areas not noted as being used by the individual in question (Figures 5.5 and 5.7). The MCP method, although biased by outlying

fixes (Harris *et al.* 1990), appeared to be better at estimating home range within fragmented environments, despite potentially elongating the home range shape.

Collar success

Problems were experienced with the suitability of the three varieties of radio collar attachments. The cable tie collars were highly susceptible to damage by black-footed tree-rats with the majority of animals dropping their collars within a few weeks of attachment. This form of collar attachment was discontinued not only because of its unsuitability for large rodents capable of biting through the plastic, but also because the cable ties cut into the necks of the animals. To investigate a suitable form of collar attachment, 10 bird transmitters were re-potted and modified into collar formations by the author. These used a leather collar lined with wool and required attachment via stitching with nylon thread. These collars also proved unsuitable as the attachment process was cumbersome and time consuming, resulting in animals having to be sedated during fitting. These collars were also highly susceptible to damage by the black-footed tree-rats; however the damage occurred to the transmitter, not the collar. The transmitter components had been enclosed in shrink-wrap plastic and coated with epoxy resin. Although this design proved suitable for the common brushtail possum *Trichosurus vulpecula*, in previous trials, they were no match for the incisors of black-footed tree-rats. The severe damage caused to the transmitters resulted in all of these failing short of their expected lifespan. It is recommended that future studies of large rodents and other species that can inflict significant damage to radio collars investigate a range of different attachment mechanisms in a pilot study before they start collecting radio-tracking data.

The third variety of collar (commercially produced by Sirtrack) had the leather/wool collar secured with a nylon nut and bolt. This meant that radio collars could be fitted in the field without the need for sedation. Being made of natural fibres, the leather/wool collar would eventually perish and drop off, hence allowing for animals that were never recaptured to lose their collars. However, these collars also suffered damage by black-footed tree-rats with a large number failing before their expected lifespan. This was more pronounced in the wet season, with moisture penetrating into the electronics of the transmitters. I lost 10 transmitters over the course of a three week period after the first rains, all of which had only recently been attached. This had a significant effect on home range estimates with only a small number of the animals collared having the required number of fixes needed to estimate home range.

Tracking Success

The low number of fixes obtained by the radio-telemetry towers also contributed to the limited data available for home range analyses. Initially, intensive radio-tracking sessions were to be conducted on foot for a few nights each month. However this method proved unsuccessful, with the animals detecting our presence and fleeing long before we were able to obtain an accurate fix. This left the option of remote radio-telemetry using stationary towers. Once the towers were obtained there was a limited time frame in which data could be collected as the telemetry towers could not be used during the wet season, because of the regularity of electrical thunder storms.

Signal reception and location accuracy can be affected by many factors, including mapping error, signal bounce, vegetation cover, nature of the terrain, atmospheric conditions, animal movements, operator error, distance to radio-tagged animals and electromagnetic interference (Harris *et al.* 1990; Schmutz and White 1990; White and Garrott 1990; Nams and Boutin 1991; Withey *et al.* 2001a). Many of these factors had to be overcome during this study; however the effects of electromagnetic interference at one site and differences in vegetation cover between the sites caused substantial problems.

The first intensive tracking session was carried out at the Tipperary study site, with no problems encountered. Error in location accuracy was minimized for operator error, with observers being trained for approximately half a day before the commencement of each session. Observers were also required to take bearings on dummy transmitters as frequently as true transmitters, without prior knowledge of which frequencies were dummy transmitters. The error associated with animal movements and the distance to the radio-tracked animal could be assessed from notes collected on signal strength, quality and ease of signal detection.

The intensive tracking session at the Humpty Doo site encountered problems with electromagnetic interference. This site has a higher density of human habitation and man-made structures (Figure 9a and b). While few studies have investigated this effect, a study by Parker *et al.* 1996) found a significant negative difference in bearing error the closer towers were to power lines. Despite the towers in this study being located as far away from power lines as possible, interference was still detected. Many signals were hard to detect because of background static, and on a number of occasions observers were able to detect television and radio signals as well as what appeared to be a telephone conversation. Only a small number of fixes obtained over the four night period were able to be used in the analysis as all triangulation calculations with an error ellipse > 1 ha were eliminated.

Differences in vegetation cover between the study sites also created problems. The vegetation at the un-fragmented site was taller and denser than that at the Tipperary site. Towers at the un-fragmented site were initially set up at a similar distances to those at the Tipperary site. The thicker vegetation reduced the distance at which transmitters could be detected. To overcome this problem two of the towers were moved closer to reduce the distance between towers. Although this overcame the problem, the wet season rains arrived early, before we had time to complete four nights of tracking with the new tower locations.

Many authors have recommended a site-specific pilot study be carried out to determine the best radio-tracking regime and to assess the accuracy in all radiotelemetry studies (Harris *et al.* 1990; White and Garrott 1990; Withey *et al.* 2001b). Although this would highlight problems such as those encountered during this study, the amount of time required to conduct a pilot study at each site is unrealistic and could not be justified for this study, with radio-tracking only being a small part of a larger project.

Conclusion

Black-footed tree-rats have a large home range. Home range and activity area size decreased significantly under fragmented conditions however, movements in large patches (i.e. greater than home range requirements) are similar to unfragmented conditions. Black-footed tree-rats were able to cross relatively large areas of cleared land (~700 m). Although they are able to move among fragments, they do not appear to use cleared land. Requiring large areas in order to obtain enough resources, it appears they are able to cope with low levels of habitat fragmentation, using many smaller patches to achieve this. Home ranges were smaller where black-footed tree-rat densities were high.

These data suggests that black-footed tree-rats are responding positively to low levels of habitat fragmentation. Alternatively, the configuration of fragments in Lambells may be more productive than the continuous and Tipperary sites. Some agricultural landscapes may provide areas of higher quality habitat as the agricultural matrix can protect sites from fires that in turn promote a higher diversity of understory fruiting plants (Chapter 6).

Livistona humilis

Sand Palm

Habitat

TROPICAL SAVANNAHS
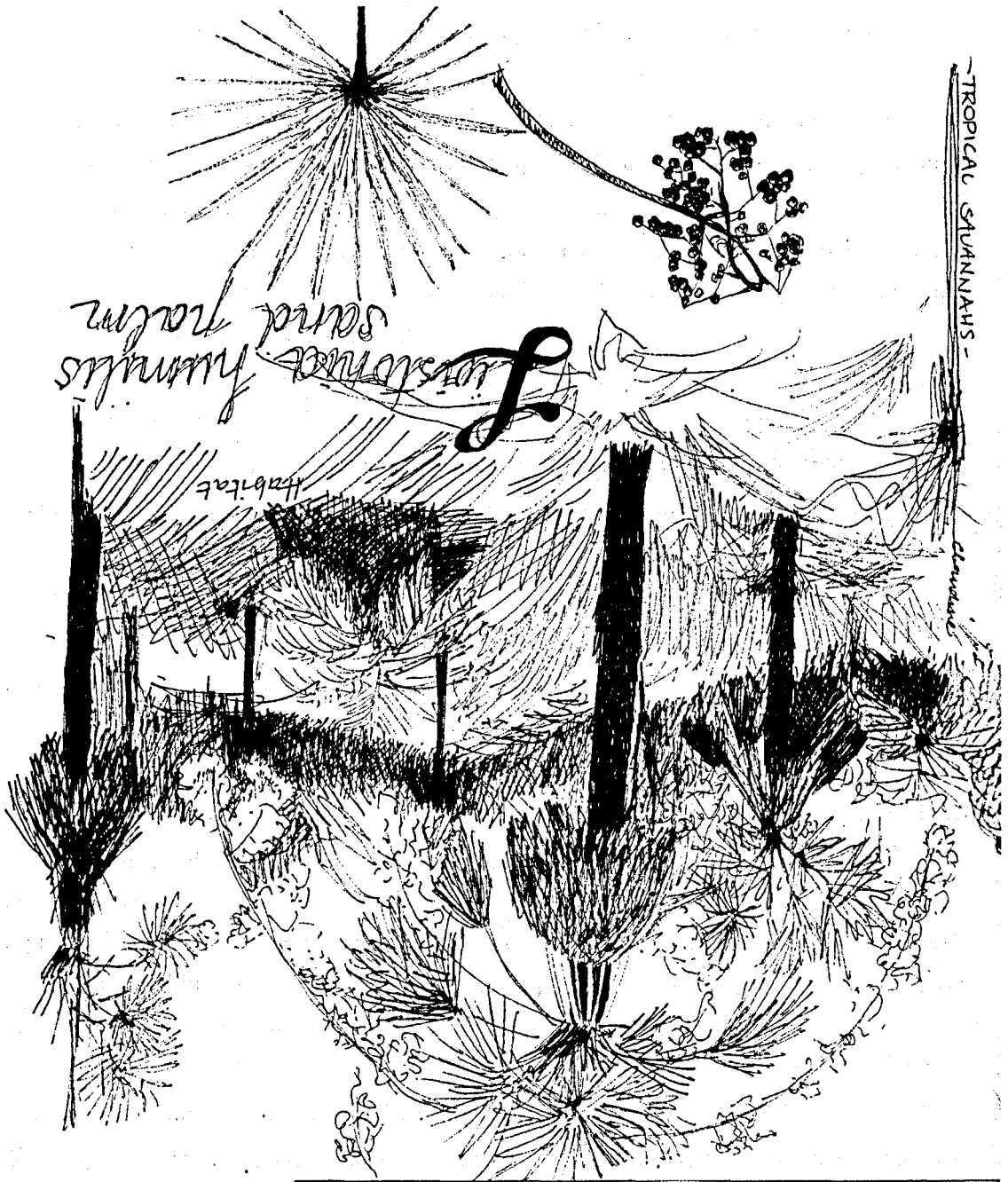
CHAPTER 6

Habitat preference and availability for the black-footed tree-rat Mesembriomys gouldii within a fragmented landscape.

Introduction

It is widely accepted that small habitat patches will contain fewer species than large patches, with species richness often being positively correlated with patch size (e.g. Kitchener *et al.* 1980; Suckling 1982; Bennett 1987; Saunders and de Rebeira 1991). However, the 'Biotic Interactions Model' (Ambuel and Temple 1983) proposes that species composition is regulated by area-dependent changes in the structural characteristics of a fragment rather than the area of the fragment *per se*. Large habitat fragments are more likely to contain greater habitat diversity than smaller fragments (Saunders *et al.* 1991), and as a result the number of species within a patch will reflect to some degree the number of different habitats that are available (Bennett 1990b). For species to persist within a fragmented environment they must have access to adequate resources that provide food and shelter. The availability of these resources will limit not only the number of species but also the number of individuals of each species capable of persisting.

Tree hollows are considered an important resource for wildlife world-wide. They are particularly important in Australian forests and woodlands with 15% (approximately 300 species) of terrestrial vertebrates using this resource for shelter (Gibbons and Lindenmayer 2002). Tree hollows are used to provide shelter from predators and adverse weather conditions, and as a place to rear young. Many studies have shown the dependence of a wide range of species on tree hollows (Rowston 1998; Inions *et al.* 1989; Smith and Lindenmayer 1988; Lindenmayer *et al.* 1990; Mawson and Long 1994). Within the Top End of the Northern Territory approximately 40% of mammals, 18% of birds, 20% of reptiles and 13% of frogs are known to use tree hollows (Taylor *et al.* 2003). Within fragmented habitats, the availability of hollows may be a critical determinant of habitat quality for these species (Gibbons and Lindenmayer 2002).

Abundance and availability of food resources are also considered to be important factors influencing natural populations (Batzli and Lesieutre 1991). Differences in food abundance and/or availability between or within habitats occurs naturally, as some areas are more productive than others, but can also be created by human induced changes to the environment such as land clearing and habitat fragmentation. At the landscape scale, habitat fragmentation is

not a random process (Burgman and Lindenmayer 1998). Land clearing usually occurs on a selective basis, with the most productive soils being cleared first for agriculture (Hobbs and Hopkins 1990; Saunders *et al.* 1991; Hobbs and Saunders 1993; Burgman and Lindenmayer 1998). Remaining habitat patches are more likely to exist on land with low quality soils or are located in areas that are unsuitable for proposed land uses, such as areas with high slopes, valleys and gullies. This pattern may lead to significant and selective loss or elimination of some habitat types, while others may remain relatively intact. At the patch scale, a range of alterations to light levels, humidity, soil moisture and rates of litter desiccation (Lovejoy *et al.* 1986) will affect wildlife, either directly or indirectly through changes to habitat (Harris 1988; Yahner 1988; Angelstam 1992; Bierregaad Jr. *et al.* 1992). Changes in plant communities and habitat structure will lead to altered habitats for animals (Bennett 1998), thus influencing wildlife communities (Yahner 1988).

Eucalypt forests and woodlands dominate northern Australia, extending over 180,000 km^2 in the Northern Territory (Wilson *et al.* 1990), they are simple in structure and have similar species composition across a large area (Woinarski 1992; Woinarski *et al.* 2005). However, this hides a finer-level of spatial and temporal variability and patchiness (Whitehead *et al.* 2005). Fire is considered to have the most broadly encompassing influence on the condition of fauna habitat in northern Australia (Whitehead *et al.* 2005). The black-footed tree-rat is one of a group of species that prefers vegetation that is relatively long-unburnt (Friend and Taylor 1985), as these areas tend to support higher densities of fruiting understorey plants (Williams *et al.* 1999b) and may have larger trees and thus more hollows (Woinarski 2004). Studies investigating the effects of fire on vegetation structure have found that individual fires increase plant mortality, particularly in the broad-leaf deciduous mid-storey species (Williams *et al.* 1999a). In the longer term, fire frequency has also been found to influence the abundance of savanna species with the density of non-eucalypt species increasing with increased fire interval (Bowman *et al.* 1988; Fensham 1990; Bowman and Panton 1995; Woinarski *et al.* 2004).

In this chapter I investigate the preferences and availability of den trees and food resources of the black-footed tree-rat *Mesembriomys gouldii*. The study aims to identify the characteristics of den trees selected by black-footed tree-rats and to determine and compare the availability of potential den trees in fragmented and unfragmented environments. The study also aims to examine the influence of fire history (timing and frequency) on vegetation structure and composition and to investigate the indirect effects of fire on the density of black-footed tree-rats at the site. On this basis, the key questions of interest for this study are:

- What is the availability of tree hollows at the sites?
- What are the environmental factors that affect hollow availability?

- What are the characteristics of dens selected by black-footed tree-rats?

- Does the availability of trees with these characteristics limit black-footed tree-rat populations?

- What are the habitat preferences of black-footed tree-rats?

- Which fruit species are important?

- What environmental factors influence fruit availability?

Methods

Study Area

Radio-tracking and mark-recapture of black-footed tree-rats was conducted at a subset of nine sites (Table 6.1) (see Chapter 4 for details and maps). Sites were selected based on the presence of black-footed tree-rats and/or northern quolls, during the original survey, and the size of the fragment (Chapter 4). Because of the low level of land clearing that has occurred in the study area it was not possible to replicate the fragment size. Although mark-recapture and radio-tracking was conducted at sites within the Tipperary study area, these were not included within the den tree and vegetation analyses as the vegetation assessment at Tipperary was carried out using a different methodology. Thus the analyses in this chapter include only sites within Litchfield Shire.

Table 6.1: The Litchfield Shire study sites used to investigate habitat preferences of the black-footed tree-rat, showing the level for fragmentation (see chapter 4), size of each site in hectares and the number of 1 hectare mammal trapping and 20m x 20m vegetation quadrats per site. Site # provides the number allocated to each site in the initial study to allow the sites to be located on maps (See chapter 4 for map).

Site Name	Site #	Level of Fragmentation	Size (ha)	No. quadrats Mammal Trapping	Vegetation
Continuous	35	Un-fragmented	2304	6	24
Lilly Mays	1	Medium	6.0	1	4
Ons	2	Medium	49.7	4	16
Metcalfes	5	Medium	13.2	2	8
Henning	36	Low	1.2	1	4
Collins	37	Low	8.3	1	4
Pearces	39	Low	7.8	1	4
Wilsons	40	Low	29.6	2	8
TOTAL				68	72

Field Data

Radio-tracking

Diurnal telemetry conducted between August 2001 and March 2003 was used to determine the day-time den locations of black-footed tree-rats in seven fragments of remnant eucalypt

woodland and one area of uncleared 'continuous' woodland. Animals were tracked to their den sites once a day, for as many days as possible during a 3 month period (the duration of the transmitter battery). Up to 10 animals were radio-tracked at once (Table 6.2). A detailed methodology of collar attachment and radio-tracking procedures are discussed in Chapter 5. Radio-tracking to locate nesting sites was conducted on foot using a collapsible 3-element Yagi antenna (Sirtrack, New Zealand) and an Icom IC-R10 receiver. Once a den tree was located information on tree characteristics were collected.

Tree Measurements

All den trees identified during this study were marked with flagging tape and allocated a unique number using an aluminium tag marked with reflective tape. Although animal species usually select hollows based on their physical characteristics, the actual dimensions of hollows are hard to assess from the ground (Gibbons and Lindenmayer 2002; Gibbons *et al.* 2002). Instead, a range of tree measurements was collected to describe the attributes of each tree. These included: (1) tree species (based on the features of the bark, leaves, fruit and buds); (2) diameter at breast height (dbh) (placed into 4 broad categories <5, 5-20, 20-50, >50 cm); (3) number of hollows (a count of the number of hollows (greater that 5 cm diameter and visible from the ground); (4) hollow location (the location of visible hollows – trunk, main branch, secondary branch); (5) termite activity (observation of the presence of wood-eating termites); (6) trunk slope (whether the trunk of the tree was sloping or straight). Trunk slope was included as it was considered that animals may select trees with a degree of slope as they may be easier to climb than vertical trees. Animals may also select particular tree species over others as the type of bark may also assist or hinder ease of climbing.

Vegetation Assessment

To assess habitat structure and composition within sites, four 20 m x 20 m quadrats, located at each corner of the 1 ha animal trapping quadrats (Chapter 4) were sampled. (Figure 6.1) Within each 20 m x 20 m quadrat environmental variables were recorded, including: levels of disturbance (weeds, feral animals, and human rubbish), soil colour and depth, and number and height of termite mounds. The total canopy cover and cover at six different height classes (>10 m, 5-10 m, 3-5 m, 1-3 m, 0.5-1 m, 0-0.5 m) in the vegetation profile were visually estimated. For each woody stem within the 20 m x 20 m quadrats the following variables were recorded: species, dbh, height, presence and location of hollows, termites, and trunk. Trees counted using

this method were identified and placed into four broad size classes (<5 cm, 5-20 cm, 20-50 cm, >50 cm dbh).
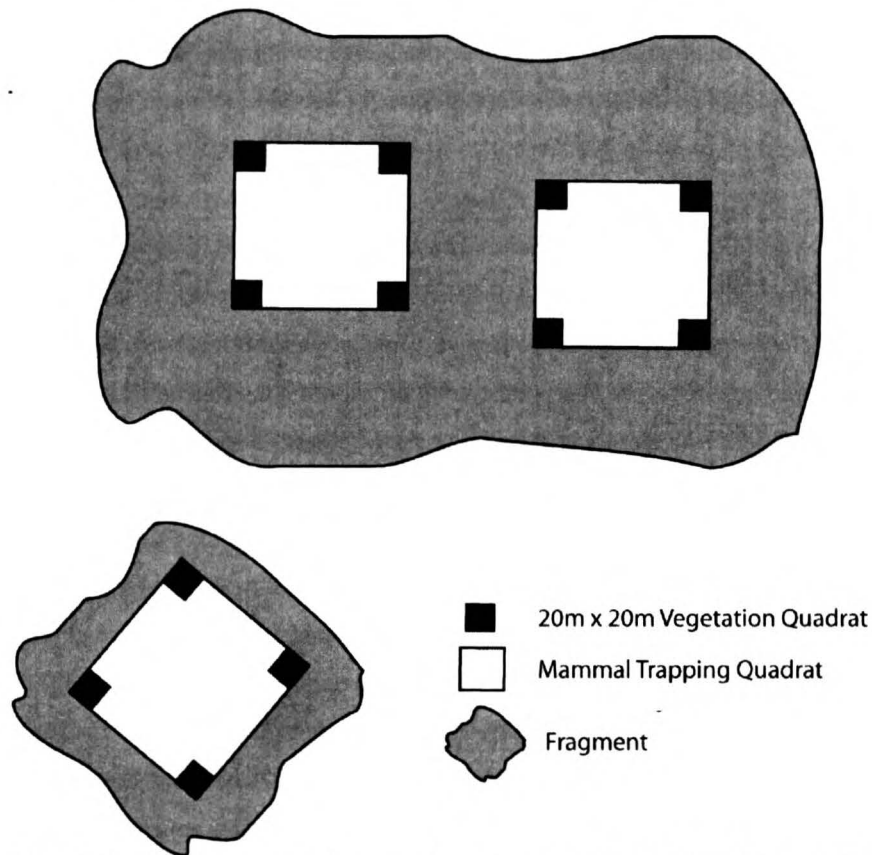
Figure 6:1: The design layout of mammal trapping quadrats and 20 x 20 m vegetation quadrats within a site.

Population Estimates

The population estimates for black-footed tree-rats and northern brushtail possums at each site (Chapter 4) were modified to provide the average abundance estimate for each one hectare mammal trapping quadrat rather than each site. Abundance estimates were calculated using the formula (n/p) where n is the number of individuals captured and p is the estimated capture probability (see Chapter 4). In chapter 4, the number of captures was pooled for all quadrats in the site to provide a population estimate for the fragment. In this chapter, the number of captures for each quadrat was used to provide a quadrat based abundance estimate.

Statistical Analysis

The limited number of sites (n = 8) used to evaluate habitat associations prevented analyses being conducted at the patch level. For this reason analyses were conducted with each trapping quadrat considered a sample. Although there is a level of pseudo-replication in this study design, generalised linear modelling with mixed effects allows for pseudo-replication with site identified as a random effect.

Patterns of vegetation composition and abundance within the 20 x 20 m vegetation quadrats were examined using ordination, in the program PRIMER (Clarke and Gorley 2001). The ordination was based on the untransformed abundances of all woody species recorded within the four 20 m x 20 m vegetation quadrats. The compositional similarity of sites was compared using the Bray-Curtis similarity index. ANOSIM was used to assess whether the pattern of similarity in plant species composition between quadrats was related to site.

Generalised linear modelling (GLM) was used to investigate a number of questions (see sections below). The variables analysed for each analysis are presented in Table 6.2. For all GLM analyses, Akaike's information criterion (AIC) was used to determine the best model. The best model was selected on the basis of low AIC score and parsimony (number of terms in the model). All models were compared and ranked by calculating the AIC difference (Δ_i), with increasing values of Δ_i the less plausible that the model is the best model. As a general rule, values of <2 are well supported, while values >10 have essentially no support and can be omitted from further consideration (Burnham and Anderson 2002). The AIC differences were used to calculate the weight of support (w_i) for each model in the candidate set (Burnham and Anderson 2002). This provides the probability for each model that it is the best model (summing to one across all models). The goodness of fit of the best model was calculated using the equation (which is analogous to r^2):

$$1- (\ln(L_M)/(\ln(L_0)))$$

where L_M is the likelihood of the best model and L_0 is the likelihood for the model with only the intercept (Quinn and Keough 2002). The estimates for the best model were also examined to investigate the strengths and directions of the relationships. All analyses were conducted using Statistica ver.6 (StatSoft 2000).

Den Tree Use

The relationship between the number of dens used and the length of time that a black-footed tree-rat was radio-tracked was investigated using linear regression. Mann-Whitney U-tests were used to examine differences in the number of dens used by male and female black-footed tree-rats and between tree-rats in fragmented and un-fragmented sites.

Table 6.2: A list of the explanatory variables used in the five Generalized Linear Models (a list of all variables initially investigated for each model is found in Appendix 6.2)

Variable	Description
Hollow availability	Measured at the scale of mammal trapping quadrat (n = 18)
Termite mounds	The mean number of termite mounds for each trapping quadrat (averaged over the 4 vegetation quadrats)
Number late fires	Number of late fires at the site (after August, 10 year history from Landsat) (Note: values are identical for all quadrats at each site)
Patch size	Area (ha) of the eucalypt woodland patch in which the quadrat is located (Note: values are identical for all quadrats at each site)
Hollow formation	Measured for trees >20cm DBH (n=219)
Termites	Presence/absence of piping termites in the tree
Trunk	Slope of the tree trunk (straight or sloping)
DBH	The diameter of the tree at breast height (4 categories; <5, 5-20, 20-50, >50 cm)
Species	Tree species
Number of fires	Number of fires at the site (10 year history from Landsat) (Note: values are identical for all quadrats at each site)
Number late fires	As above
Den Characteristics	Measured for all trees (den and non-den) of species recorded as having den trees (n=860)
Termites	As above
Trunk	As above
DBH	As above
Species	As above
Habitat Preferences	Measured at the scale of mammal trapping quadrat *(n = 18)*
Number trees >20cm dbh	A count of the number of trees >20cm dbh within each 20x20 m quadrat, averaged for each trapping quadrat
Structure_SW	Shannon-Wiener equitability measure of structural diversity for each trapping quadrat (based on proportions of tree girths in each of 4 size classes
Fruit_sp_div	The number of different fruiting species recorded for each trapping quadrat
Environmental impacts on habitat	Measured at the site scale (n=9).
Patch size	Area (ha) of the eucalypt woodland patch in which the quadrat is located
Number late fires	Number of late fires at the site (after August, 10 year history from Landsat)

Hollow Availability

Hollow availability was calculated as the number of trees within the 20 m x 20 m vegetation quadrats with visible hollows from the ground averaged over the four quadrats for each 1 hectare mammal trapping quadrat, providing a density of hollows. This analysis investigates if there are environmental and or historical factors that may affect the abundance of tree hollows in an area. Generalised linear modelling with mixed effects was used to investigate the relationship of environmental variables on the number of hollows within quadrats. A mixed model was used to allow for any site based effect to be considered, avoiding the problem of pseudo-replication. A correlation matrix identified explanatory variables that were collinear a priori. Correlated variable were removed from further analysis.

Hollow Formation

Differences in the number of hollows among trees of differing size (dbh) and species were investigated with Kruskal-Wallis non-parametric ANOVA tests, using all trees recorded in all quadrats as a sample (n=219). Generalised linear modelling was used to investigate the effects of various tree characteristics on hollow formation in individual trees. This was a binomial model of presence or absence of a hollow, with logit-link function.

Den Tree Characteristics

A simple correlation was used to examine the relationship between hollow availability and the abundance of black-footed tree-rats and northern brushtail possums for each trapping quadrat (n = 18). The proportion of dens used by black-footed tree-rats that were not hollow-bearing trees was also examined in relation to hollow availability at each site (n = 9) using linear regression.

Chi-squared analyses were conducted to compare how the use of hollows by black-footed tree-rats compares with actual hollow availability. This analysis was broken down into individual components with four tree characteristics (dbh, species, termites and trunk slope) assessed separately to investigate each in more detail. For each of the four characteristics there are two questions to be investigated. For example, for dbh the questions are; (1) is the size-class distribution of den trees used by black-footed tree-rats different to the trees available in the environment? and, (2) if the size class distribution of den trees used by black-footed-tree-rats different to the size class distribution of hollow-bearing trees in the environment?

GLM was then used to identify which of these tree characteristics were the best determinants of a tree being selected as a den tree. This was a binomial model of know den trees or non-den tree, with logit-link function.

Habitat Preferences

A correlation matrix was used to investigate the relationship between black-footed tree-rat abundance and the abundance of each individual fruiting plant species detected at the study sites. This analysis provides information on the importance of particular fruiting species (Appendix 6.2).

A GLM with mixed effects was used to investigate the habitat variables selected by black-footed tree-rats. A large set of habitat variables were recorded for the assessment of habitat associations for black-footed tree-rats. After inspection of the correlation matrix of those variables, many were excluded because of high co-linearity (see Appendix 6.1 for a full description of variables and Table 6.6 for correlations). The only variables remaining and therefore included in further analysis were fruit species richness, structural diversity (Structure_SW) and the number of trees greater than 20 cm dbh.

Environmental impacts on habitat

The influence of fragment area and fire history on the species richness of fruiting species at each site was investigated using GLM, with Poisson error distribution and log link function. A correlation matrix identified explanatory variables that were colinear. The number of late fires was significantly correlated with the overall number of fires and was removed from further analysis. This allowed the investigation of fire frequency, but prevented the investigation of the timing of fires on vegetation.

Results

There was a distinct difference in vegetation composition between sites (Figure 6.2). Site was highly significantly related to vegetation composition at the quadrat level (ANOSIM R = 0.63, P = 0.001).
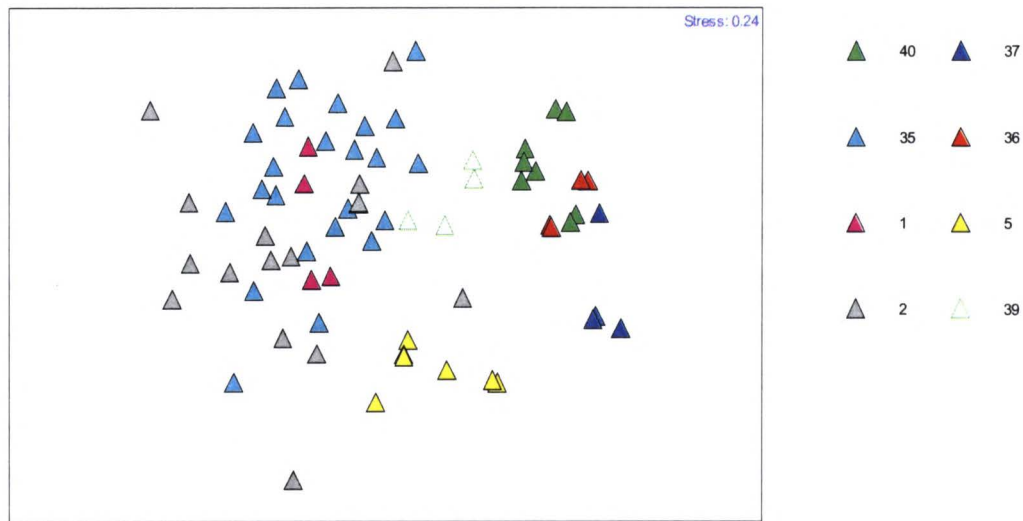
Figure 6:2: Ordination of all vegetation quadrats by their species composition in relation to site.

Den Tree Use

Thirty-seven black-footed tree-rats (22 males and 15 females) were radio-tracked during this study. Seven individuals disappeared soon after being collared and thus were removed from further analysis. A total of 97 trees with hollows were used by the remaining 30 individuals. The total number of dens used by each individual is shown in Table 6.3. There were eight records of black-footed tree-rats using places other than hollow-bearing trees, including a house and shed roof, a caravan, an introduced Carpentaria palm and *Pandanus spiralis*. The number of different dens used by an individual ranged from 1-13 (Table 6.3). The mean number of different den trees used per animal was 3.4 for males and 2.9 for females, however this difference between sexes was not significant (U = 164, p >0.1). Animals at the un-fragmented site used slightly more den trees than animals at fragmented sites (3.8 and 2.2 respectively), however this was also not significant (U = 94.5, p > 0.1).

Table 6.3: The number of den-trees used by individual black-footed tree-rats in Litchfield Shire. * indicates animals that were not included in subsequent analysis.

Site #	Animal	Sex	No. den trees	No. other dens	No. dens	No. days tracked
1	18	F	2	3	5	17
1	34	M	0	0	0	1*
1	52	F	1	1	2	8
1	58	F	0	0	0	1*
1	60	M	0	0	0	1*
1	587	M	0	1	1	22
1	1065	F	0	0	0	1*
1	4065	F	0	2	2	17
1	1b	F	0	0	5	18
2	24	M	2	0	2	17
2	74	M	4	0	4	9
2	76	M	3	0	3	11
2	02b	M	1	0	1	9
5	22	F	1	0	1	2
5	12b	M	11	0	11	43
35	4	M	13	0	13	51
35	48	F	1	0	1	3
35	50	M	3	0	3	24
35	368	M	0	0	0	1*
35	667	M	1	0	1	3
35	12a	M	5	0	5	18
35	14a	M	6	0	6 -	22
35	14b	M	2	0	2	24
35	28b	F	5	0	5	23
35	2a	M	2	0	2	3
36	4765	F	1	0	1	22
37	36	M	0	0	0	1*
37	02a	F	2	1	3	38
39	289	M	2	0	2	4
39	44a	M	3	0	3	6
39	46b	F	0	0	0	1*
40	6	F	6	0	6	25
40	9	M	1	0	1	13
40	44	M	1	0	1	2
40	718	F	3	0	3	19
40	08a	F	1	0	1	2
40	08b	M	1	0	1	13
Total			84	8	97	495

The number of trees used by each animal increased with the length of time over which the individual was tracked ($r^2 = 0.58$, p <0.000) (Figure 6.3).
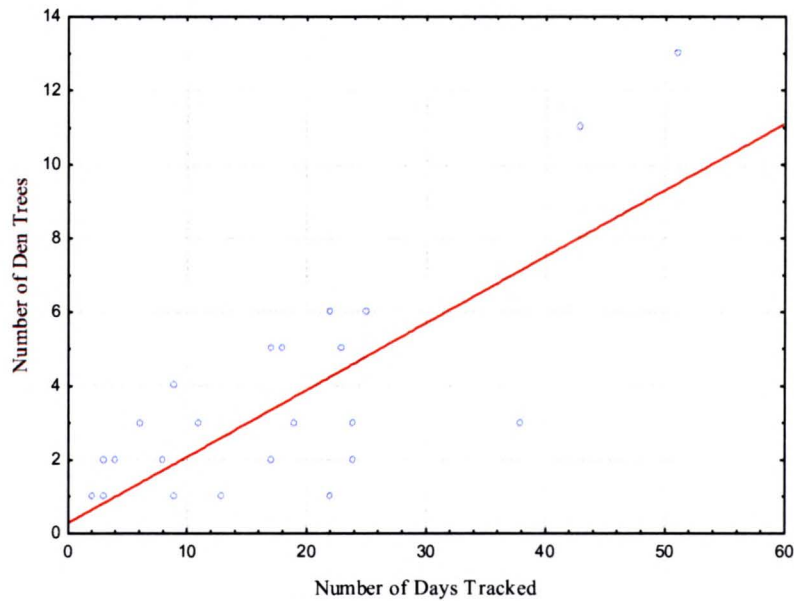
Figure 6:3: Linear regression of the number of different den trees used by each individual in relation to the length of time it was radio-tracked.

Hollow Availability

The best model of hollow availability at a site was 'termite mounds + the number of late fires' (Table 6.4). This model has an AIC_c weight of 28.3% and explained 17.3% of the variation in the data (Table 6.4)

Table 6.4: The results of the 'Best Model' for the Generalised linear models conducted. Definition of variables can be found in Table 6.2. n.s. = not significant.

Analysis	Independent Variable	Variable 1	Variable 2	Best Model Variable 3	% deviance	AICc weight
Hollow availability	Hollow availability	Termite mounds	Number of late fires		17.3	28.3
Hollow formation	presence/absence of a hollow	DBH	Termites	Trunk	4.0	48.7
Den tree characteristics	den tree/ non-den tree	DBH			17.7	
Habitat preferences	tree-rat abundance	Fruit_sp div	Number trees >20cm dbh		15.5	33.0
Environmental impacts on habitat	Fruiting Species Richness	Number of fires			29.6	49

Hollow Formation

There was a highly significant relationship between the number of hollows formed by a tree and tree dbh (KW = 1539, p < 0.001). There were significantly more hollows in trees with a large dbh (Figure 6.4). Based on these results, all trees less than 20 cm dbh were removed from further analysis, and hence the Kruskal-Wallis ANOVA was used to investigate whether hollow formation in trees > 20 cm dbh differed among species. Tree species was significantly related to hollow formation (KW = 21.53, p = 0.01). Three species did not form hollows (Figure 6.5). These species were removed and the data were re-analysed. With the removal of these species there was no significant difference in the number of hollows per tree among the remaining species (KW = 11.45, p = 0.07). The best model 'DBH + termites + trunk' only captured 4% of the deviance (Table 6.4).
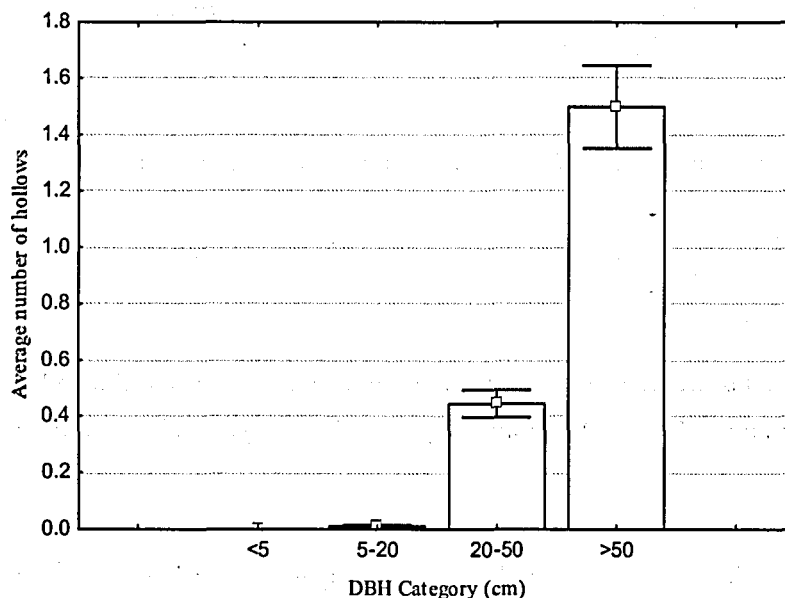
Figure 6:4: The average number of hollows found in trees for each dbh category, showing standard errors.
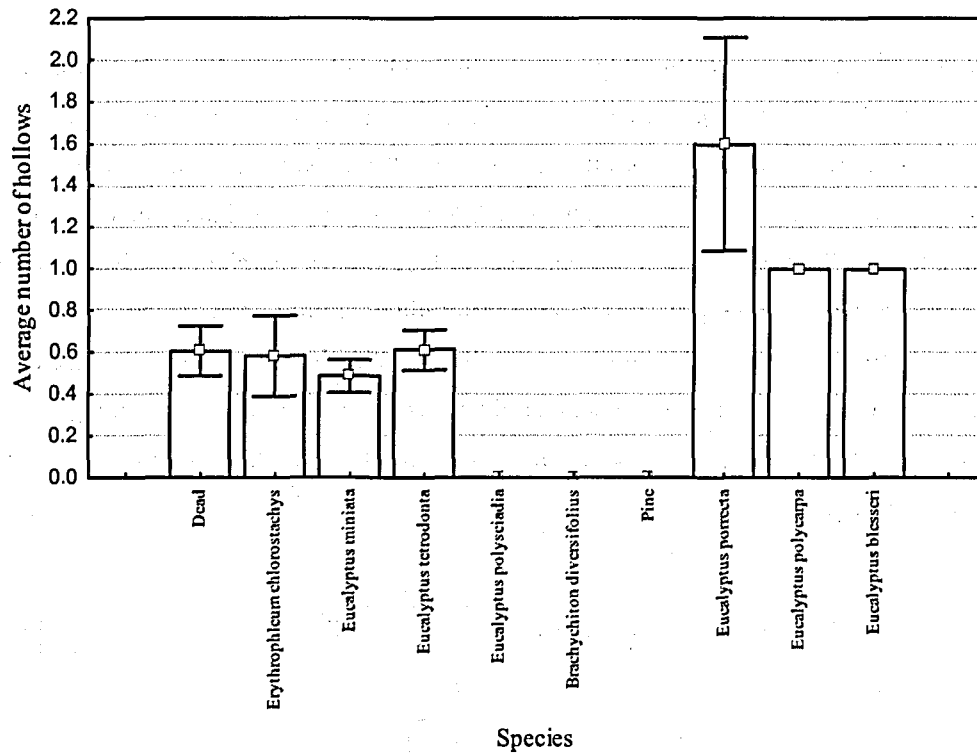
Figure 6:5: The average number of hollows found for each tree species for stems >20cm DBH, showing standard error bars.

Den Selection

For black-footed tree-rats and possums, abundance was not significantly correlated with hollow availability (black-footed tree-rats C = -0.30; brushtail possums C = -0.23) (Figures 6.6 and 6.7).

The proportion of dens other than tree hollows used at a site was significantly inversely related to hollow availability (r^2 = 0.7, p = 0.009) (Figure 6.8).
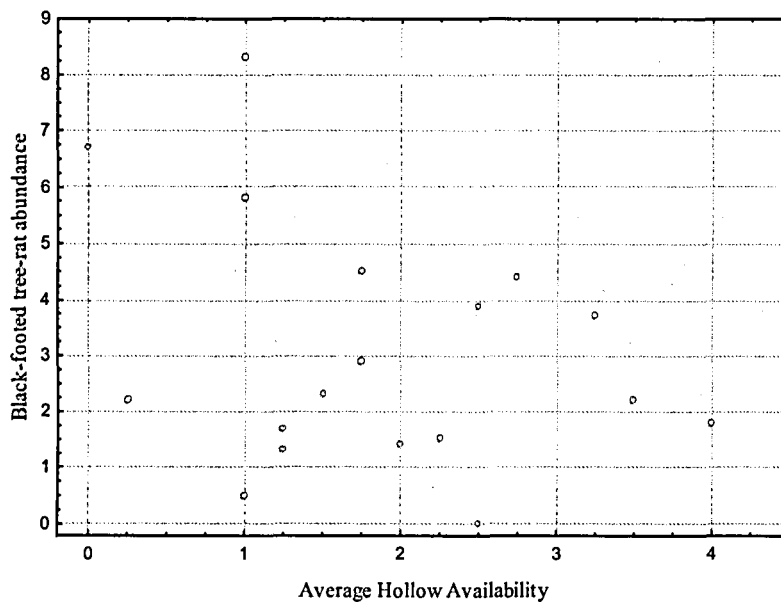
Figure 6:6: A scatterplot of the relationship between black-footed tree-rat abundance and the average hollow availability per trapping quadrat.
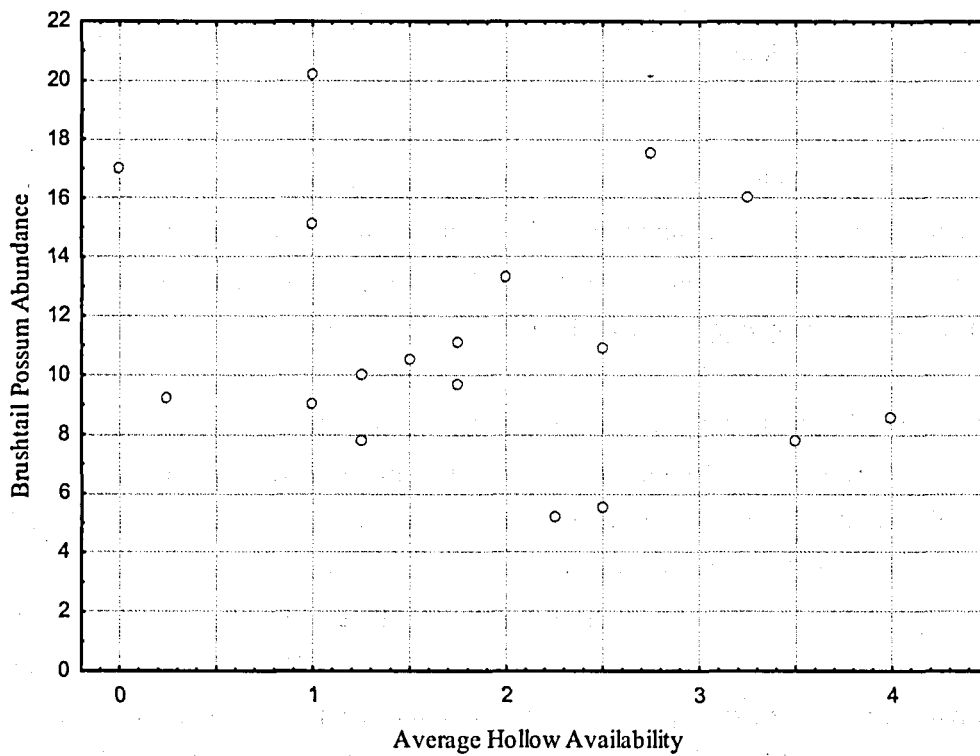
Figure 6:7: A scatterplot of the relationship between brushtail possum abundance and the average hollow availability per trapping quadrat.
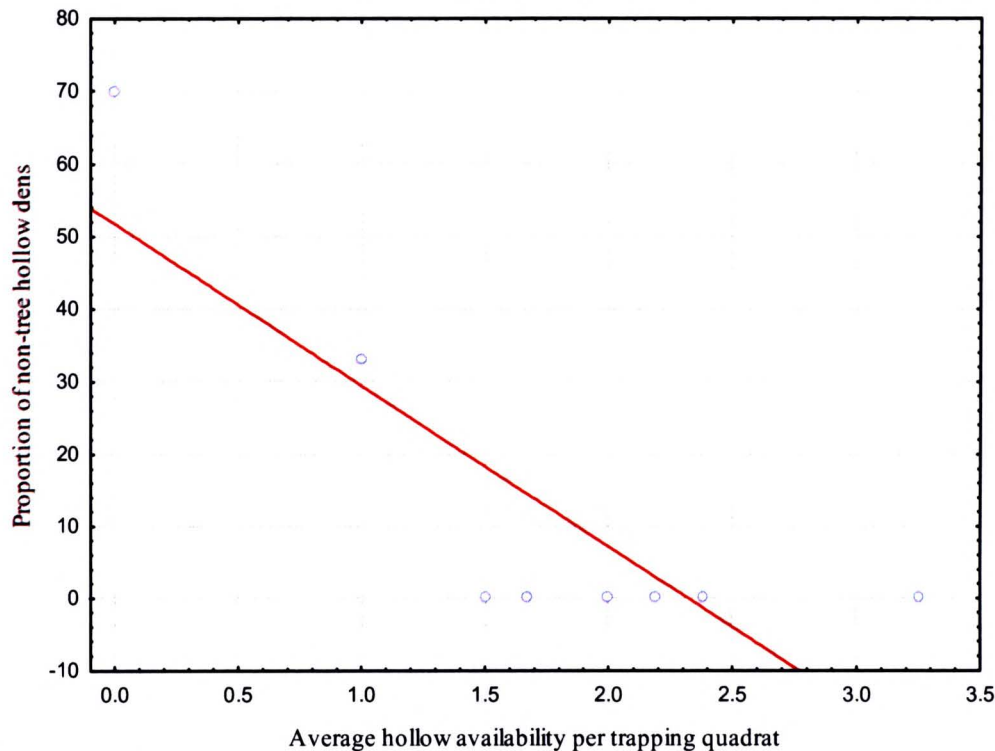
Figure 6:8: A linear regression of the average hollow availability for each site in relation to the proportion of dens that were not tree hollows.

Of the dens that were in hollow-bearing trees, the average tree diameter at breast height (dbh) was 42.3 cm (range 18 – 64.5). Of all the den trees observed, 96% had at least one visible hollow, with 47% having more than one hollow visible. Thirty percent of den trees had piping termites present at the base of the tree and 31% had a sloping trunk.

The distribution of hollow-bearing trees across size classes was significantly different to the distribution of all trees, with hollow-bearing trees having a greater representation among the larger size classes (χ^2 = 475.5, p = <0.001). This trend was repeated for tree-rat dens (χ^2 = 502.7, p = <0.001) (Figure 6.9a). For all seven tree species analysed, the distribution of hollow-bearing trees was not significantly different from the distribution of all trees of each species (χ^2 = 5.5, p = 0.48), however the proportion of tree–rat dens was significantly different from the proportion of trees available for each species (χ^2 = 13.5, p <0.05), with particular over-representation in den trees of *Eucalyptus tetrodonta* followed by *Corymbia porrecta* (Figure 6.9b). The presence of piping termites was significantly higher in trees with hollows and trees with tree-rat dens than the proportion available (χ^2 = 236.3, p <0.001) and (χ^2 = 263.2, p <0.001). There was no significant difference in termite presence between the number of trees with hollows and tree-rat dens (χ^2 = 3.59, 0.58) (Figure 6.9c). This trend was repeated when investigating the trunk slope, with hollow-bearing trees and tree-rat dens having a significantly higher proportion of sloping

trunks than available, but no significant difference between trees with hollows and trees with tree-rat dens ($\chi^2 = 201.8$, p <0.001), ($\chi^2 = 97.9$, p <0.001) and ($\chi^2 = 1.1$, p = 0.30) (Figure 6.9d).

The best model to determine the likelihood of a tree being selected as a den tree was diameter (dbh) (Table 6.4). This model was selected as the 'best model' based on parsimony, with six models having an AIC difference (Δ_i) of <2. The best model explained 17.7% of the deviance (p < 0.001).
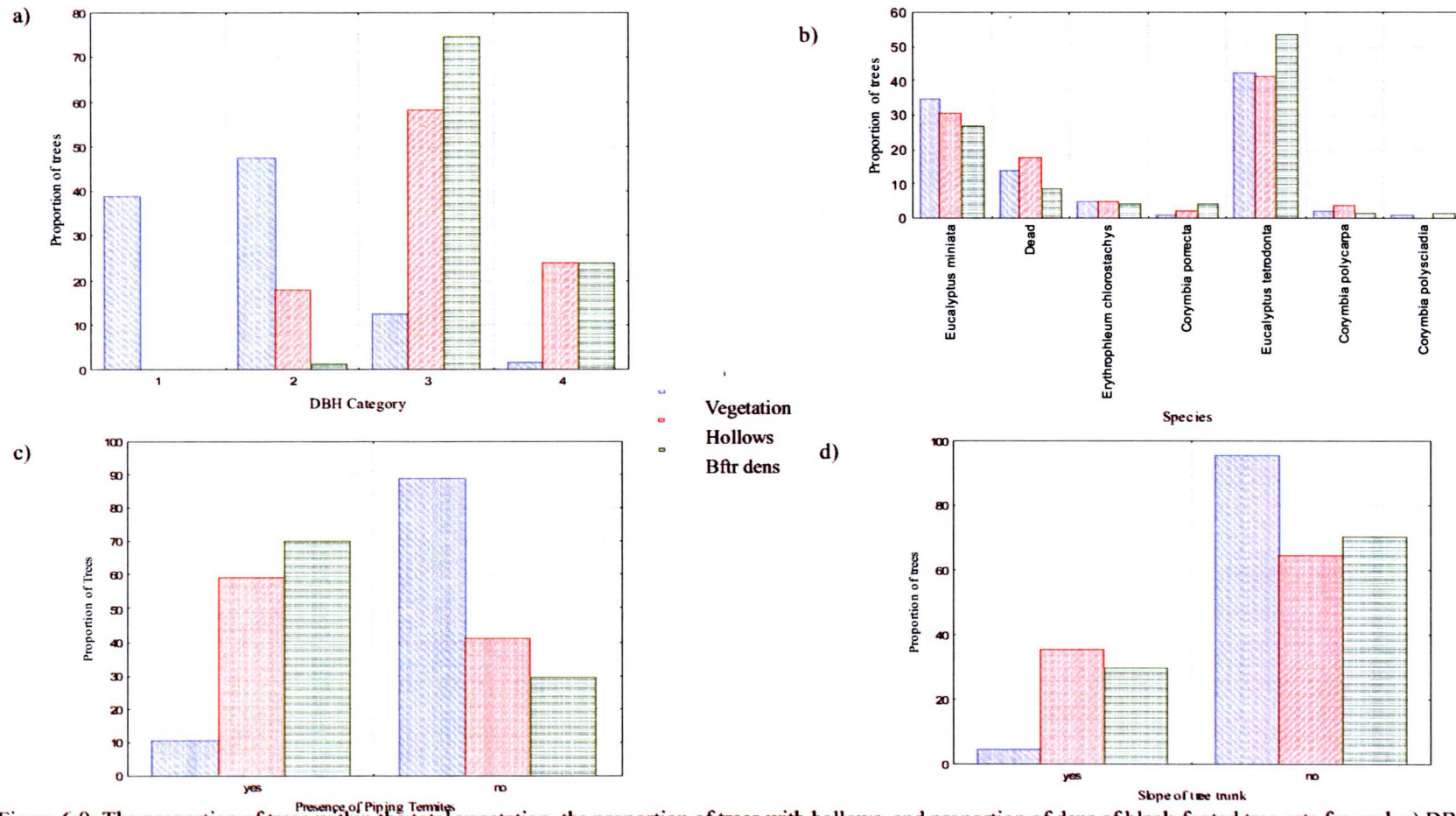
Figure 6:9: The proportion of trees within the total vegetation, the proportion of trees with hollows, and proportion of dens of black-footed tree-rats for each a) DBH category, b) species, c) presence of piping termites and d) straight or sloping tree trunk.

Habitat Preferences

The abundance of black-footed tree-rats was strongly correlated with the abundance of three species of fruiting tree (Appendix 6.2).

The best model to explain black-footed tree-rat abundance was 'fruit species diversity + the number of trees greater than 20cm dbh'. This model has an AIC_c weight of 33% and explained 15.1% of the deviance (Table 6.4). The random effect of 'site' explained a further 57% of the residual deviance. This was a positive relationship with black-footed tree-rat abundance increasing with increasing richness of fruiting species.

The number of fires at a site significantly reduced the diversity of fruiting species, explaining 29.6% of the variation (Table 6.4).

Table 6.5: Correlation matrix of dependant and independent variables investigating habitat preferences of black-footed tree-rats. Values above 0.47 are significantly correlated.

	>20cm dbh	Struct SW	1-5m cover	fruit_sp abund	fruit_sp richness	litter	grass cover	tot_sp abund	tot_sp richness	B. tomentosa	E. latifolius	P. pubescens
bftr	-0.23	-0.08	0.47	0.27	0.61	0.39	-0.34	0.38	0.36	0.65	0.65	0.62
>20cm dbh	1.00	0.33	-0.41	-0.06	-0.28	-0.43	0.32	-0.14	-0.10	-0.24	-0.37	-0.28
struct_SW		1.00	-0.27	-0.09	-0.33	-0.23	0.33	-0.13	-0.27	-0.18	-0.41	-0.47
1-5m cover			1.00	0.54	0.66	0.63	-0.60	0.58	0.76	0.52	0.68	0.55
fruit_sp_abund				1.00	0.76	0.26	-0.39	0.89	0.64	0.40	0.55	0.30
fruit_sp_div					1.00	0.45	-0.42	0.84	0.61	0.57	0.70	0.52
litter						1.00	-0.88	0.40	0.55	0.46	0.46	0.40
grass cover							1.00	-0.37	-0.57	-0.41	-0.52	-0.52
tot_sp_abund								1.00	0.72	0.41	0.49	0.21
tot_sp_div									1.00	0.61	0.65	0.48
B. tomentosa										1.00	0.91	0.81
E. latifolius											1.00	0.92
P. pubescens												1.00

Discussion

Den Tree Use

This is the first study to investigate the den use and preferences of black-footed tree-rats in detail. However, other short term studies have demonstrated that black-footed tree-rats use several den sites. A study by Griffiths *et al.* (2002) observed one individual occupying five den trees, while another study conducted in the Kimberley radio-tracked a male black-footed tree-rat to four different den sites (Friend and Calaby 1995). Those results are within the range of den trees used by individuals in this study (Table 6.3). Although most individuals used multiple dens, there were 5 individuals that were tracked for more than 10 days that only ever used one den tree.

The evidence of multiple den use by black-footed tree-rats is similar to the results obtained by a number of other investigations of arboreal mammals, demonstrating similar behaviours. These include studies of the common brushtail possum (Kerle 1984; Green and Coleman 1987); the mountain brushtail possum (Lindenmayer *et al.* 1996); the sugar glider (Suckling and Macfarlane 1983; Suckling 1984) and the feathertail glider (Ward 1990).

A number of reasons have been proposed to explain why animals use multiple dens. This behaviour may be a form of predator avoidance, with regular movement between den sites reducing the chance that predators will learn the pattern of emergence (Lindenmayer *et al.* 1996). This could be an important factor for black-footed tree-rats as they often descend to the ground to feed after emerging (pers. obs.). Movements between den trees may also reflect changes in the foraging area used by an animal. As black-footed tree-rats are predominately frugivores they may have to move relatively large distances as many of these plants are patchily distributed (Friend and Calaby 1995; Rankmore 2003). Although there are other possible reasons for this behaviour these are the main factors that may have an important influence on this behaviour in black-footed tree-rats.

Although the sample size was so limited that I could not test for significance, animals within the un-fragmented site appeared to use more den trees than those in fragments. This would support the findings from Chapter 5, that animals in the un-fragmented area had larger home ranges. With a larger home range it would be expected that animals would require more den sites to provide shelter when foraging in different areas of the home range.

A general trend in the data showed that, if the length of radio-tracking had been extended, the number of trees used would have increased (Figure 6.2). Other studies have also found an

increase in the number of den sites with increased length of radio-tracking (Green and Coleman 1987; Lindenmayer *et al.* 1996).

Den Availability and Hollow Formation

Hollow availability differed between sites, with a higher number of termite mounds present at a site increasing hollow availability. A causal relationship is supported by the presence of 'termites' as a variable in the best model predicting hollow formation (Table 6.2). The findings of this study suggest that hollows are more likely to form in large diameter trees with piping termites and a sloping trunk. A parallel study by Pitman (2003) investigating hollow formation and availability at a subset of sites within the current study, also identified tree diameter along with canopy width and the number of dead branches as tree characteristics influencing hollow formation. A number of studies from southern Australia have investigated the relationship between tree characteristics and hollow occurrence. These studies have linked hollow formation to canopy condition (Lindenmayer *et al.* 1993b), tree age (Whitford 2002), presence of fire scars (Inions *et al.* 1989) and tree diameter (Lindenmayer *et al.* 1993b; Gibbons *et al.* 2000). Ultimately, tree diameter increases with age and as tree diameter increases so does the likelihood of hollow formation. Other characteristics are more likely to be influenced by historical environmental conditions. The width of the canopy, the number of dead branches and trunk slope may all be affected by exposure to wind and storm activity.

Fire plays a major role in hollow formation within tropical savanna systems, with a higher number of late season fires having a negative impact on hollow availability. In one respect, fire has been found to reduce the age at which hollows form (Inions *et al.* 1989), but it also reduces the survival of large diameter trees (Williams *et al.* 1999a).

Den Selection

Hollow availability did not influence the abundance of black-footed tree-rats or possums at a site, but it did influence den selection by tree-rats. At sites with a low availability of hollows, tree-rats used a higher proportion of non-hollow dens. This behaviour was also observed by Pittman (2003) for tree-rats and possums, with black-footed tree-rats also altering their preferred hollow dimensions at sites where hollow availability was low and possum densities were high, possibly because the larger possums are likely to out-compete tree-rats (Pittman 2003). Studies have revealed that larger species usually succeed when competition occurs for a hollow suitable for both species (Menkhorst 1984).

Black-footed tree-rats showed a clear preference for hollows in large diameter trees. It is likely that only trees with a large diameter will develop hollows large enough to be used by tree-rats. Although this study found no preferences by tree-rats for particular tree species, tree-rats did select *E. tetrodonta* and *C. porrecta* as den trees more than was proportionately available (Figure 6.10b). The other dominant eucalypt species within tropical woodland, *E. miniata*, was selected less than would be expected. These results support the findings of Griffiths *et al.* (2002), who also found tree-rats preferred *E. tetrodonta* over *E. miniata*. This may relate to the ease of climbing, as *E. tetrodonta* and *C. porrecta* have thick fibrous bark, while *E. miniata* has smooth bark, other than at the base.

Habitat Preferences

The abundance of black-footed tree-rats was influenced by the richness of fruiting species at the quadrat, with a greater abundance of tree-rats able to persist at quadrats with more fruiting species. While little is known about the diet of black-footed tree-rats, they are considered to be mostly frugivorous (Friend 1991; Friend and Calaby 1995; Rankmore 2003). A higher diversity of fruiting species provides a larger variety of food resources that will fruit during different periods of the year, providing a more sustained and permanent food supply. Black-footed tree-rats are considered to be patchily distributed throughout the tropical savannas (Friend and Calaby 1995). These findings suggest that black-footed tree-rats may be limited by the availability and diversity of food resources more than by hollow availability. The abundance of black-footed tree-rats was also influenced by the number of trees >20 cm.

The number of fires that occurred at a site over the past 10 years influenced the diversity of the fruiting species present at the site. Sites that were long unburnt had a greater fruiting species diversity and hence were able to support a greater abundance of black-footed tree-rats. These findings are consistent with the findings of Friend (1987). The habitat preference correlation matrix (Table 6.6) also highlighted the influence of fire on habitat structure and composition. Sites with an extensive mid-storey (1-5 m) cover also had reduced grass cover and increased litter cover. This set of inter-related responses to fire are consistent with previous studies examining vegetation response to fire (Williams *et al.* 2003; Woinarski *et al.* 2004).

Fragment size was not a significant predictor of the diversity of fruit species. This may be because of the uniform structure and composition of Australia's tropical savannas (Chapter 2).Within this relatively homogeneous environment finer-level variability can be influenced by a mosaic of fire histories (Price *et al.* 2005b). However, fire regimes are currently more frequent, intense and homogeneous than previously experienced in Australia's tropical savannas (Lacey *et al.* 1982; Haynes 1985; Bowman and Panton 1993; Braithwaite 1996; Russell-Smith

et al. 2000). Ultimately, fire has the most pervasive influence on the condition of wildlife habitats in northern Australia (Whitehead *et al.* 2005).

Conclusions

Across the set of sites considered here and potentially more generally across the tropical woodlands, black-footed tree-rats are influenced by the diversity of food resources and the availability of hollows. Ultimately fire regimes have a direct effect on the habitat quality by influencing vegetation structure and composition. Inevitably habitat fragmentation by definition provides barriers to the extensive homogeneous fires occurring in the landscape. Fragmentation of native vegetation may provide a range of fire frequencies increasing habitat heterogeneity. Within human-dominated landscapes some areas will be burnt under control burns annually to prevent intense late fires and protect human property, while other areas are actively maintained unburnt. Hence, a low level of fragmentation may assist species that prefer long unburnt habitats, such as the black-footed tree-rat, providing habitat rich in resources.

Appendix 6.1: A full list of the explanatory variables used in the five Generalized Linear Models

Variable	Description
Hollow availability	Measured at the scale of mammal trapping quadrat (n = 18)
Termite mounds	The mean number of termite mounds for each trapping quadrat (averaged over the 4 vegetation quadrats)
Number of fires	Number of fires at the site (10 year history from Landsat) (Note: values are identical for all quadrats at each site)
Number late fires	Number of late fires at the site (after August, 10 year history from Landsat) (Note: values are identical for all quadrats at each site)
Weeds	The mean weed count for each trapping quadrat (averaged over the 4 vegetation quadrats)
Disturbance	The sum of all disturbance categories (pig, horse/cattle, human)average over the 4 vegetation quadrats.
Patch size	Area (ha) of the eucalypt woodland patch in which the quadrat is located (Note: values are identical for all quadrats at each site)
Hollow formation	Measured for trees >20cm DBH (n=219)
Termites	Presence/absence of piping termites in the tree
Trunk	Slope of the tree trunk (straight or sloping)
DBH	The diameter of the tree at breast height (4 categories; <5, 5-20, 20-50, >50 cm)
Species	Tree species
Number of fires	As above
Number late fires	As above
Den Characteristics	Measured for all trees (den and non-den) of species recorded as having den trees (n=860)
Termites	As above
Trunk	As above
DBH	As above
Species	As above
Habitat Preferences	Measured at the scale of mammal trapping quadrat (n = 18)
Number trees >20cm dbh	A count of the number of trees >20cm dbh within each 20x20 m quadrat, averaged for each trapping quadrat
Structure_SW	Shannon-Wiener equitability measure of structural diversity for each trapping quadrat (based on proportions of tree girths in each of 4 size classes
1-5 Cover	The percentage cover of the vegetation profile from 1-5 m.
Fruit_sp_abund	The number of stems of fruiting species for each trapping quadrat
Fruit_sp_div	The number of different fruiting species recorded for each trapping quadrat
Litter	The percentage cover of litter for each 20x20 m quadrat averaged for each trapping quadrat.
Grass cover	The percentage cover of perennial and annual grass for each 20x20m quadrat averaged for each trapping quadrat and standardised as a score out of 10.
Tot_sp_abund	The number of woody stems within the four 20x20 m quadrats for each trapping quadrat
Tot_sp_div	A count of the number of different woody species for each trapping quadrat
Bridelia tomentose	A count of the abundance of this species in each trapping quadrat
Exocarpos latifolius	As above

Petalostigma pubesens	As above
Environmental impacts on habitat	Measured at the site scale (n=9).
Patch size	Area (ha) of the eucalypt woodland patch in which the quadrat is located
Number of fires	Number of fires at the site (10 year history from Landsat)
Number late fires	Number of late fires at the site (after August, 10 year history from Landsat)

Appendix 6.2: Correlation matrix of the abundance of black-footed tree-rats and the abundance of individual fruiting species.

	A. ghaesembilla	B. tomentosa	B. obovata	C. philippinensis	C. armstrongii	E. latifolius	F. opposita	G. megasperma	L. humilis	P. spiralis	P. nonda	P. falcata	P. pubescens	P. quadriloculare
BFTR	0.23	0.65	0.16	-0.07	0.14	0.65	0.45	0.44	-0.24	-0.22	-0.17	0.12	0.62	-0.16
Antidesma ghaesembilla	1.00	0.34	0.69	0.16	-0.22	0.44	-0.09	0.57	-0.26	-0.10	0.06	0.73	0.09	-0.12
Bridelia tomentosa		1.00	0.25	0.06	0.17	0.91	-0.04	0.77	-0.01	-0.20	-0.03	0.24	0.81	-0.13
Buchanania obovata			1.00	0.04	-0.12	0.30	-0.23	0.37	-0.37	-0.18	0.34	0.62	0.07	-0.26
Celtis philippinensis				1.00	-0.08	0.33	-0.08	-0.08	-0.23	-0.18	0.42	-0.10	0.35	-0.08
Cycas armstrongii					1.00	0.12	-0.11	0.02	0.13	-0.31	-0.20	-0.38	0.20	0.07
Exocarpos latifolius						1.00	-0.05	0.57	-0.14	-0.22	-0.04	0.25	0.92	-0.14
Ficus opposita							1.00	-0.13	-0.26	0.27	-0.09	-0.20	-0.03	-0.09
Gardenia megasperma								1.00	0.04	-0.23	0.15	0.50	0.34	0.09
Livistona humilis									1.00	0.18	-0.26	-0.13	-0.09	0.18
Pandanus spiralis										1.00	-0.30	0.06	-0.23	0.17
Parinari nonda											1.00	0.16	-0.05	-0.17
Persoonia falcata												1.00	0.03	-0.16
Petalostigma pubescens													1.00	-0.11
Petalostigma quadriloculare														1.00
Planchonia careya														
Syzygium bleeseri														
Syzygium suborbiculare														
Terminalia ferdinandiana														
Vitex glabrata														
Xanthostemsum paradoxus														
Species Richness														

	P. quadriloculare	P. careya	S. bleeseri	S. suborbiculare	T. ferdinandiana	V. glabrata	X. paradoxus	Species Richness
BFTR	-0.16	0.19	-0.05	-0.27	0.05	-0.10	0.43	0.37
Antidesma ghaesembilla	-0.12	-0.37	-0.25	-0.17	-0.20	-0.10	0.40	0.53
Bridelia tomentosa	-0.13	-0.12	0.05	-0.19	-0.05	-0.11	0.45	0.70
Buchanania obovata	-0.26	-0.07	0.28	0.16	0.09	0.06	0.30	0.58
Celtis philippinensis	-0.08	-0.25	-0.03	-0.12	-0.01	-0.07	0.59	0.32
Cycas Armstrongii	0.07	0.48	-0.15	0.26	0.79	0.85	-0.04	0.13
Exocarpos latifolius	-0.14	-0.16	0.05	-0.20	-0.03	-0.11	0.75	0.75
Ficus opposita	-0.09	0.24	-0.06	0.01	0.10	-0.06	-0.10	-0.26
Gardenia megasperma	0.09	-0.22	-0.25	-0.28	-0.17	-0.16	0.15	0.64
Livistona humilis	0.18	-0.13	0.03	0.13	-0.14	0.06	-0.30	-0.03
Pandanus spiralis	0.17	-0.27	0.18	0.27	-0.24	-0.15	-0.27	-0.08
Parinari nonda	-0.17	0.13	0.20	0.30	0.10	-0.14	0.13	0.30
Persoonia falcata	-0.16	-0.52	-0.28	-0.19	-0.45	-0.18	0.37	0.44
Petalostigma pubescens	-0.11	-0.05	0.13	-0.16	0.03	-0.09	0.77	0.61
Petalostigma quadriloculare	1.00	0.11	-0.12	0.01	0.09	-0.07	-0.14	0.06
Planchonia careya		1.00	0.27	0.51	0.78	0.32	-0.24	-0.07
Syzygium bleeseri			1.00	0.57	0.17	-0.17	-0.06	0.17
Syzygium suborbiculare				1.00	0.59	0.35	-0.20	0.18
Terminalia Ferdinandiana					1.00	0.77	-0.10	0.14
Vitex glabrata						1.00	-0.11	0.03
Xanthostemsum paradoxus							1.00	0.58
Species Richness								1.00

Black-footed tree-rat Mesembriomys gouldii

CHAPTER 7

General Discussion

Introduction

The overarching aim of this thesis was to explore the effects of habitat fragmentation on the vertebrate fauna of the open forests of Australia's tropical savanna in the Northern Territory. I have investigated and presented data on several aspects of the fragmentation process and their effects on vertebrate fauna, and in particular medium-sized mammals. As this is the first study in this region to investigate the processes of habitat fragmentation on biodiversity, I had to firstly identify which species were affected by habitat fragmentation. I investigated the effects of various components of landscape structure and vegetation on vertebrate abundance. Having established that several species of medium-sized mammals were affected, I considered the influence of habitat fragmentation on the population dynamics of these species. The objective of this approach was to gain information to support the development of management strategies to conserve biodiversity values in agricultural landscapes. During this study I have sought to address the following question: What are the landscape requirements needed to maintain important biodiversity values in land primarily under agricultural management?

In this final chapter, I provide an overview of the major findings of this research and discuss the implications for the conservation of vertebrate fauna of the tropical savannas of northern Australia.

Impacts of Habitat Fragmentation on Vertebrate Fauna

Abundance and Species Richness: Overview of Results

When compared to southern Australia, the tropical savannas of the north are relatively intact and in good ecological condition Woinarski and Braithwaite 1990. The natural vegetation remains extensive with limited modification, and has not suffered the loss of species that has plagued most of the rest of the continent since European settlement (Woinarski and Braithwaite 1990; Braithwaite 1991; Woinarski 1992). Factors including low levels of human habitation, isolation and poor soils have limited agricultural development. However, land use pressures are increasing and land managers are confronted with an increasing need to understand the ecological processes of savanna ecosystems, to allow sustainable land management (Winter and Williams 1996).

In the first component of the study, the abundance of all vertebrate species was measured in a range of fragments of varying size and isolation, including continuous forest and completely modified sites. Faunal species richness was highest in continuous woodland and lowest in mango orchards (Chapter 3). The vertebrate fauna fell into one of three groups in relation to their response to fragmentation. The first group of species actively used the new matrix. The second group do not use the matrix, but appear to remain at their previous levels of abundance in woodland fragments. The third group showed a negative response to fragmentation. These species have not only been lost from areas that have been cleared, but have also declined in abundance in remaining fragments.

Numerous studies investigating the effects of habitat fragmentation on species richness have focused on biogeographical features of remnants, such as remnant size, to explain the loss of species (see Chapter 1). Fewer studies have investigated the effect of other landscape or habitat characteristics of habitat fragments on species richness (Yahner 1988; Laurance 1991a; Laurance 1997; Dunstan and Fox 1996). Without considering such factors it is difficult to determine which features of the fragmentation process influence the persistence of species within habitat fragments. For this reason, the current study measured a wide range of parameters that could potentially influence the species present in fragments.
The responses of individual species varied greatly and included both biogeographical and habitat-related variables (see Chapter 3).

The edges of fragments differed from the interior, but edge effects did not penetrate far into fragments. Most species occurred within corridors, confirming that corridors may have an important role in maintaining wildlife in the landscape. Because of the limited replication of corridor widths sampled in the study, I was unable to define a corridor width that was appropriate for most species. Several management issues that affect wildlife in fragments were also identified, and their consideration is important to maintaining the value of retained fragments. The most important of these was fire frequency.

Ultimately, the design of future landscapes needs to focus on optimising three important fragmentation indices: the area of the fragment, the amount of woodland within 4 km of the fragment and connectivity. Although they are not able to support a high diversity, small fragments provide useful habitat for some species. Most species, even those that are affected by fragment size, occurred in some small fragments (Chapter 3). Thus fragments of any size are useful, but larger ones are better than smaller ones. Connectivity allowed many species to be present in fragments that would otherwise be too small to maintain them. Most species occurred

within corridors, confirming that corridors have an important role in maintaining wildlife in the landscape. However, this result only showed that some species use corridors for habitat, with no evidence of corridors facilitating movement. Despite this, incorporating habitat corridors into landscape plans will become an important component of the conservation of wildlife in Australia's tropical woodlands. Several environmental variables that consistently influenced the abundance of species were also identified, including fire. Their consideration is important to maintaining the value of retained fragments.

The second component of the study aimed to investigate the underlying basis or reason for the responses observed in medium-sized mammals and in particular, the black-footed tree-rat *Mesembriomys gouldii.*

Mammal Population Dynamics: Overview of Results

The abundance of all four medium-sized mammals was greatest in the fragmented sites (Chapter 4). As land clearing and habitat fragmentation are only a recent phenomenon in the study area, these fragments may still be subject to increased population densities and over-crowding, especially for the northern brushtail possum *T. vulpecula* and northern brown bandicoot *I. macrourus.*

Despite this higher abundance, survival rates were lower in the fragmented sites than continuous site. Although, in general these survival rates were not substantially lower than in continuous areas they do highlight the fact that habitat fragmentation is having an effect on the survival of small mammals in this study. This supports the findings of Soulé *et al.* (1988) that the time since a patch was isolated had a negative influence on the survival probabilities of species within the patch. Inevitably, studies conducted within a few years of clearing events (such as this study) may portray a more optimistic picture than is likely to occur over the long term. These results underscore a paradox: although present in high densities within fragmented sites, the future of these mammal species may be insecure.

Ultimately, the speed with which species re-adjust to fragmentation is dependent on generation time (Brook *et al.* 2003), suggesting that small rodents and dasyurid marsupials will adjust quickly. However, for specialised species like the northern quoll (a carnivore that naturally exists at low densities, with a large home range) re-adjusting to the new environment may have been overtaken by localised extinction. The northern quoll showed a strong negative response to fragmentation, with none recorded in the initial survey from fragments with less than 65% woodland within 4 km (Chapter 3) and none recorded from these same sites during the mark-

recapture study (Chapter 4). Survival rates were also substantially lower in sites with a low level of fragmentation than in the continuous area.

Another explanation may be that individuals are more transient in fragmented environments. Although recapture rates account for temporary emigration, permanent emigration cannot be differentiated from survival probability. Animals dispersing from the fragment would be recorded as absent and thus contribute to lower levels of survival. The radio-tracking of black-footed tree-rats (see Chapter 5) showed that animals were able to move between fragments.

Although abundance of all four medium-sized mammals was greatest in the fragmented sites, abundance varied widely between fragments (Chapter 4). As these differences may be attributed to differences in habitat quality, a more intensive study of denning and food resources preferred by black-footed tree-rats was conducted to further investigate the resources that influence populations of small mammals in fragmented landscapes (Chapter 6). Black-footed tree-rat populations were limited by the diversity of food resources and the availability of hollows. A higher diversity of fruiting species provides a larger variety of food resources that will fruit during different periods of the year, providing a more sustained and continuous food supply, while large dhb trees provide more hollows for shelter. Fire history influenced the diversity of the fruiting species present at the site (Chapter 6). Sites that were long unburnt had a greater fruiting species diversity and hence were able to support a greater population of black-footed tree-rats. Hence, fire regimes were found to have a direct effect on the habitat quality by influencing vegetation structure and composition and in turn affecting mammal populations.

The space used by individuals of a species provides important information about factors that limit the species. The black-footed tree-rat was radio-tracked in fragmented and continuous habitats to investigate possible differences in movement, activity area and home range. The size of home range estimates for black-footed-tree-rats in the un-fragmented environment suggests that tree-rats require large areas (67.3 ± 10.4 ha) when compared to many other mammal species of comparable size in Australia's tropical savannas (Chapter 5). Home range and activity area size decreased significantly under fragmented conditions, but black-footed tree-rats were able to cross relatively large areas of cleared land. This suggests that the area of a fragment may be an important factor limiting the home range size of black-footed tree-rats, supporting the findings from the initial survey (Chapter 3) of a positive relationship with the area of a fragment (i.e. black-footed tree-rats prefer larger fragments). Ultimately, black-footed tree-rats depend on a certain amount of woodland to maintain a population, but this may be achieved either in a single large patch, or via several small patches.

Implications for Conservation and Management

Most habitat fragmentation studies have been conducted in areas where extensive clearing has resulted in an extreme loss of native vegetation. For these areas, the aim is usually to report on the effects that habitat fragmentation and loss has had on the biota of the region and to suggest the best ways to restore and manage the remaining vegetation (Brook et al. 2003). In contrast, the main aim here was to determine the requirements of the region's fauna in order to guide the design of future agricultural landscapes. The amount of land clearing in the Northern Territory has increased markedly since the early 1990s, although it is still limited compared to southern Australia. Consequently, planners in the Northern Territory have a rare opportunity to enact clearing controls, informed with the principles of ecological sustainability, to help ensure the long-term maintenance of the Northern Territory's native flora and fauna. The configuration of habitat patches capable of maintaining viable wildlife populations can be pre-determined, with guidelines being put into place before vegetation clearance occurs.

The open forest and woodland fragments in this study were all isolated within the last 30 years, and many of them within the last 10 years. This is insufficient time for most populations of animals or plants to adjust to the new landscape. Studies of fragmentation around the world show that species continue to disappear from fragments more than 70 years after isolation (Diamond et al. 1987; Sieving and Karr 1997). Consequently, these results are an optimistic assessment of the impact of fragmentation because time since isolation is yet to have had its full impact. Thus many animals will continue to decline in abundance in the open forest and woodland fragments in the Northern Territory.

Guidelines

Here I discuss some guidelines for the design of future agricultural landscapes in the tropical savannas of the Northern Territory. These guidelines are based on the findings of this study and are an attempt to provide strategies to reduce the ecological impacts of habitat fragmentation. It should be noted, however, that being based on the findings of this study, these recommendations are based solely from a biodiversity perspective and do not consider agricultural requirements or the economic effects of these recommendations.

Species living in the tropical savanna woodlands and forests of the Northern Territory fall into three groups in relation to their needs under fragmentation scenarios. Many species can actively use the new matrix and thus there is no need to implement measures for their conservation.

Many more do not use the matrix, but appear to remain at their previous levels in woodland fragments. However, for such species, their populations have been reduced by whatever percentage of the woodland the land clearing has removed. Where habitat fragmentation is severe the populations may become unviable in the long-term because there are too few individuals left in the whole landscape. Obviously, this problem will be most acute for the rarest species. For these two groups of species, it is probably not necessary to implement specific conservation measures because they will benefit from the measures needed for the third group of species.

This third group is comprised of the species that showed a negative response to fragmentation. Not only have they been lost from the woodlands that have been cleared, they have declined in the remaining fragments as well. In this study, there were 28 species in this group (Chapter 3). It is this group of species that are the focus of the guidelines for the retention of fragments. The aim is to describe landscape design rules that maximise the probability that this group of species will remain in the landscape. It should be pointed out that although 28 species were identified, there may be many more species that have the same response. Most of the species that live in woodlands were recorded too infrequently to undertake statistical analysis, and such rare species are likely to suffer from fragmentation (Saunders et al. 1991).

The guidelines focus on optimising the three fragmentation indices that were found to be important in Chapter 3: the amount of woodland within 4 km radius of the site, fragment area, and connectivity, and are additional to current legislation (briefly discussed in Chapter 2).

1: The total amount of clearing should not exceed 60% within any 4 km radius.

The majority of species (five of nine) with a significant relationship with the amount of woodland within 4 km, were not detected from fragments with less than 30% of woodland in the surrounding landscape, and the abundance of another two species had declined to less than one fifth of that in un-fragmented woodland (Chapter 3). Three of these species were still absent in fragments with less than 45% of bush remaining in a 4 km radius of the site and the quoll was not recorded in any patch with less than 65% of bush remaining in a 4 km radius of the site (Chapter 3). In order to balance conservation and development aims, it is accepted that not all species may be retained. The guideline is to retain a mininum of 40% of woodland, and this would retain all but one of the 67 species analysed (or about 99%). The probable absence of the quoll from such a landscape is a concern, but there may be alternative measures that can be taken to promote their retention. There are no areas in Litchfield Shire that do not currently meet this guideline, while at Tipperary, about one quarter of the landscape does not.

2: Guideline 1 should be applied at a regional scale

The guidelines should be seen as a tool for planning at a landscape scale. As guideline 1 sets targets over an area that is larger than most rural or horticultural properties, it is logical to apply the guideline in a regional or multi-property context. It is not envisaged that they be applied retrospectively, in areas where land has already been subdivided into small, freehold lots. Nor is it strictly necessary to retain woodland and corridors on all small properties. For example, properties may vary in their percentage retention of woodland due to variation in the agricultural or wildlife values of the land they contain. Alternatively, it may be better to set aside some land into public ownership for conservation purposes before the lots are created. These kinds of decisions can only be made in the context of regional planning, where the rule applied to each property is guided by the land uses in the surrounding properties. Since it is important to manage woodland in a 4 km radius (or units of about 5000 ha), the guidelines should be applied by the Government, and by the developers of large properties and should be applicable to any tenure.

Riparian areas and land considered unsuited for development (i.e. valleys with a steep slope), would form the basis of the fragment and corridor network. In some cases, additional areas of woodland will need to be retained to satisfy the guidelines and to provide an adequate representation of all habitat types. Since the 40% landscape retention applies over an area of about 5000 ha, it may be possible on small properties to retain less than 40% as long as it is compensated for in other properties. If the process were to function properly landholders would be informed where clearing was permitted on the property in question before purchasing.

Ultimately, the implimentation of guidelines during the planning and development process allows us to obtain a balance between biodiversity conservation and human land uses. The implementation of guidelines at this stage would eliminate the need for expensive post-hoc initiatives to re-vegetate degraded areas, to re-establish isolated areas.

3: At least 60% of the total area of retained woodland should be in fragments at least 10 ha in size.

Of the 11 species with a significant area relationship, two appear to be absent from fragments smaller than 1 ha (black-footed tree-rat). Two others fell to an abundance about one tenth of that in un-fragmented woodland in the smallest fragments, and the rest showed a gradual decline or erratic pattern (Chapter 3). Thus most species, even those that are affected by fragment size, will occur in patches smaller than 1 ha. It seems that fragments of any size are useful, but larger ones are better than small ones, especially if a long-term perspective is considered. In light of the loss

of two species from sites as small as 1 ha, a decline with fragment size in several other species and the high potential edge effects in small fragment, it is important that some large patches be retained. Patches larger than 10 ha appear to maintain abundances of most species at close to those expected in un-fragmented woodland.

4: Connect fragments with at least two corridors of retained woodland at least 100 m wide.
Fifteen species were related to connectivity in models, more than any other variable (Chapter 3). Four of these were not present in fragments where connectivity was below 0.2 and another three declined to abundances less than one fifth of that in un-fragmented woodland (Chapter 3). Five of these seven were still at very low abundance in fragments with less than 40% connectivity. It is clear that connectivity allows many species to be present in fragments that otherwise would be expected to be too small to maintain them. For example, agile wallabies and black-footed tree-rats were found in fragments 0.8 ha and 2.0 ha respectively, but in these cases connectivity was above 0.6. The connectivity index used here is a measure of how easy it is to move to and from a fragment through woodland. A value of 1 could only be achieved in un-fragmented woodland, but values of 0.8 or more can be achieved if a fragment is surrounded by corridors on many sides that link to extensive woodland within 2 km. Thus connectivity reflects the presence of corridors, although the width of corridors does not influence the calculation of the index. The study also found that the great majority of species do occur in corridors. Combining this information with the results from the statistical modelling, it seems that corridors have a very important role in maintaining wildlife in the landscape. Therefore, the recommendations for this section are to promote the retention of corridors.

Fragments should always be connected by corridors to at least two other areas of woodland, and more corridors are better. Recommendations in the Conservation Plan for the Daly Basin (Price *et al.* 2003a) aim to retain riparian vegetation to a width of 250 m either side of rivers and 100 m either side of creeks. These corridors can form the backbone of a system of corridors connecting all of the fragments in any landscape. It is important that these corridors include Eucalypt forest or woodland, since many of the animals studied here are restricted to these vegetation types.

The width of a corridor influences which species will use it and how serious edge effects will become. In general, a corridor is likely to be more effective where animals can live in the corridor as well as move through it. Since a number of animals in the tropical savanna woodlands have large home ranges (i.e. the black-footed tree-rat, Chapter 5) corridors should be as wide as possible. There is very little evidence to determine how wide a corridor should be. Studies in other parts of the world have concluded that corridors should be wide. In this study,

there were nine species that had a significant relationship with connectivity, did not occur in cleared land and did occur in corridors. Only one of these, the grey butcherbird, occurred in the two corridors less than 40 m wide (Chapter 3). However, I did not study enough corridors to give a confident estimate of the width required. Considering the literature and my results, I recommend that corridors should be at least 100 m wide.

5: Manage fragments for moderate fire regimes (by avoiding annual fires and late dry season fires), to minimise weed invasion, to avoid high densities of exotic animals and to promote the growth of large trees.

Several management issues that affect the wildlife in fragments were identified in this study, and their consideration is important to maintaining the value of the retained fragments. There is widespread agreement that fire regimes in northern Australia are currently more frequent, intense and homogeneous than they were when indigenous people routinely managed fire across this land (Haynes 1985; Bowman and Panton 1993; Braithwaite 1996; Russell-Smith *et al.* 2000). It is not possible from the nature of this study to provide recommendations of an optimum fire frequency, and arguably there is no such ideal that encompasses all species. However, the results are consistent with other studies, which suggest that a mosaic of fire histories is a better goal (Russell-Smith *et al.* 1997; Bowman 1999; Gill *et al.* 2000; Woinarski *et al.* 2001b; Yibarbuk *et al.* 2001; Williams *et al.* 2002b; Price *et al.* 2005a). Price *et al.* (2005b) suggests that low levels of habitat fragmentation may actually increase habitat heterogeneity in the landscape, in the form of new vegetation types and a variety of fire regimes

Future research and Directions

As this is the first study to investigate the effects of land clearing and habitat fragmentation on the vertebrate fauna of the open forests of the tropical savannas of northern Australia, a large number of questions have arisen as a result and require further investigation. Unlike fragmentation studies conducted in most other areas, one of the initial challenges for this study was obtaining enough sites that could be defined as fragments. Limited and mostly small-scale land clearing meant that many of the patches are small in size (the majority are less than 5 ha), recently isolated and are separated from other wooded areas by small distances. Also, time since isolation is low. Consequently, these results are an optimistic assessment of the impact of fragmentation. To overcome these uncertainties, long term monitoring (preferably investigating survival rates using mark-recapture) should be set up to follow populations of targeted species over time.

There are many topics that I have not been able to investigate in this study, but which are important, if we are to understand fragmented systems and to confidently design future agricultural landscapes. These include:

- long term fate of unmanaged fragments
- socio-economics of vegetation retention. Incentives for vegetation retention (how do we promote their adoption)
- strategies for improving management of privately owned fragments
- optimal corridor width
- ecological traits related to fragmentation sensitivity
- long-term monitoring including before habitat fragmentation occurs.

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