

Spatial Ecology of the Tasmanian Spotted-Tailed Quoll



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Declaration of Originality

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and to the best of my knowledge and belief no material previously published or written by another person except where due acknowledgement is made in the text of the thesis, nor does the thesis contain any material that infringes copyright.

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Statement of Ethical Conduct

The research associated with this thesis abides by the international and Australian codes on human and animal experimentation, the guidelines by the Australian Government's Office of the Gene Technology Regulator and the rulings of the Safety, Ethics and Institutional Biosafety Committees of the University.

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Shannon Troy

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“Our collective effort to try to understand the immense diversity of interactions in living nature amounts to an attempt to navigate through a narrow passage between the Scylla of dogmatism and the Charybdis of resignation. We must be critical, see nature as it is, and pursue the limitations of our favorite hypotheses. However, we also need general ideas, showing that everything is not a hopeless maze of special cases.”

Oksanen and Oksanen (2000)

Abstract

The importance of top predators in maintaining ecosystem structure, function and resilience is increasingly apparent as predators decline worldwide. Habitat loss and fragmentation are leading causes of these declines. Therefore, knowledge of habitat preferences is needed for conservation of predators, but is often lacking.

Mainland Australia's marsupial carnivore guild is severely depleted. In south-eastern Australia, only the endangered spotted-tailed quoll (*Dasyurus maculatus*) remains, and is sympatric with the introduced red fox (*Vulpes vulpes*), feral cat (*Felis catus*), wild dog (*Canis familiaris*) and dingo (*Canis dingo*). In contrast, Tasmania retains a relatively intact guild: the spotted-tailed quoll, Tasmanian devil (*Sarcophilus harrisi*), and eastern quoll (*Dasyurus viverrinus*), as well as the feral cat. The red fox is historically and probably functionally absent. The spotted-tailed quoll is not well studied in Tasmania. Extrapolation of habitat preferences from mainland populations may be inappropriate as the predator and prey assemblages and environments differ in the two regions. This study aimed to determine the biotic and abiotic correlates of Tasmanian spotted-tailed quoll distribution, abundance, space use, and movement, at individual-, population-, and distribution-scales.

I used live-trapping and camera survey data to investigate the distribution and abundance of the spotted-tailed quoll in relation to environmental factors and competitors across Tasmania (i.e. first-order habitat selection). Abundance was best explained by climatic correlates of productivity and by mean annual net primary production. The most suitable habitat for Tasmanian quolls occurs off-reserve, highlighting the role of private landholders in

quoll conservation. Optimal habitat of quolls and foxes overlaps extensively. Spotted-tailed quoll abundance was independent of the Tasmanian devil, feral cat, or prey.

I used GPS and VHF telemetry tracking of adult females in a fragmented agricultural landscape to investigate the influence of vegetation composition on home range size, habitat selection, activity, movement and den use (i.e. second-, third- and fourth-order scales). Quolls preferred forest and avoided pasture for home range placement (second-order selection scale), within-home range movement (third-order) and non-maternal den site selection (fourth-order). Home range size increased with habitat loss and fragmentation, suggesting quolls in fragmented landscapes needed larger areas to meet their resource requirements. Activity times were unrelated to vegetation composition. Quolls moved more quickly across pasture than through forest, indicating higher risk and/or low resources in open areas, but showed similar selection of interior *versus* edge of vegetation cover. High use of foliage/grass dens (57.5%), suggests that either secure den resources are limited in the study area or that risk of predation is low.

This study provides new insights for management of spotted-tailed quolls. Habitat management in Tasmania should focus on retaining remnant forest in productive landscapes with high predicted habitat suitability, restoring forest in heavily cleared landscapes, and increasing engagement with private landholders. Habitat requirements of the Tasmanian spotted-tailed quoll are more flexible than for the south-eastern mainland populations. The differences may be attributed to competition with the red fox on the mainland. Habitat requirements of the Tasmanian spotted-tailed quoll could therefore indicate potential habitat on the south-eastern mainland under fox-control programs.

This study highlights that observed patterns of wildlife habitat associations are influenced by both bottom-up environmental factors and top-down constraints on habitat availability. Extrapolating across spatial scales or geographic regions may underestimate the

area of potential habitat and lead to ineffective conservation actions. Effective conservation of predators requires knowledge of habitat preferences across their distribution at multiple scales.

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Chapter 1: General Introduction

1.1 Habitat

1.1.1 Habitat loss and fragmentation

The Earth is facing an extinction crisis, with extinction rates for flora and fauna up to 1000 times higher than the background rate in the fossil record (Barnosky *et al.* 2011; Pimm *et al.* 1995; Wilson 1999). One fifth of the world's vertebrates are either recently extinct or globally threatened (IUCN 2013). Across all taxa, habitat loss and fragmentation are considered to be the greatest contributors to past and potential future extinctions (Brook *et al.* 2008; Henle *et al.* 2004; Tilman *et al.* 1994). For mammals, habitat loss is a particularly pervasive threat; of the 22% of extant mammals worldwide listed as threatened, 80% are negatively impacted by habitat loss (IUCN 2013). As the human population continues to grow, protecting remaining habitat is central to conserving the species that inhabit it. Thus, an understanding of the habitat a species requires and where that habitat occurs is a critical first step in preventing and mitigating the effects of habitat loss and fragmentation.

1.1.2 Definition of habitat

There has been considerable debate on the interchangeable use of the terms habitat and niche (Guisan and Thuiller 2005; Kearney 2006; Whittaker *et al.* 1973), which are related, though not synonymous, concepts. For the purposes of this thesis, habitat is defined as “the resources and environmental conditions present in an area that allow persistent occurrence by a given organism” (Hall *et al.* 1997). Similarly, the definition of niche used is “...the

hypervolume defined by the environmental dimensions within which a species can survive and reproduce” (Hutchinson 1957). This definition is further distinguished as the fundamental (physiological or potential) niche, defined as “the response of species to environment (resources) in the absence of biotic interactions (competition, predation)” and the realized (ecological, actual) niche, defined as “the environmental dimensions in which species can survive and reproduce in the presence of biotic interactions” (Hutchinson 1957). Thus, habitat is a function of the environment with which a species interacts, while the niche is an attribute of a species itself (Kearney 2006; Pulliam 2000). In the absence of constraints, animals select habitats to acquire resources that maximize survival and reproductive success e.g. fundamental niche (Hutchinson 1957). However, animals experience biotic constraints (e.g. competition and predation) that prevent them using parts of their fundamental niche; what remains is their realised niche (Hutchinson 1957).

1.1.3 Spatial scales of habitat selection

Conservation management strategies often focus on retention of the most important habitat for a given species. Management of species threatened by habitat loss requires protection and restoration of habitat. For many species, particularly wide-ranging habitat generalists, it is not feasible to protect all habitats that could be used. We can identify critical habitat for a species by studying habitat selection. Although the terms ‘habitat selection’, ‘habitat use’ and ‘habitat preference’ are often used interchangeably, they technically describe different processes (Hall *et al.* 1997; Johnson 1980). Habitat selection is the process of decision making by animals that involves a series of innate and learned behaviour decisions resulting in occupation of certain habitats rather than others with equal availability (Morrison *et al.* 2006). Preference and avoidance refer to the disproportionate use of habitat relative to

availability, for example as time spent or number of locations used in a habitat, where availability is defined as the quantity and accessibility of habitat components (Johnson 1980; Thomas and Taylor 1990). Due to the impracticalities of assessing accessibility from an animal's point of view, habitat availability usually refers to the quantity of focal habitat components in the area of interest (Hall *et al.* 1997). Thus, investigations of wildlife-habitat relationships often compare the use of habitat by animals relative to its availability (i.e. quantity) to infer preference or avoidance.

Habitat selection is a hierarchical process, operating from broad to fine spatial scales that involve population- to individual-level processes (Hall *et al.* 1997; Johnson 1980; Wiens 1989). I follow Johnson's (1980) hierarchical scheme, which recognises four orders of habitat selection. First-order selection defines the selection of the geographical range or distribution of a species. Second-order selection determines the home range of an individual within that distribution. Third-order selection relates to the use of habitat components within the home range. Fourth-order selection describes procurement of resources within the home range. Within Johnson's (1980) framework, Thomas and Taylor (1990; 2006) classified designs for resource selection studies into four categories. In Design 1 studies, individual animals are not identified and availability is assumed to be the same for all animals, a scenario that usually corresponds to landscape-scale and population-level studies of wildlife habitat preference. In Design 2 studies, individual animals are identified, and use is measured individually. Availability however remains the same for all animals, allowing for assessment of landscape-scale habitat selection. In Design 3 studies, use and availability are measured separately for individual animals, allowing assessment of patch-scale habitat selection. Finally, in Design 4 studies, use and availability are measured multiple times for each individual animal around a use site (e.g. nest or den) allowing assessment of microhabitat selection.

At any level in the hierarchy, it is assumed that preference for certain habitat components improves the fitness of animals (Morris 2003; Thomas and Taylor 2006), and that the distribution and abundance of species should reflect the quality of the environment they inhabit. Maladaptive habitat selection can lead to use of resource-poor habitats (e.g. sink populations), where individuals are found but do not contribute to population growth (Pulliam 1988; Van Horne 1983). To identify preferred habitat through alternative approaches, such as assessment of individual-based measures of performance (e.g. survival or reproductive status) or success across multiple generations (McLoughlin *et al.* 2005; Pollock *et al.* 1989), is almost always infeasible for rare and cryptic species. Thus, with appropriate caveats, I consider selection of habitat components to reflect choices and trade-offs that are made by animals to access resources that maximize their fitness.

1.2 Carnivore conservation

The conservation management of carnivores and their habitat is a focus of conservation management efforts globally (Dalerum *et al.* 2009; Gittleman *et al.* 2001; Sergio *et al.* 2008) for a number of reasons. First, mammalian carnivores often possess biological traits that are positively correlated with high risk of population decline or extinction in response to threats such as habitat loss and fragmentation (Duffy 2003; Woodroffe 2001). These include low population density, large area requirements, high trophic level, slow life history, specialized niche requirements, and large body size (Pimm *et al.* 1988; Purvis *et al.* 2000). However, species do not respond equally to habitat loss and fragmentation, and even within predator guilds some species are more susceptible to these processes than are others (Crooks 2002; Gehring and Swihart 2003; Ryall and Fahrig 2006). Understanding species-specific habitat preferences are an important first step in predicting the effect of past and ongoing habitat loss

and fragmentation. For this reason, many predator species are listed as threatened (e.g. 24% of species in the Order Carnivora, IUCN 2013), and specific management actions to assist their recovery may be legislated.

Second, changes in the abundance and distribution of high trophic level predators can have profound effects on lower trophic levels, so understanding their likely response to habitat loss and fragmentation is key to understanding the effects on the broader ecosystem and its conservation. For example, the decline of apex predators such as wolves (*Canis lupus*) and jaguars (*Panthera onca*) has resulted in increases in abundance of herbivore prey, which in turn has led to overgrazing, habitat loss for smaller species, and ecosystem degradation (Berger *et al.* 2001; Terborgh *et al.* 2001). In contrast, generalist predators may thrive in heterogeneous landscapes, causing declines in prey species (Crooks and Soule 1999; Prugh *et al.* 2009).

Finally, due to their large area and prey requirements, conservation of top carnivores also requires the preservation of large areas of suitable habitat (and associated vertebrate prey). Conservation planning and management for top predators can therefore be a useful proxy for conservation at the broader landscape scale (Carroll *et al.* 2001; Noss *et al.* 1996).

1.3 Australian mammal decline

Australia presents a stark example of the global extinction crisis and its relationship with habitat loss. Australia has the highest rate of mammal extinction in the world, with 28% of terrestrial mammals becoming extinct since 1600 AD, and 22% of extant species currently threatened with extinction (EPBC 1999). Habitat loss, modification and fragmentation have been implicated in the extinction of all Australian mammals, and are considered to be threatening processes for all currently threatened species (EPBC 1999). Habitat loss and degradation has been extensive in most parts of Australia. Agricultural practices have destroyed

or modified approximately 50% of all forest and woodland ecosystems and 70% of the remaining forests are degraded (Kingsford *et al.* 2009). In the productive eastern temperate zone, 90% of native vegetation has been removed for agriculture, industry and human habitation in just over 200 years of European occupation (ABS 2006). Habitat loss alone does not, however, fully explain patterns of Australian mammal declines and extinctions (Johnson 2006). Predation and competition from introduced eutherian predators, particularly the European red fox (*Vulpes vulpes*) and the feral cat (*Felis catus*), have also been identified as primary factors in the extinction and decline in distribution and abundance of Australia's small- and medium-sized (critical weight range 35 to 5500 g body weight) terrestrial mammal fauna (Johnson 2006; Saunders *et al.* 2010; Short and Smith 1994)

All of Australia's largest marsupial predators, the thylacine (*Thylacinus cynocephalus*), Tasmanian devil (*Sarcophilus harrisi*) and the four species of quolls (*Dasyurus sp.*) have declined in distribution and abundance since European settlement (Jones *et al.* 2003). These declines have been most severe on mainland Australia where the thylacine, Tasmanian devil and eastern quoll are now extinct, the northern and spotted-tailed quolls are Endangered, and the western quoll is Vulnerable (EPBC 1999). Habitat loss and fragmentation and predation and competition from introduced eutherian predators pose the greatest threats to the ongoing persistence of these species (Johnson 2006; Jones *et al.* 2003).

In contrast to the situation on mainland Australia, the large (68 000 km²) island State of Tasmania, situated 350 km south of south-eastern Australia, has retained an almost intact marsupial carnivore guild, although extant species face ongoing threats. The thylacine was last recorded in 1933 and is formally listed as extinct (EPBC 1999; McKnight 2008). The Tasmanian devil is extant, although listed as Endangered; primarily as a result of population-wide spread of the invariably fatal contagious cancer Devil Facial Tumour Disease (DFTD)

(EPBC 1999; Hawkins *et al.* 2008). The eastern quoll is also extant, but declining (Fancourt *et al.* 2013). The spotted-tailed quoll is listed as Vulnerable under Commonwealth legislation (EPBC 1999) and Rare under the Tasmanian legislation (TSPA 1995).

The better conservation status of Tasmanian mammals relative to those on mainland Australia has been attributed to the historical absence of the red fox (*Vulpes vulpes*) (Short and Smith 1994). Indeed, with the exception of foxes, all of the threats to mammals that are present on mainland Australia are also present in Tasmania, yet many mammal species such as the eastern quoll (*Dasyurus viverrinus*), Tasmanian bettong (*Bettongia gaimardi*), eastern barred bandicoot (*Perameles gunnii*) and Tasmanian pademelon (*Thylogale billardierii*) that are now extinct on mainland Australia persist in Tasmania.

1.4 The spotted-tailed quoll

In this thesis, I investigate the distribution and habitat associations of the Tasmanian spotted-tailed quoll (*Dasyurus maculatus maculatus* Tasmanian population). Habitat loss, modification and fragmentation have been posited as the greatest threat to the spotted-tailed quoll (Jones *et al.* 2003; Long and Nelson 2008; Mansergh 1984). The spotted-tailed quoll is the largest extant marsupial carnivore on mainland Australia, and in Tasmania is second in size only to the devil. Males can reach up to 7 kg and females 4 kg (Jones *et al.* 2001). The species exhibits many of the behavioural and life history traits common to extinction-prone placental predators, including relatively large body size; large home range size (Female 88 – 1, 515 ha; Male 359 – 5, 512 ha (Andrew 2005; Belcher and Darrant 2004; Claridge *et al.* 2005; Glen and Dickman 2006b; Nelson 2007); female territoriality and natal philopatry (Firestone 1999; Glen *et al.* 2009); low population density (Belcher 2003; Glen 2008; Körtner *et al.* 2004);

and dietary specialization (Belcher 1995; Belcher *et al.* 2007; Dawson *et al.* 2007; Glen and Dickman 2006a; Jarman *et al.* 2007; Jones and Barmuta 1998). These attributes theoretically limit the ability of the species to tolerate disturbance to their habitat, or to recolonize fragmented habitats (Firestone 1999).

The spotted-tailed quoll occurs throughout eastern Australia as two subspecies: *D. m gracilis*, in northern Queensland, and *D. m. maculatus*, found in south-eastern Australia and Tasmania (Figure 1.1). Two populations of *D. maculatus maculatus* are recognised: a south-eastern mainland population, which is listed as Endangered and a Tasmanian population, which is listed as Vulnerable (EPBC 1999). A genetic study indicated that *D. m. maculatus* (Tasmanian population) should be raised to the subspecies level, and that *D. m. gracilis* and *D. m. maculatus* (south-eastern mainland population) should be treated as separate management units of the same subspecies (Firestone 1999). To date, this has not occurred. In this thesis, spotted-tailed quoll refers to all subspecies and populations of *Dasyurus maculatus*; the Tasmanian spotted-tailed quoll refers to *Dasyurus maculatus maculatus* Tasmanian population; the south-eastern mainland spotted-tailed quoll refers to *Dasyurus maculatus maculatus* south-eastern mainland population; and the northern spotted-tailed quoll refers to *Dasyurus maculatus gracilis*.

Most information on the ecology and habitat preferences of the spotted-tailed quoll derives from research on south-eastern mainland populations. At the time of European settlement, the species was distributed continuously throughout its range, including the Victorian coastal forests, and along the length of the Murray River into South Australia (Mansergh 1984). The south-eastern mainland spotted-tailed quoll has suffered an estimated 50% range contraction (Maxwell *et al.* 1996). The species has become extinct in South

Australia, is uncommon west of the Great Dividing Range, and remaining populations are disjunct and fragmented. Historically, the south-eastern mainland spotted-tailed quoll has been recorded from a wide range of habitat types, including rainforest, wet and dry sclerophyll forest and woodland, coastal scrub and heath, and grassland or pasture adjacent to forested areas (Long and Nelson 2008), but is now considered to be a primarily forest dependent species that is largely restricted to wet forests (Belcher 2004; Mansergh 1984). Habitat considered critical to the survival of the spotted-tailed quoll includes large patches of forest with a high density of potential den resources and high densities of small- to medium-sized mammalian prey (Belcher and Darrant 2006b; Glen and Dickman 2006b).

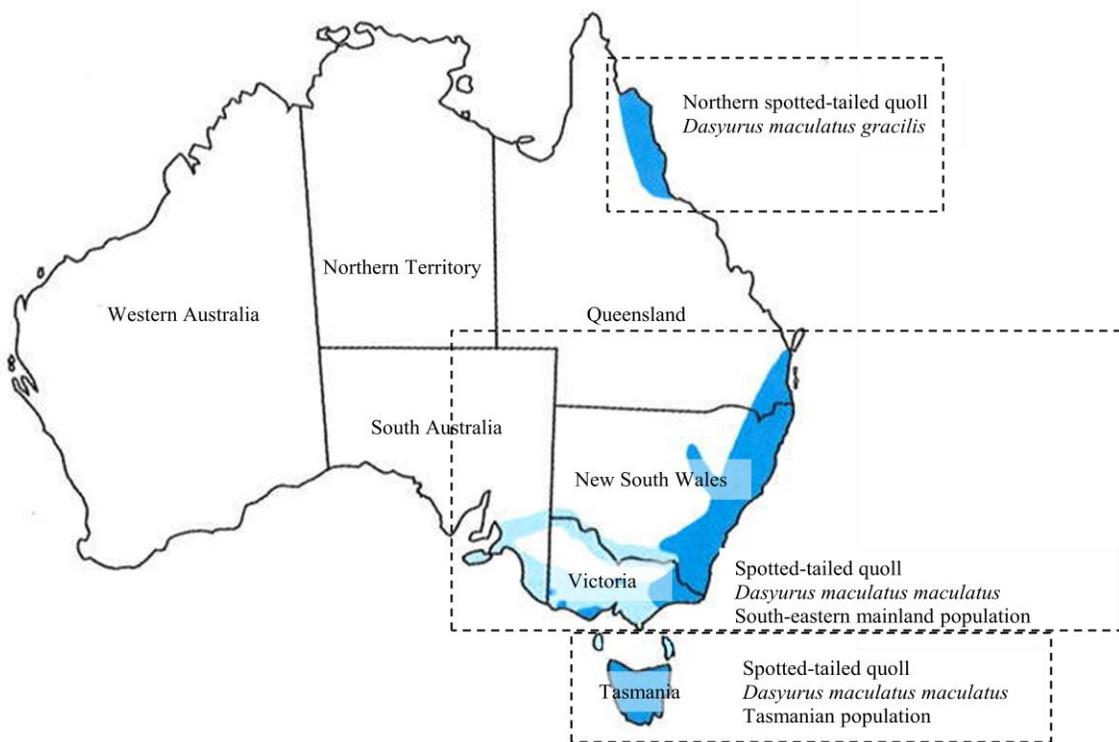


Figure 1.1: Current (dark blue) and former (light blue) distribution of spotted-tailed quoll subspecies and populations in eastern Australia. Modified from (Edgar and Belcher 2008)

At the first-order scale, the distribution of the mainland spotted-tailed quoll appears most strongly associated with extensively forested areas at high elevation on productive soils in regions of high and predictable seasonal rainfall (Burnett 2001; Catling *et al.* 2002; DNR 1997; Mansergh 1984; Wintle *et al.* 2005). At the second-order scale, quoll home ranges preferentially include gullies, flats and escarpments and avoid mid-slopes; factors related to the availability of den sites and prey (Belcher and Darrant 2006a). However, in the same study area, a different study found that adult female spotted-tailed quolls showed no selection for topographic features (Nelson 2007). Within a contiguously forested landscape, a study of use of selectively logged and unlogged forest found that quolls preferred forest more than 50 years of age and avoided young (< 10 year old) forest (Belcher 2008). In the only study conducted in a partially forested and naturally heterogeneous landscape, quoll home range placement in the landscape was associated with forest, woodland and shrub cover and avoids open sedgeland, heathland, grassland, and cleared land (Andrew 2005). Similarly, in the same study area but at the third-order scale, the spotted-tailed quoll showed strong preference for forest and woodland, used shrubs in proportion to availability, and avoided sedgeland, heathland, grassland, and cleared land (Andrew 2005). At the fourth-order scale, the spotted-tailed quoll has been recorded using a variety of den structures including burrows, rock outcrops and piles, and tree hollows (Andrew 2005; Belcher and Darrant 2006a; Glen and Dickman 2006b; Nelson 2007; Ruibal *et al.* 2011). The type and frequency of den use differs among studies. Similarly, although mammals are always the most frequent prey item in the diet, the size of the prey consumed and the degree of supplementation with other taxa varies among study regions (Belcher 1995; Belcher *et al.* 2007; Dawson *et al.* 2007; Glen and Dickman 2006a; Glen *et al.* 2011; Jarman *et al.* 2007).

In contrast to the well-studied south-eastern mainland spotted-tailed quoll, there is little quantitative information on the ecology and habitat preferences of the Tasmanian spotted-tailed quoll. The species is widespread at low abundance across Tasmania. The only known range contractions in Tasmania are the species extirpation from King and Flinders Islands (Bass Strait), where the last confirmed sightings were in 1923 (Green and McGarvie 1971) and 1893 (Gabriel 1984) respectively. Extirpation from these islands has been attributed to land clearance, human persecution and attacks by domestic dogs (Green and McGarvie 1971). At the first-order scale, the distribution of the Tasmanian spotted-tailed quoll has been qualitatively associated with wet forest and scrub in the west and north-west of the state (Rounsevell *et al.* 1991). Similarly, a visual inspection of predicted distribution from a presence-only model indicated that the species' core distribution occurs in northern Tasmania and coincides with areas of high productivity, as inferred by association with predictable seasonal rainfall, warm annual mean temperature and low altitude, although these relationships have not been quantified (Jones and Rose 1996). There have been few studies of higher-order resource selection by the Tasmanian spotted-tailed quoll. The only detailed study of Tasmanian spotted-tailed quoll habitat use (third-order) investigated niche partitioning and the potential for interspecific competition among the devil, spotted-tailed quoll and eastern quoll (Jones 1997; Jones and Barmuta 1998; Jones and Barmuta 2000). While that study found that the spotted-tailed quoll has higher arboreal activity than the devil and the eastern quoll and made greater use of rainforest and habitats with a structurally complex understory than the other two sympatric marsupial carnivores. However, habitat use was not quantified relative to the availability of habitats in the landscape, making assessment of preference difficult.

The dearth of information on the ecology of the Tasmanian spotted-tailed quoll is hindering its effective conservation management (Jones and Rose 1996). The Tasmanian

spotted-tailed quoll has been isolated from mainland populations for ~13,000 years (Firestone *et al.* 1999; Lambeck and Chappell 2001), and now occurs within a guild of predators and assemblages of prey that differ significantly from mainland Australia. Most importantly, the south-eastern spotted-tailed quoll co-occurs with and probably experiences competition from the red fox (Glen and Dickman 2005; Glen and Dickman 2008), while the Tasmanian spotted-tailed quoll co-occurs with and probably experiences competition from the devil (Jones 1997; Jones and Barmuta 1998; Jones and Barmuta 2000). These differences in apex predators may result in the Tasmanian and south-eastern mainland spotted-tailed quoll exhibiting divergent habitat associations in the two regions. To date however, management of the Tasmanian spotted-tailed quoll has largely, but unavoidably, been informed by the ecology and habitat associations of the south-eastern mainland subspecies. Given the known differences in habitat use and behavior and co-occurring predators, it seems unlikely that extrapolation of for the management of the Tasmanian subspecies is valid.

The need for information on the ecology and habitat preferences of the Tasmanian spotted-tailed quoll has become more pressing in light of two recent and significant events in the Tasmanian ecosystem. First, the ongoing decline of the Tasmanian devil as a result of DFTD (Hawkins *et al.* 2006) is expected to result in changes to the distribution and abundance of mesopredators such as the feral cat and the spotted-tailed quoll. Second, the contemporary (~1999) introduction of the red fox (Sarre *et al.* 2013) is expected to adversely impact lower trophic levels and potentially impact directly on spotted-tailed quolls through predation or competition. The fox is currently considered rare but widespread in Tasmania (Sarre *et al.* 2013). The high rate of conversion of native Tasmanian forest to other land uses (Jones and Rose 1996) also the need for quantitative information on Tasmanian spotted-tailed quoll distribution and habitat preferences to apply to the development of conservation management

strategies for the species.

1.5 Thesis objectives

The purpose of this study was to investigate the distribution and habitat associations of the Tasmanian spotted-tailed quoll. I had three specific objectives:

1. Determine the biotic and abiotic correlates of Tasmanian spotted-tailed quoll distribution, abundance, space use, and movement.
2. Compare environmental associations of Tasmanian spotted-tailed quoll to mainland conspecifics.
3. Use the results to inform the development of recommendations for the conservation management of the spotted-tailed quoll.

1.6 Thesis structure

This thesis contains six chapters. Chapters 2-5 are written as stand-alone research papers that have been formatted for future submission to peer-reviewed scientific journals. This formatting has resulted in some repetition among chapters, particularly in descriptions of the study site and background information on the study species. The data chapters were prepared with advice and feedback from supervisors and collaborators, and their contributions are recognised with co-authorship where appropriate. I was primarily responsible for all aspects of the thesis, including acquiring research funding, formulating the research questions, literature reviews, planning and conducting field data collection, data analyses, and writing.

Chapter 1: General Introduction

This chapter introduces the context, theory, previous research, and knowledge gaps that led to this study.

Chapters 2-5: Data Chapters

In the four data chapters, I use data from trapping surveys, camera surveys, and GPS / VHF telemetry to investigate the biotic and abiotic factors associated with spotted-tailed quoll distribution, abundance, space use, and movement. The chapters are arranged in increasing selection orders, from state-wide extent to individual extent, and first- to fourth-order selection.

Chapter 2 Explaining and predicting the distribution of the Tasmanian spotted-tailed quoll

First-order, Design 1

Species distribution models provide an invaluable first step in understanding patterns in the occurrence of wildlife. In this chapter, I combine data on quoll abundance collected during trapping surveys with spatial data on environmental characteristics and devil habitat suitability to build a species distribution model for the Tasmanian spotted-tailed quoll. I use the model-averaged parameter estimates to explain the abiotic and biotic correlates of quoll abundance, and to generate a map of predicted habitat suitability for the Tasmanian spotted-tailed quoll across Tasmania.

Chapter 3 Influence of environment and competitors on probability of occupancy by the Tasmanian spotted-tailed quoll

First-order, Design 1

Understanding the role of top-down processes such as interspecific competition and bottom-up processes such as productivity, landscape structure and prey abundance are key to predicting potential future changes to ecosystems following the decline or loss of apex predators. There is currently limited information available on the bottom-up and top-down processes influencing the abundance and co-occurrence of Tasmanian predators. In this chapter, I use camera survey data, occupancy modelling and quantile regression to quantify the role of bottom-up environmental processes and top-down regulation by higher order carnivores in determining the activity and abundance of three predator species and their common prey.

Chapter 4 Multi-scaled habitat selection by the spotted-tailed quoll in a fragmented agricultural landscape

Second-, Third-, & Fourth-Order, Design 2, 3, 4

Due to their intrinsic biological traits, terrestrial mammalian carnivores are predicted to be at greatest risk of decline from habitat loss. However some species, particularly some species of mesopredators (middle-sized predators), can persist and flourish in agricultural landscapes. The spotted-tailed quoll is an unusual case in that it is considered forest-dependent, but in Tasmania reaches high abundance in agricultural landscapes. In this chapter I use telemetry data to investigate how the composition, amount and contiguity of vegetation influences adult female spotted-tailed quoll home range size and placement, intra-home range habitat preferences and den use.

Chapter 5 Movement ecology of a forest-dependent mesopredator in a fragmented agricultural landscape

Third-Order, Design 3

Studying the movement decisions of individuals inhabiting heterogeneous landscapes can provide insight into the mechanisms driving species-specific responses to habitat loss and fragmentation. In this chapter, I use high temporal frequency GPS telemetry data to investigate how vegetation community composition and landscape structure influence the activity times, movement decisions and behaviour of adult female spotted-tailed quolls in a fragmented agricultural landscape.

Chapter 6 General Discussion

In this chapter I synthesise the key findings of the data chapters, relate this synthesis to the broader issues in the conservation management of spotted-tailed quolls and mammalian mesopredators, and discuss the importance of spatial scale and niches in interpreting wildlife habitat preferences. I conclude with suggestions for future directions in research and management of the spotted-tailed quoll in Tasmania.

Chapter 2: Explaining and Predicting the Distribution and Habitat Associations of the Tasmanian Spotted- Tailed Quoll



Photo: Thea Shell

2.1 Abstract

Wildlife conservation and management requires robust information on the distribution and habitat preferences of focal species. Species distribution models are a powerful tool for investigating the environmental associations and predicted distribution of wildlife and developing conservation management strategies. This is especially true for wide-ranging, low density, and cryptic predators, for which direct observation is difficult and whose populations are typically threatened, increasing the need for landscape-scale conservation planning.

In this study, we investigated the influence of bottom-up and top-down factors on the relative abundance and distribution of the spotted-tailed quoll (*Dasyurus maculatus maculatus*) using a combination of trapping occurrence data, spatial environmental data, and predicted habitat suitability for the local apex predator, the Tasmanian devil (*Sarcophilus harrisii*).

Relative abundance was best explained by two bottom-up drivers of environmental productivity: annual mean temperature and rainfall seasonality. The Tasmanian spotted-tailed quoll is less associated with high elevation, cool, high rainfall, forested areas than their mainland conspecifics. We hypothesise that the high abundance of the introduced red fox (*Vulpes vulpes*) on mainland Australia has resulted in a niche contraction in the south-eastern spotted-tailed quoll. In contrast, there was no evidence for a top-down effect of devil occurrence on Tasmanian spotted-tailed quoll relative abundance.

Spatial model predictions indicated that Tasmanian spotted-tailed quoll relative abundance is highest in north and north-western Tasmania, with a high proportion of core habitat occurring off reserve on private land. The high proportion of overlap in predicted optimal habitat suggests that the recent introduction of the red fox to Tasmania poses a significant risk to the spotted-tailed quoll.

We conclude that eradication of foxes from Tasmania should be considered a priority for

spotted-tailed quoll conservation efforts in Tasmania. More generally, our study highlights the importance of considering both top-down and bottom-up processes in determining the abundance, distribution and habitat preferences of wildlife, especially where predator guilds differ geographically.

2.2 Introduction

Wildlife conservation and management requires robust information on the distribution and habitat preferences of focal species (Margules and Pressey 2000). For many species, particularly those that are threatened, naturally rare, or cryptic, quantitative information on habitat requirements is lacking, and distributions are not well resolved. Accurate prediction of the likelihood of species occurrence in unsurveyed locations is essential for land managers with responsibility for landscape-scale conservation of threatened species and their habitats. Species distribution models (SDMs) provide a powerful means of relating information on species occurrence or abundance to environmental determinants of distribution (Austin 2002; Hirzel and Le Lay 2008). Spatially predicted maps of habitat suitability from SDMs have been used to assist conservation prioritization and planning (Araujo and Williams 2000; Ferrier *et al.* 2002), identify regions and habitat important for species recovery (Cianfrani *et al.* 2010; Davis *et al.* 2007; Gavashelishvili and Lukarevskiy 2008; Jedrzejewski *et al.* 2008; Spencer *et al.* 2011), and locate suitable areas for reintroductions (Schadt *et al.* 2002). Thus, SDMs are often used as a first step to improve ecological understanding of species-habitat relationships and develop conservation management strategies (Carroll *et al.* 2001; Le Lay *et al.* 2010; Thorn *et al.* 2011).

Although SDMs commonly include only abiotic variables describing the fundamental niche, in reality, species occurrence and distribution is often strongly influenced by biotic

components of the environment, such as predators and competitors (Cianfrani *et al.* 2010; Marcer *et al.* 2013). On the largest scale, competition may exclude a species from a given habitat (Anderson *et al.* 2002; Creel *et al.* 2001). For example, dogs (*Canis familiaris*) negatively influence the spatial distribution of the Indian fox (*Vulpes bengalensis*) at the landscape level, and may exclude them from accessing high quality habitat (Vanak and Gompper 2010). Therefore, interspecific interactions can be an important determinant of distribution, abundance, and observed environmental associations by enforcing ecological and geographical separation.

Mammalian predators often possess intrinsic biological traits such as low population density and large area requirements that render them vulnerable to threatening processes (Purvis *et al.* 2001). These traits also mean that carnivores are frequently rare, cryptic, and difficult to detect during surveys. Consequently, information on their distribution, habitat requirements and status is often uncertain or incomplete (Le Lay *et al.* 2010; Thorn *et al.* 2011). Carnivore species have important effects on ecosystem structure, function, and resilience (Estes *et al.* 2011; Ritchie and Johnson 2009). Therefore, the protection and recovery of populations of terrestrial mammalian carnivores, including identification and preservation of important habitat, is a primary focus of conservation management globally (Dalerum *et al.* 2009; Gittleman *et al.* 2001; Sergio *et al.* 2008).

The spotted-tailed quoll (*Dasyurus maculatus*) is a medium-sized marsupial predator endemic to eastern Australia, where it occurs as two subspecies: the northern spotted-tailed quoll (*Dasyurus maculatus gracilis*) and the south-eastern mainland spotted-tailed quoll (*Dasyurus maculatus gracilis*). The southern subspecies occurs as two genetically distinct subpopulations: south-eastern mainland and Tasmanian. The species is naturally rare, owing to its obligate carnivory, large home range size, female territoriality, and low lifetime fecundity,

and is also listed as threatened under the Australian Commonwealth Environmental Protection and Biodiversity Conservation Act 1999 (EPBC 1999), largely due to habitat loss and competition with introduced predators (Long and Nelson 2010; Maxwell *et al.* 1996). To date, the majority of information on the habitat requirements of the Tasmanian spotted-tailed quoll derives from south-eastern mainland Australian populations, where quoll occurrence is most strongly associated with large, contiguous tracts of high elevation forest in areas of high annual mean rainfall (Catling *et al.* 2002; Mansergh 1984). In contrast, the status and distribution of the Tasmanian subspecies is poorly understood, hindering its effective conservation management (Jones and Rose 1996). The Tasmanian spotted-tailed quoll has been isolated from mainland populations for ~13,000 years (Firestone *et al.* 1999; Lambeck and Chappell 2001). It occurs within a guild of predators and assemblages of prey that now differ significantly from mainland Australia, in respect of the historical absence of the European red fox (*Vulpes vulpes*) and presence of another dasyurid, the larger Tasmanian devil (*Sarcophilus harrisi*), both of which are known to exert top-down control on smaller predators (Dexter and Murray 2009; Hollings *et al.* 2014; Kinnear *et al.* 2002). It is unclear whether extrapolation of knowledge of the ecology of the spotted-tailed quoll from mainland populations to the management of the Tasmanian subspecies is valid. The potential for establishment of the red fox following recent (~ 1999) introductions (Sarre *et al.* 2013), predicted increases in quoll abundance with devil decline, and high rate of conversion of native forest to other land uses all highlight the need for better information with which to manage the Tasmanian spotted-tailed quoll.

The goal of this study is to better understand the factors determining the distribution and abundance of the Tasmanian spotted-tailed quoll to assist in its conservation management. Specifically, we aim to test the role of bottom-up environmental processes and potential for top-down interspecific competition from the devil in driving the distribution and abundance of

the Tasmanian spotted-tailed quoll. To this end, we have two hypotheses. First, on the basis of prior knowledge from both mainland and Tasmanian subspecies, we expect the Tasmanian spotted-tailed quoll to be most abundant in warm, wet, densely forested areas (Catling *et al.* 2002; Jones and Rose 1996; Mansergh 1984) . Second, because competition from the larger devil is hypothesised to restrict the abundance and habitat preferences of the Tasmanian spotted-tailed quoll (Jones and Barmuta 2000), we expect to find a significant negative effect of devil habitat suitability on spotted-tailed quoll abundance. The feral cat is also distributed throughout Tasmania, and as a potential competitor of the spotted-tailed quoll (Glen and Dickman 2008, Glen *et al.* 2011) could also be expected to have an effect on its abundance and distribution. However, there were insufficient data on cat distribution, abundance or habitat suitability to assess the effect of feral cats on spotted-tailed quoll abundance in this study.

I use mapped habitat suitability as predicted by the SDM to assess the spatial characteristics of preferred habitat in relation to reservation status and land tenure to identify areas where the Tasmanian spotted-tailed quoll is particularly susceptible to potential habitat loss through land use change and to identify priority areas and stakeholders for quoll management. Finally, I compare predicted habitat suitability of the Tasmanian spotted-tailed quoll to model-predicted habitat suitability for the introduced red fox (Sarre *et al.* 2013) to evaluate the threat that this potential competitor poses.

2.3 Methods

2.3.1 Study location

This study spans the full extent of the island state of Tasmania, Australia (Figure 2.1). Tasmania has a cool maritime climate that is characterised by mild to warm summers and cool

winters. This climate, combined with substantial variation in elevation, geology, and precipitation, has resulted in a complex mosaic of vegetation communities, including temperate rainforest, sclerophyll forest, coastal scrub and heath, sedge, and grasslands (Jackson 2005).

2.3.2 Field data collection

Trapping surveys were conducted by researchers from the Tasmanian Department of Primary Industries, Parks, Water and Environment and the University of Tasmania between 2004 and 2011 inclusive. The primary intent of trapping was to detect the presence of Devil Facial Tumour Disease (DFTD) in the Tasmanian devil, and to investigate disease induced changes in population trends. Trapping regions were selected to sample variation in devil population density, and spatial and temporal aspects of DFTD distribution (Hawkins *et al.* 2006; Lachish *et al.* 2007). Although the purpose of these surveys was to capture the Tasmanian devil, the spotted-tailed quoll was frequently trapped as by-catch, and in fact both of these carnivore species can be detected using identical field survey methods (e.g. Jones and Barmuta 1998).

Each trapping trip was between three and ten nights in duration and trap locations covered a region of approximately 25-35 km². PVC pipe traps (diameter 315 mm, length 875 mm) baited with a variety of meats were set a minimum of 200 m apart in areas that were considered likely to intercept the movements of marsupial carnivores, as judged by the presence of animal trails, drainage lines, saddles, and road junctions. Traps were set in a wide range of vegetation communities, and sampled the majority of the extent of the spotted-tailed quoll's known distribution (Figure 2.1). The position (± 10 m) of each trap was recorded on a handheld GPS unit (Garmin 76CSX), and mapped in ArcGIS v 9.2 (ESRI, Redlands, California, USA).

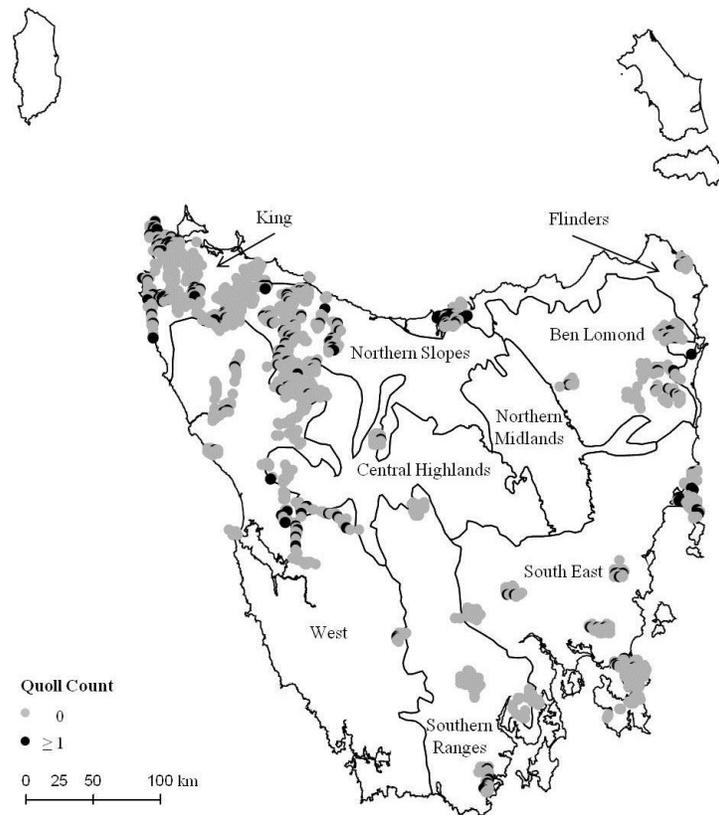


Figure 2.1: Location of trap sites across Tasmania, Australia. Black lines indicate Interim Biogeographic Regionalisation for Australia 6.1 (IBRA) bioregion boundaries.

Some locations were surveyed once, while others were surveyed repeatedly, both seasonally and/or annually (Figure 2.2). To ensure a comparable and representative sample was used in analysis, only one trapping survey for each location was selected for modelling. We selected the survey with the highest adult spotted-tailed quoll trap-rate to maximise the prevalence of positive counts in our response data. The consistent relative abundance of quolls at localities that were surveyed more than once suggests that our strategy of selecting data from just one trapping survey for modelling is a reliable representation of spotted-tailed quoll abundance at those locations (Figure 2.2). The Narawntapu population is a notable exception to this; data collected subsequent to July 2007 were not considered in analyses.

2.3.3 Spotted-tailed quoll data

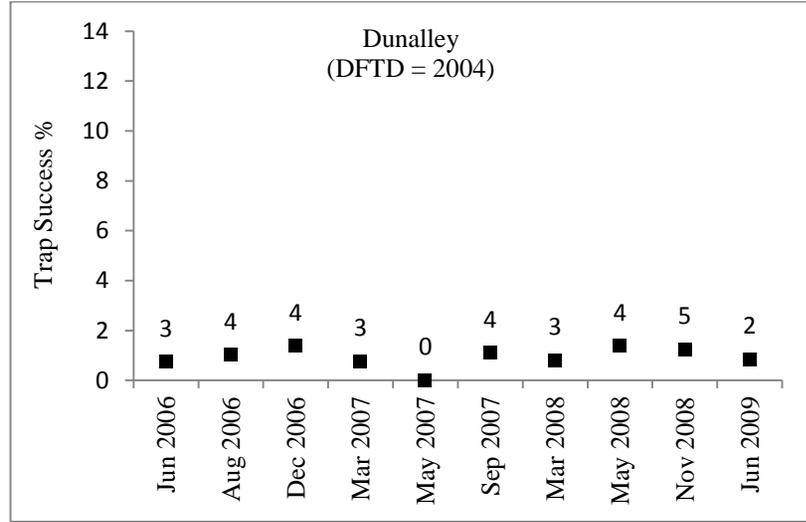
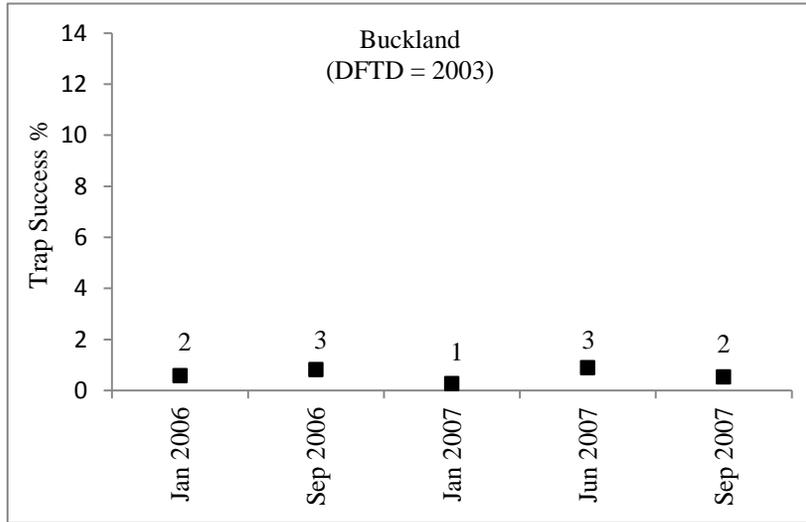
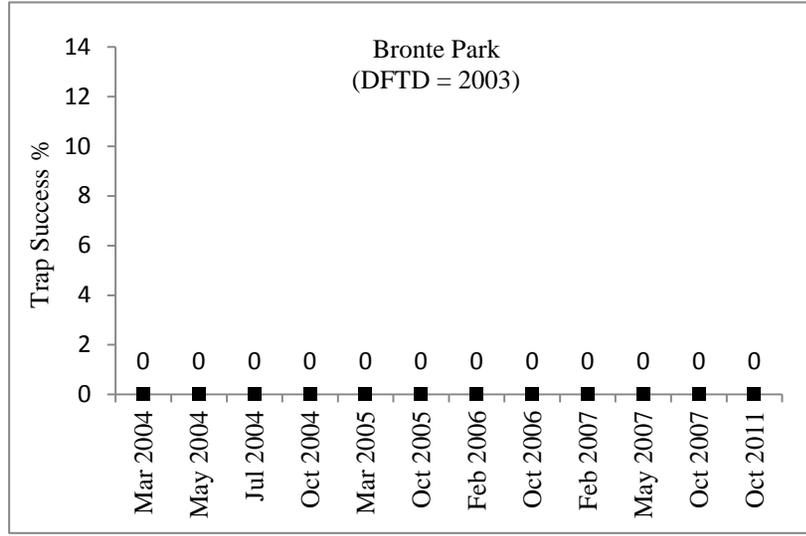
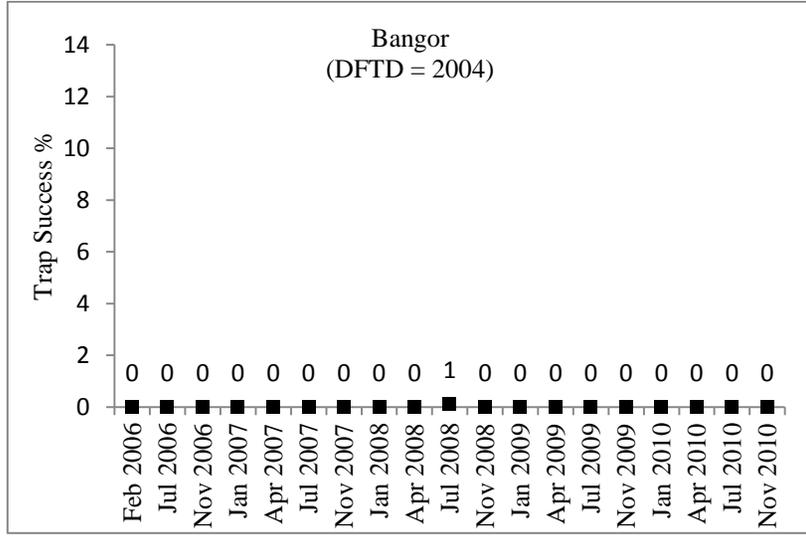
Individual trap sites were treated as separate data points, which were imported into ArcGIS v 9.2 (ESRI, Redlands, California, USA) and aggregated into 1 km² grid cells. A 1 km² resolution approximates the smallest home range size recorded for the spotted-tailed quoll, and was expected to represent the spatial scale at which spotted-tailed quolls respond to their environment (Andrew 2005; Belcher and Darrant 2004; Claridge *et al.* 2005; Glen and Dickman 2006b; Nelson 2007). On first capture each quoll was uniquely micro-chipped for future identification (Allflex ®, New Zealand). This provided us with a total count of the number of individual quolls recorded at each trap. Quolls were also weighed and sexed. When combined with information on time of year, these data allowed us to determine the age class of individuals (adult female > 1.6 kg, adult male > 2.6 kg Jones and Barmuta 1998). We used only adult quoll records for model building, because their habitat associations are more likely to reflect preference than are the habitat requirements of subadults, which may be dispersing or may occupy suboptimal habitat due to competition from larger intraspecifics. Values for the total number of unique individual quolls captured were summed, and stored in a 1 km² grid cell spatial layer. This count of spotted-tailed quolls across 1, 679 grid cells formed the modelling response data.

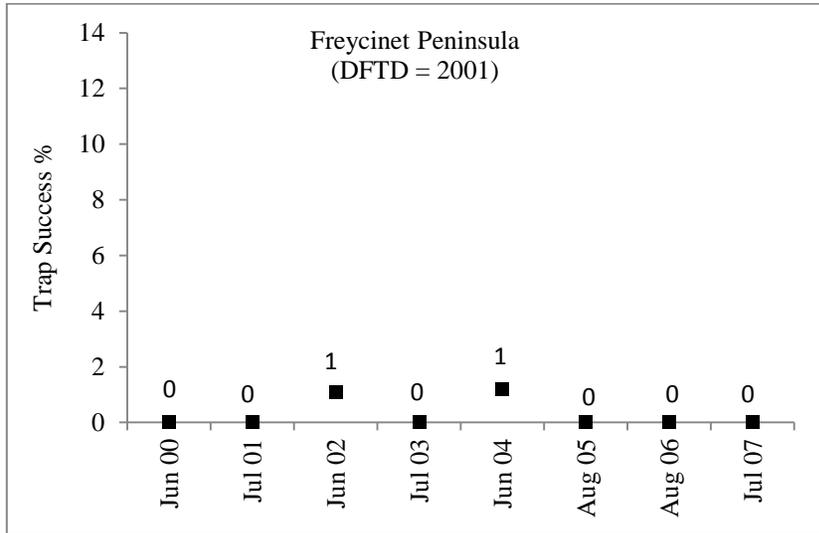
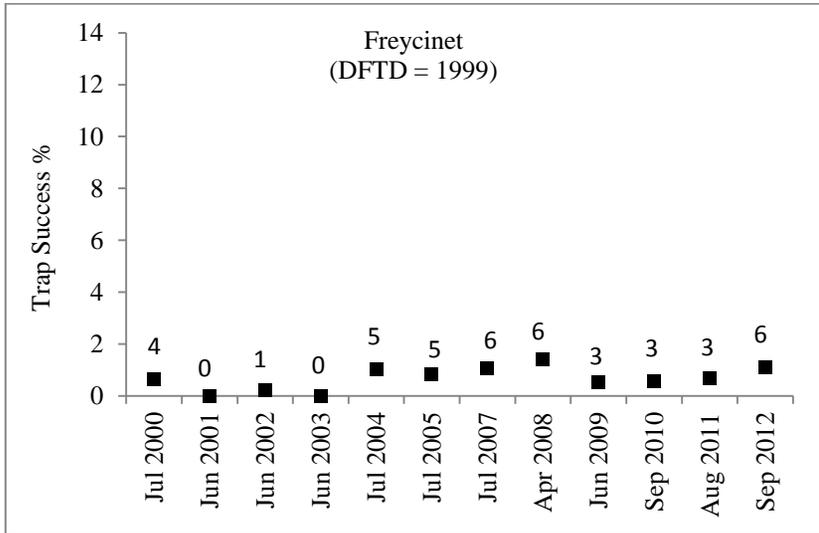
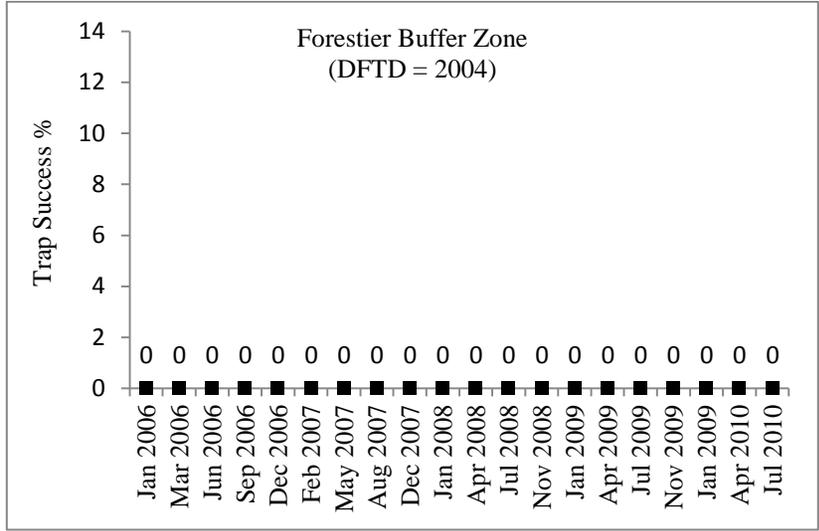
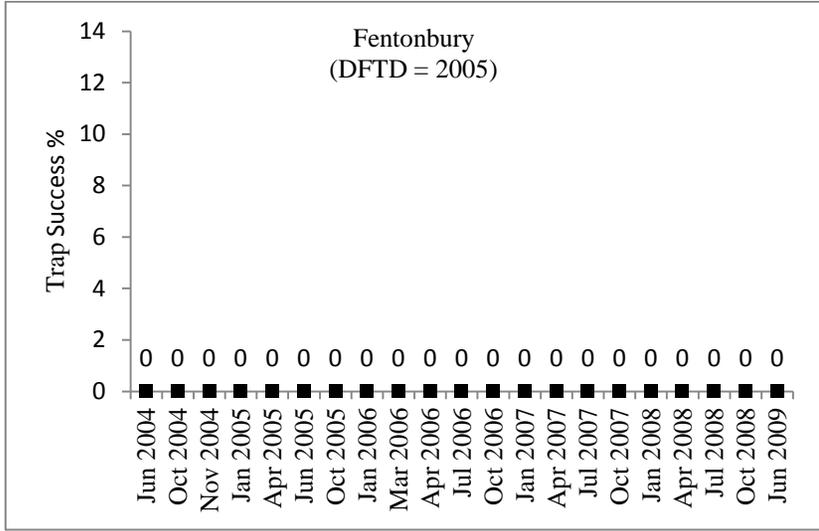
2.3.4 Predictor variable data

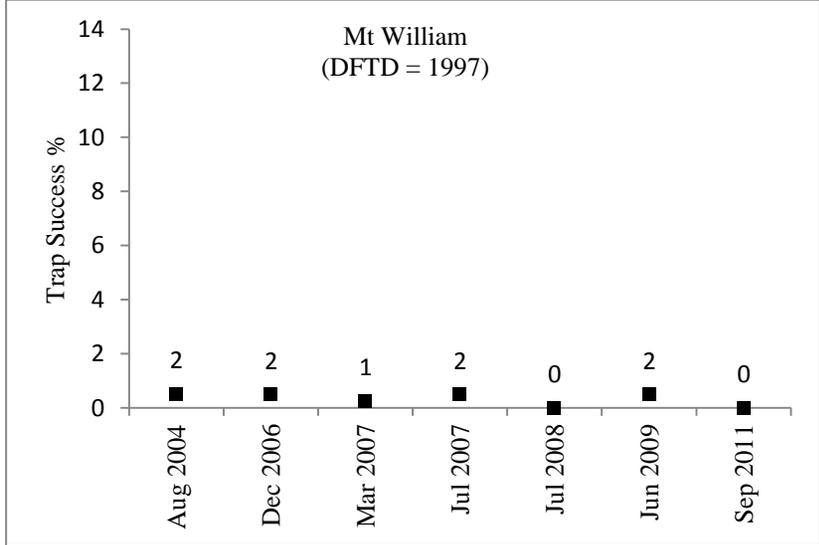
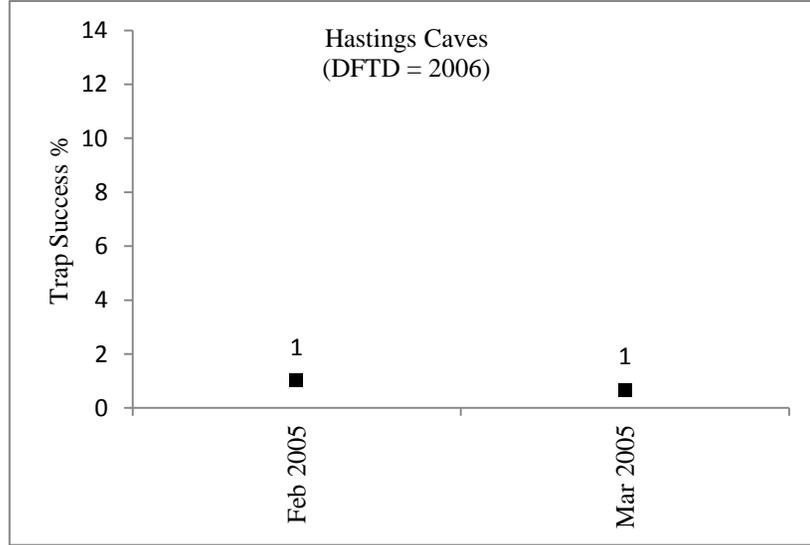
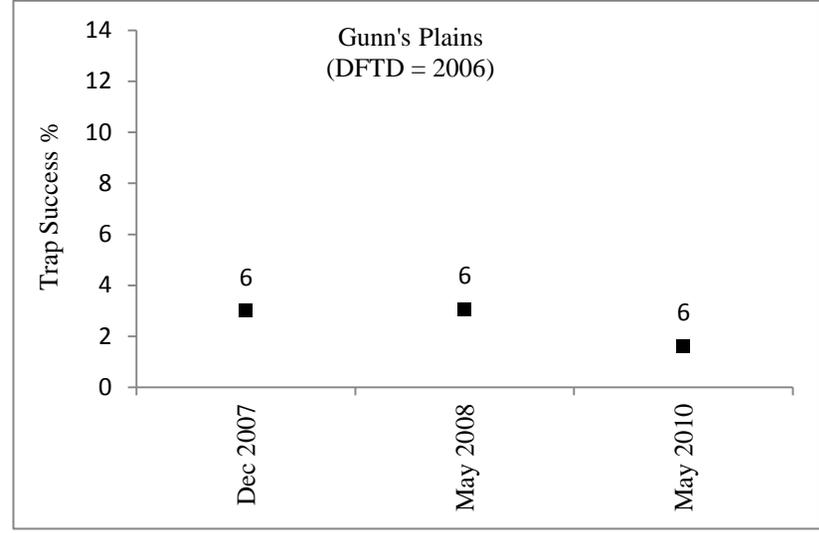
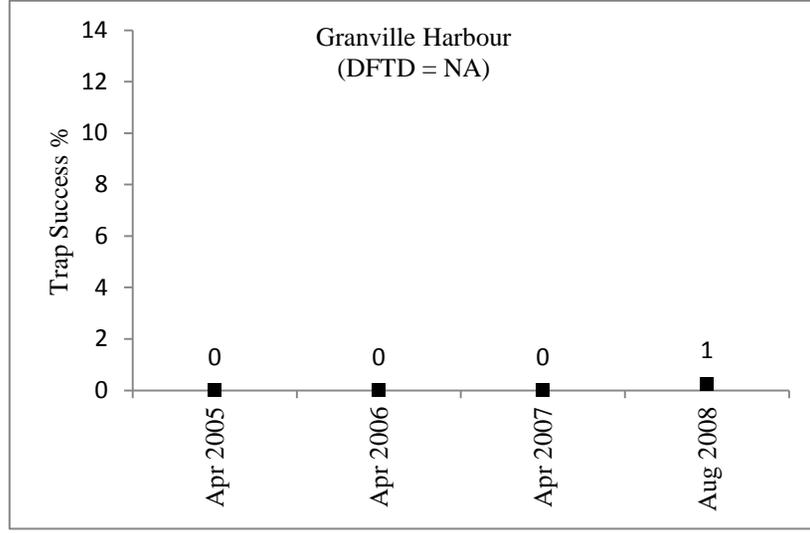
Spatial environmental data were compiled from a range of digital sources (Table 2.1), imported into ArcGIS v 9.2 (ESRI 2006) and rasterized at 100 m² resolution for GIS analysis. We developed a preliminary set of 17 candidate environmental covariates that were considered likely to influence the spotted-tailed quoll's ecological requirements (Table 2.1, Jones and Rose

1996, Mansergh 1984, Belcher and Darrant 2006, Belcher 2008, Jones and Barmuta 1998, 2000, Green and Scarborough 1990, Rounsevelle 1991). To obtain the proportion of each vegetation community and forest structure type in each 1 km², we used a moving window that assigned to each focal grid cell the mean value of the 100 cells in the surrounding 1 km² neighbourhood. We constructed a forest fragmentation index (GYRATE) in the program FragStats 3.3 by using a moving window that assigned to each forest focal cell the mean distance to every other forest cell that fell within the surrounding 1 km² neighbourhood (McGarigal *et al.* 2002).

To investigate the relationship between the occurrence of quolls and their main competitor, the Tasmanian devil, we included an index of predicted habitat suitability for the Tasmanian devil. It was not possible to use direct estimates of devil abundance due to the arrival of DFTD because state-wide data (e.g. every cell has a value) is needed for spatial prediction of the SDM. It was also not sensible to build a separate habitat model for the devil using abundance data from the same survey as that used for the spotted-tailed quoll, because devil decline is independent of habitat factors. Thus, predicted devil habitat suitability was derived from a species distribution model that used presence records collected prior to the arrival of DFTD, climate data, and the Maximum Entropy algorithm to delineate probability of devil occurrence State-wide (Johnson *et al.* 2012). As quoll relative abundance appeared independent of time since DFTD arrival (Figure 2.2), we assumed that the pre-DFTD habitat suitability was likely to be a reasonable proxy of devil abundance.







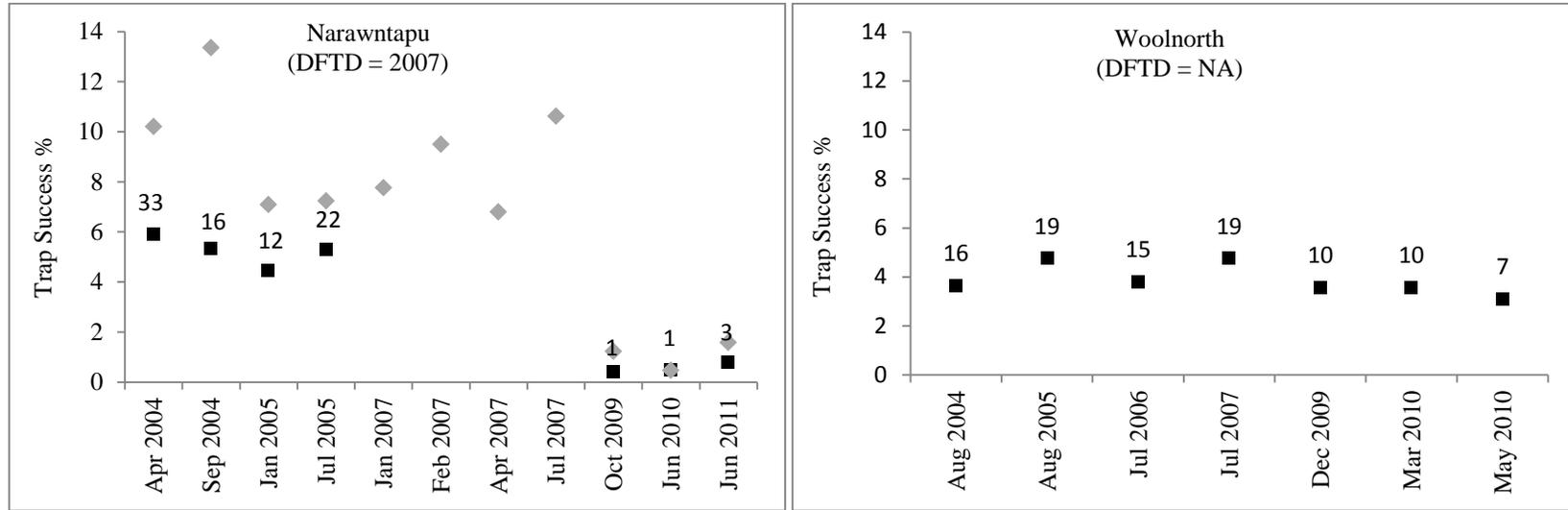


Figure 2.2: Abundance of the spotted-tailed quoll across sites and years for localities surveyed more than once. Plot title gives site name. DFTD = year indicates the year that Devil Facial Tumour Disease (DFTD) arrived at the site. Y-axis gives trap success: black squares = number of individual adult quolls trapped / number of trap nights * 100, gray diamonds (Narawntapu only) = number of quoll captures / number of trap nights * 100. X-axis gives dates of trapping survey. Labels above data points indicate number of unique spotted-tailed quolls.

After covariates were derived, data were aggregated to 1 km² to match the resolution of the spotted-tailed quoll relative abundance data. The modelling dataframe was constructed by sampling the value of environmental covariates at each quoll sample site using the extract tool in the Spatial Analyst extension of ArcGIS v 9.2. Each row of data contained the survey observation (0 = species absent, ≥ 1 species present) and values for each of the candidate covariates at the sample sites. The dataframe was then exported to R 3.0 (R Core Team 2013) for data exploration and analysis. Inclusion of correlated covariates may induce instability in parameter estimation in regression models (Quinn and Keough 2002). We removed eight potential environmental covariates from candidacy because they were correlated (Spearman's $r > 0.6$) with another predictor that was considered a more proximal variable (Austin 2002), leaving nine environmental covariates available for modelling (Table 2.1).

2.3.5 Data analysis

Our response data had a high frequency of zero counts, with 90 % of data points having a value of zero. In addition, the variance of the response data was almost double the mean (mean 0.142, variance 0.257) indicating some overdispersion in the response data. Overdispersion can occur due to a large proportion of zero counts, high variation in the positive (≥ 1) count data, or both (McCullagh and Nelder 1989). A high proportion of zero counts can arise from two situations: true zeros, where a species is absent from many sites because it is intrinsically rare, or because of ecological conditions; and false zeros, where a species is present at a site but not detected due to sampling error (Martin *et al.* 2005; Potts and Elith 2006). Given the natural rarity and cryptic nature of the spotted-tailed quoll, the zeros in our data are likely to a mixture of both true and false zeros. To date, no method to model data sets that contain both excess true zeros and false zeros has been developed (Martin *et al.* 2005).

Predictor Variable	Predictor Variable Description	Expected Response
<u>Climate</u>		
Annual Mean Temperature ¹	Annual mean temperature (mm)	Positive
Annual Mean Precipitation ¹	Annual mean precipitation (mm)	Positive
Rainfall Seasonality ¹	Coefficient variation of mean monthly precipitation (mm)	Positive
Driest Month Precipitation ¹	Precipitation of driest month (mm)	Positive
Wettest Quarter Precipitation ¹	Precipitation of wettest three months of the year (mm)	Positive
<u>Terrain</u>		
Elevation ²	Cell elevation (meters above sea level)	Negative
Topographic Ruggedness ²	Standard deviation in elevation. Flat sites have low values	Positive
<u>Vegetation Community</u>		
Dry Eucalypt Forest ⁴	Proportion of dry eucalypt forest in 1 km ² site	Negative
Wet Eucalypt Forest ⁴	Proportion of wet eucalypt forest in 1km ² site	Positive
Rainforest ⁴	Proportion of rainforest in 1km ² site	Positive
Forest Cover ⁴	Proportion of native forest in 1km ² site	Positive
Agricultural ⁴	Proportion of agricultural land in 1km ² site	Negative
<u>Forest Structure</u>		
Low Eucalypt Forest ⁵	Proportion of low eucalypt forest in 1km ² site	Negative
Tall Eucalypt Forest ⁵	Proportion of tall eucalypt forest in 1km ² site	Positive
<u>Fragmentation</u>		
Forest Fragmentation Index ⁴	Radius of gyration	Negative
<u>Competition</u>		
Devil Habitat Suitability	Index of devil habitat suitability	Negative
<u>Survey Effort</u>		
Effort	Number of traps * Number of nights	Asymptote

Table 2.1: List and description of potential candidate covariates. Covariates in bold were used in model building; covariates not in bold were correlated and removed from candidacy.

¹BIOCLIM variables ²Digital Elevation Model (DEM) from Geoscience Australia elevation data ³Derived from 1:250,000 Geology layer, Mineral Resources Tasmania ⁴Tasmanian Department of Primary Industries, Parks, Water, and Environment ⁵TasVeg 2.0 and ⁶Forest Groups data.

We initially planned to model the data within a site occupancy framework to account for false zeros, with joint estimation of the influence of habitat covariates on both abundance and detectability (MacKenzie *et al.* 2002). However, differences in survey length among sample sites and the short period of surveys at some sample sites resulted in low detection probability and associated non-convergence of models, so this method of analysis was not possible. We therefore used generalised linear models (GLMs) to model the relationship between the relative abundance of quolls and their environment. GLMs were fit with a negative binomial distribution, which we found provided better fit than the Poisson distribution and equivalent fit to the zero-inflated Poisson and zero-inflated negative binomial distributions during preliminary analysis.

2.3.6 Model selection

Traditional model selection approaches such as stepwise selection, that use probability thresholds to select a single “best” model, ignore the model uncertainty that commonly arises where two or more models have a similar level of support (Burnham and Anderson 2002; Wintle *et al.* 2003), which can result in underestimation of the importance of predictor variables, and overconfidence in model predictions (Grueber *et al.* 2011; Wintle *et al.* 2003). To account for this uncertainty we used a model averaging approach, which provides a robust means of making inference and predictions from a set of models in cases where two or more models have a similarly high level of support (Burnham and Anderson 2002). We first fitted a global model with all nine predictor variables, and then generated a set of candidate models that included all possible combinations of predictor variables using the R package MuMIn (Bartoń 2013). Although the “all subsets” approach has justly been cautioned against (Burnham and Anderson 2002), in this case we had *a priori* reason to believe that the candidate predictor

variables we chose contributed to quoll distribution (Table 2.1), making all sub-models ecologically plausible. In addition, our aim was to determine the relative importance of these variables and to make inference and predictions with estimates of precision that account for uncertainty in model selection. Furthermore, as recommended by (Burnham and Anderson 2002), the total number of candidate models ($n = 1,024$) did not greatly exceed the number of observations ($n = 1,679$).

Candidate models were ranked according to their conditional Akaike Information Criterion (AICc) value and assigned an Akaike weight (w_i), which represents the probability of each model being the ‘best’ model for the observed data, given all other alternative models (Burnham and Anderson 2002). A 95% confidence model set was generated by summing the Akaike weights until the total ≤ 0.95 . We also used the Akaike weights to calculate the relative importance of each predictor variable, by summing the weights of all models in which the parameter of interest appears (Burnham and Anderson 2002). Coefficients and standard errors were then averaged over the 95% confidence set to determine the magnitude and direction of the influence of the predictor variables on spotted-tailed quoll relative abundance.

2.3.7 Model evaluation

We assessed model adequacy by evaluating model fit and predictive performance. Global model fit was assessed quantitatively by estimating a pseudo- R^2 (Cameron and Trivedi 2013), and qualitatively by examination of plots of residuals against fitted values. We checked for spatial autocorrelation in global model residuals by plotting spline correlograms with 95% bootstrap confidence intervals and a lag interval of 1 km over a maximum distance of 30 km (R package *ncf*; Bjornstad and Falck 2001). Ideally, the predictive accuracy of our models would be assessed by their ability to correctly predict relative abundance in a spatially and temporally

independent data set. In the absence of an independent data set, we evaluated predictive accuracy using 10-fold cross-validation (Stone 1974). We divided the data into ten subsets, used nine subsets as training data on which model selection was conducted (as described above), and then predicted 95% model averaged to the held out tenth subset that was used as validation data. This process was repeated ten times so each of the ten subsets acted as validation data once.

Predictive performance was then assessed using three measures: Pearson's correlation coefficient r ; calibration intercept; and calibration slope (Potts and Elith 2006). Pearson's r provides an indication of the strength of agreement between observed relative abundance values and values predicted from the models. The calibration intercept and slope were derived from a simple linear regression between the observed and predicted values, using the mean and standard error of the regression slope and intercept across all ten folds. Where a model is perfectly calibrated, this regression has an intercept of zero and slope of one. A calibration intercept that differs from zero is evidence of positive or negative bias in predictions, while the slope provides information on the numerical spread of predictions relative to the observations (Potts and Elith 2006).

2.3.8 *Spatial prediction*

We used averaged coefficients from the 95% model set to predict spotted-tailed quoll relative abundance at every 1 km² cell in Tasmania. To account for the effect of trap effort, a dummy variable was created that held trap effort constant at 70 trap nights per 1 km² per 7 night survey period, which was the median value for the modelling data, and an effort commonly achieved in the field. The model averaged mean and upper and lower 95% confidence intervals of predicted relative abundance were then imported into ArcGIS and

displayed as continuous values. Predictions were displayed relative to the Interim Biogeographic Regionalisation of Australia 6.1 (Thackway and Cresswell 1995), which represents ecosystem boundaries, and is the reporting unit for the protection of native ecosystems in the Australian reserve system.

To delineate important habitat, we divided our predictions into two categories, core and potential range, as defined by the Threatened Fauna Adviser, a conservation planning tool used for forest fauna in Tasmania and an end user of this research (FPA 2014). We defined core range as all predicted values above the median predicted value; and potential range as predicted values below the median value. To identify priority areas and stakeholders for future quoll conservation management actions, we investigated the proportion of predicted core distribution occurring on reserved land and on private land by bioregion within the Tasmanian spotted-tailed quoll's current distribution (e.g. excluding offshore islands).

2.3.9 Fox-quoll overlap

To investigate the threat that the introduction of the red fox may pose to the Tasmanian spotted-tailed quoll in the future, we calculated the percent overlap in highest suitability quoll and fox habitat suitability for each bioregion and state-wide. For the fox, we used the threshold habitat suitability predictions (Sarre *et al.* 2013), which comprised the top 20% of predicted values. We thus used the top 20% of predicted quoll relative abundance values for comparison. We refer to these top 20% of predictions as “optimal habitat”.

2.4 Results

2.4.1 Trapping results

Spotted-tailed quolls were detected in 173 of the 1,679 1 km² grid cells. The number of detections per 1 km² cell was also low, with between 0 and 7 individuals detected. Our sampling effort covered approximately 2.5% of Tasmania's total area, and 8 of the 9 bioregions (Figure 1, Table 2.2). Relative abundance was low across all sites, although three locations (Woolnorth, Narawntapu, and Arthur River) were notable for their particularly high trap rates (Figure 2.2).

Bioregion	Area (km²)	Sampled Area (km²)	Sampled Area (%)
Ben Lomond	6571	112	1.70
Central Highlands	7673	193	2.52
Flinders	4717	58	1.23
King	4118	373	9.06
Northern Midlands	4151	0	0.00
Northern Slopes	6231	305	4.89
South East	10974	296	2.70
Southern Ranges	7774	118	1.52
West	15508	224	1.44
Tasmania Total	67717	1679	2.48

Table 2.2: Characteristics of sampling effort for the spotted-tailed quoll within each Interim Biogeographic Regionalisation for Australia 6.1 (IBRA) bioregion and across Tasmania, Australia.

2.4.2 Model selection

The 95% confidence set of models contained 63 models and the top model carried just 4.7 % of weight, indicating considerable model uncertainty (Appendix 2.1). The role of three of the nine predictor variables was clear. As predicted, spotted-tailed quoll relative abundance had an asymptotic relationship with trap effort, and a consistent positive association with annual

mean temperature and rainfall seasonality (Table 2.3, Figure 2.3). Although the direction and magnitude of the effect of the remaining six predictor variables was consistent among models in the 95% confidence set, their relative importance and thus effect on quoll relative abundance was lower (Table 2.3). Contrary to our expectations, there was a weak negative association between quoll relative abundance and the proportion of native forest and wet eucalypt forest cover, annual mean precipitation, and topographic ruggedness, and a positive relationship between quoll relative abundance and the proportion of cleared agricultural land (Figure 2.3, Table 2.3). In line with our predictions, there was a negative association between quoll relative abundance and devil habitat suitability, however this variable had low relative importance and the relationship was weak and non-significant (Table 2.3, Figure 2.3).

	Estimate	SE	Relative Importance
Annual Mean Temperature*	0.441	0.080	1
Trap Effort*	0.071	0.011	1
Trap Effort ² *	-0.001	0.000	1
Rainfall Seasonality*	0.031	0.012	1
Agriculture	0.539	0.380	0.53
Wet Eucalypt Forest	-0.470	0.368	0.46
Forest Cover	-0.364	0.314	0.44
Devil Habitat Suitability	-0.865	0.788	0.42
Annual Mean Precipitation	-0.004	0.036	0.31
Topographic Ruggedness	-0.002	0.006	0.27

Table 2.3: Model averaged coefficients estimates and their standard errors and relative importance of environmental covariates for the negative binomial generalised linear model of spotted-tailed quoll abundance. * indicates statistical significant (p value < 0.05).

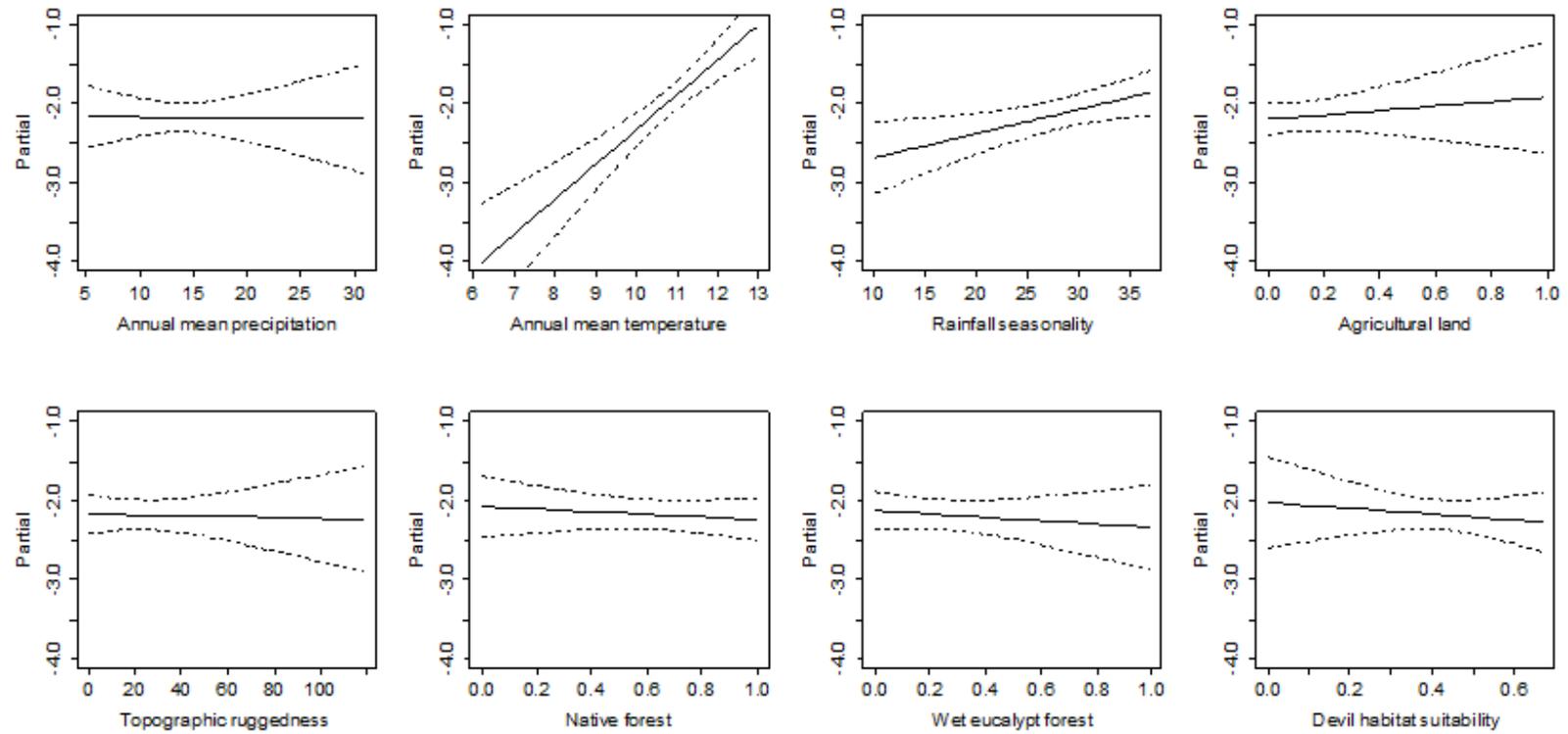


Figure 2.3: Partial dependence plots for predictor variables. Y = marginal effect, represents response of spotted-tailed quoll to predictor variable with all other predictor variables held at their mean. Plot on bottom of graph indicates the degree of sampling across values of predictor.

2.4.3 Model evaluation

Pseudo- R^2 values for models in the 95% confidence set revealed that the averaged model explained between 17.9% and 18.3% of variation in quoll relative abundance. Although there was significant positive spatial autocorrelation in the response data, model residuals were spatially independent (Appendix 2.2).

Evaluation of predictive performance from cross-validation revealed that the model had a low correlation ($r = 0.377$, $SE = 0.046$) between observed and predicted values, but that the model was well calibrated, with the intercept means not significantly different from zero (intercept = -0.021 $SE = 0.024$) and a slope means having a value close to one (slope = 1.182 $SE = 0.248$). These results indicated that although the model has a high amount of error around predictions, on average the predictions were accurate and unbiased.

2.4.4 Spatial prediction

Spotted-tailed quoll relative abundance was predicted to be highest in the north and west of the state, especially in coastal areas (Figure 2.4). The King, Flinders, and Northern Midlands bioregions contained the highest proportions of predicted core distribution, with 49-100% of predicted core distribution occurring on private land and 92-100% outside of the Tasmania's formal reserve system (Figure 2.4, Table 2.4). State-wide, approximately 89% of predicted core distribution occurs on private land, with a minimum of 49% per bioregion. While quoll habitat is well protected by the reserve system in the Central Highlands, in all other bioregions 92-100% of the predicted core distribution occurs in areas outside of reserves (Figure 2.4, Table 2.4).

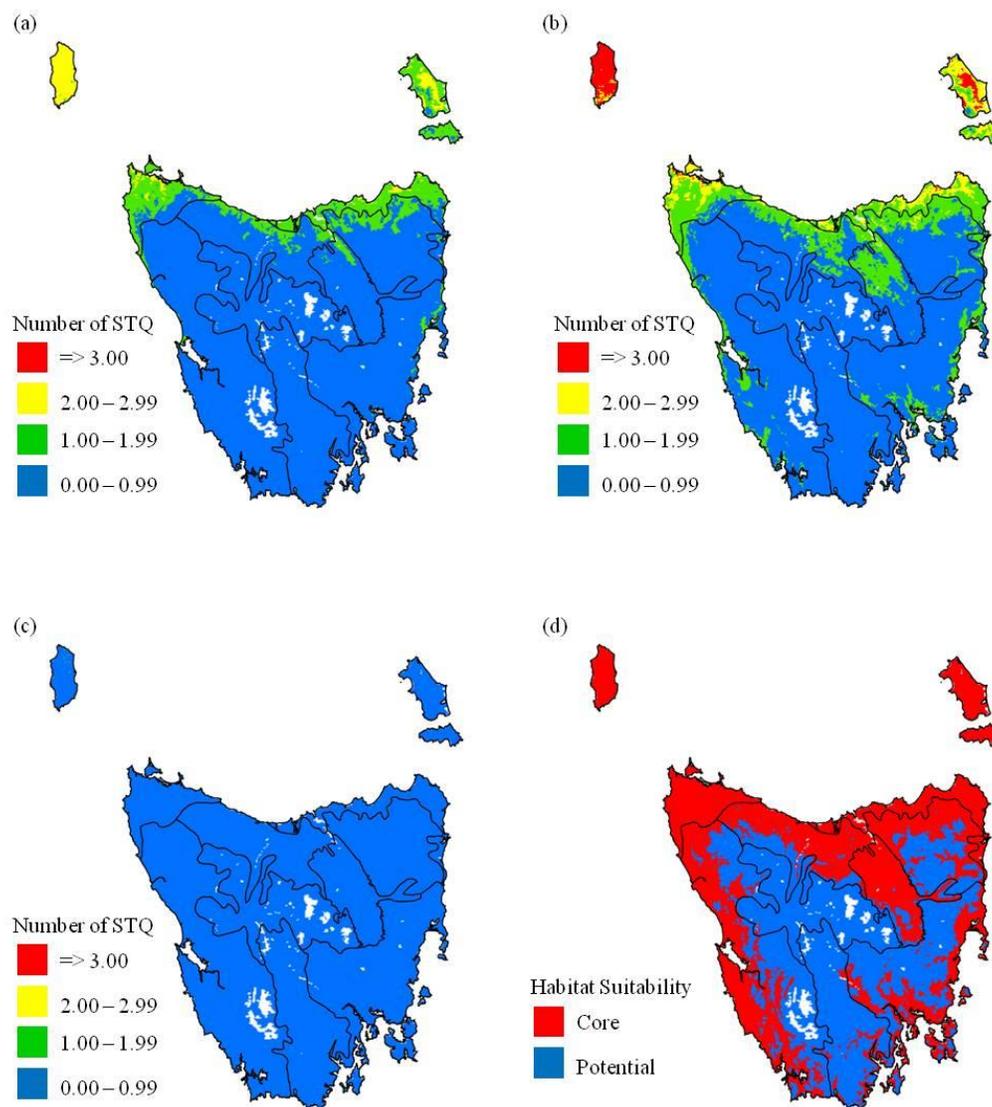


Figure 2.4: Mean predicted values of Tasmanian spotted-tailed quoll relative abundance (a), upper 95% (b) and lower 95% (c) confidence intervals, and (d) predicted potential abundance delineated into core and potential habitat from the model averaged negative binomial GLM. Black lines indicate Interim Biogeographic Regionalisation for Australia 6.1 (IBRA) bioregion boundaries.

Bioregion	Bioregion %	Private Land %	Dedicated Reserve %	Fox-Quoll Overlap %
Ben Lomond	55.09	28.76	0.65	22.24
Central Highlands	1.11	44.71	0.01	0.00
Flinders	94.06	66.71	7.86	58.51
King	96.92	48.40	1.52	13.88
Northern Midlands	82.65	98.60	0.34	93.47
Northern Slopes	70.65	67.72	0.87	47.05
South East	37.41	87.64	2.31	77.26
Southern Ranges	10.33	55.46	2.11	0.00
West	50.57	6.08	19.66	0.51
State Total	48.31	53.44	12.96	42.32

Table 2.4: Characteristics of predicted habitat suitability for the spotted-tailed quoll within each Interim Biogeographic Regionalisation for Australia (IBRA) bioregion, excluding area of and predictions to offshore islands. Bioregion % = percent of sites classified as core distribution within each bioregion; Private Land % = percent of core distribution occurring on private land. Dedicated Reserve % = percent of core distribution occurring in dedicated reserves. Fox overlap indicates the percent of optimal fox habitat that overlaps with optimal quoll habitat in each bioregion, where optimal delineates the top 20% of predicted values for each species.

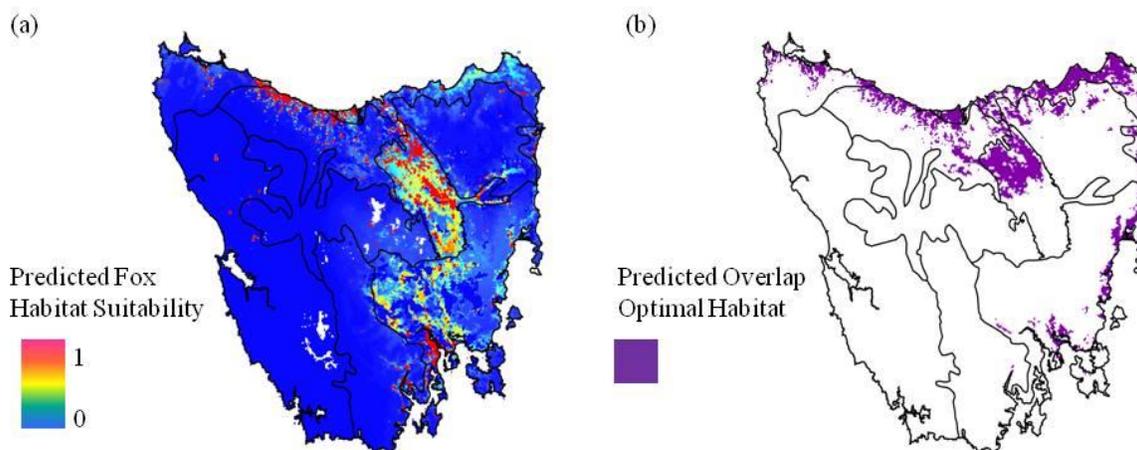


Figure 2.5: (a) Predicted values of red fox probability of occurrence (habitat suitability) for Tasmania (data from Sarre et al 2013). Values range from 0 to 1 where 0 is unsuitable and 1 is most suitable. (b) Predicted extent of spatial overlap in the top 20% of predictions of spotted-tailed quoll abundance and red fox probability of occurrence. Black lines indicate Interim Biogeographic Regionalisation for Australia 6.1 (IBRA) bioregion boundaries.

2.4.5 Fox-quoll overlap

State-wide, optimal habitat for the red fox coincided with 42% of optimal spotted-tailed quoll habitat (Figure 2.5, Table 2.4). Per bioregion, the most extensive overlap was in Northern Midlands (93%), Flinders (77%) and Flinders (59%) (Figure 5b, Table 2.4), while overlap was lowest in the Central Highlands (0%), Southern Ranges (0%) and West (0.5%).

2.5 Discussion

This study has provided novel insights into role of bottom-up environmental factors and top-down control from larger predators in driving the distribution and abundance of the Tasmanian spotted-tailed quoll. Annual mean temperature and rainfall seasonality were the strongest environmental correlates of spotted-tailed quoll abundance, with other variables previously proposed to relate to quoll occurrence having less support. The model predicted that Tasmanian spotted-tailed quoll abundance is highest in the north and northwest of the state. A large proportion of the predicted core distribution occurs on private land outside of the reserve system, which places the quoll in a vulnerable position in which it is potentially at risk from future land use change. The high degree of spatial overlap in their optimal habitat indicates that the spotted-tailed quoll is at high risk of decline with the potential establishment of the red fox, particularly in the Northern Midlands, Northern Slopes and Flinders bioregions.

2.5.1 Bottom-up environmental correlates of Tasmanian spotted-quoll abundance

As hypothesized, we found that Tasmanian spotted-tailed quoll abundance is highest in warm, low elevation areas with predictable seasonal rainfall, conditions that are positively correlated with primary productivity in Tasmania (Jones and Rose 1996). Our finding that the abundance of quolls in Tasmania is highest in warm, low elevation areas with predictable

seasonal rainfall accords with food-web theory, which states that high levels of environmental productivity can have strong bottom-up effects on the abundance of top predators (Elmhagen *et al.* 2010).

We found a number of major differences in the environmental associations of mainland and Tasmanian spotted-tailed quolls. Most notably, while the distribution of mainland quolls is most strongly associated with high annual mean rainfall (> 600 mm), high elevation, and extensive tracts of continuous forest (Burnett 2001; Catling *et al.* 2002; DNR 1997; Mansergh 1984; Wintle *et al.* 2005), our results indicate that this is not the case in Tasmania. As discussed, Tasmanian quoll distribution is best explained by warm temperature, which is correlated with low elevation, and annual mean precipitation was not an important predictor. Furthermore, while mainland quolls appear to be largely restricted to forested areas, our finding that landscapes with low forest cover can provide suitable habitat for the spotted-tailed quoll is further supported by observations that Tasmanian spotted-tailed quolls are frequently observed in woodland, pastoral areas and coastal heath as well as in forest (DPIPWE unpublished, Green and Scarborough 1990).

Correlative species distribution models such as those we have applied here should be considered representative of a species' realised niche, or environmental associations given current biotic interactions, rather than a species fundamental niche, or the full range of environmental conditions it could potentially exploit (Hutchinson 1957). We hypothesise that the realised niches of mainland and Tasmanian spotted-tailed quolls differ due to differences in the composition of their predator guilds. Specifically, we suspect that the apparent habitat preferences of the mainland spotted-tailed quoll are shaped top-down by intense competition from an invasive apex predator, the introduced red fox.

Due to their high dietary overlap, the spotted-tailed quoll is considered to be vulnerable

to both exploitation and interference competition from the introduced red fox (Glen and Dickman 2013; Glen and Dickman 2005; Glen and Dickman 2008). Foxes prey primarily on small- and medium-sized mammals that inhabit relatively open habitats (Kinnear *et al.* 2002). As well as being implicated in the decline of many small- and medium-sized mammals, for the more resilient generalist or arboreal species, this predation pressure has resulted in a niche contraction from a wide range of habitats to their current apparent ‘preferred’ habitat in structurally complex mesic forests (Bilney *et al.* 2010; Kinnear *et al.* 1998; Kinnear *et al.* 2002). Similarly, south-eastern mainland spotted-tailed quolls occur at high abundance only where foxes are rare or absent (Catling and Burt 1995; Catling *et al.* 2002), and their habitat preferences are characterised by the same features that foxes avoid: undisturbed areas with dense forests, steep topography, and rocky crevices (Kinnear *et al.* 2002; Saunders *et al.* 1995). Furthermore, where spotted-tailed quolls and foxes do co-exist, foxes prey primarily on terrestrial prey in cleared habitat, while quolls forage primarily on arboreal prey in forested habitat, potentially as means of niche partitioning to minimise competition (Glen and Dickman 2005; Glen and Dickman 2011). We suggest that rather than having a preference for cool, rugged, forested habitat, and selection for complex forests with arboreal prey, mainland quolls are now restricted to those environments where competition with foxes is less intense. Thus, the environmental correlates of quoll distribution in the forests of south-eastern mainland Australia may represent a survival niche, where rates of decline of quolls and their prey are lower compared to other, perhaps more preferred habitats, rather than being preferred habitat *per se*. Similar examples of dominant predators shaping the apparent habitat preferences of subordinate species can be seen in other ecosystems worldwide. For example, although cheetah (*Acinonyx jubatus*) always lose in direct competition with lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*), they persist in the ecosystems by seeking out “competition refuges” with

low densities of their competitors (Durant 1998). In another example, while the American mainland marten (*Marten americana*) is considered a late-successional coniferous forest specialist, the Newfoundland island subspecies (*Marten american atrata*) has evolved a more generalised niche in the absence or low abundance of larger predators (Hearn *et al.* 2010).

2.5.2 Top-down correlates of Tasmanian spotted-tailed quoll abundance

Contrary to our expectations, we did not find a significant relationship between devil habitat suitability and spotted-tailed quoll abundance. Theory (Soulé *et al.* 1988) and empirical studies (Jones 1997; Jones and Barmuta 1998; Jones and Barmuta 2000) led to the prediction that the abundance of the smaller spotted-tailed quoll should be limited by that of the larger Tasmanian devil (Jones *et al.* 2007). Although model testing and expert opinion indicated that the mapped predictions of devil probability of occurrence were reliable (Johnson *et al.* 2012), it may be that predicted habitat suitability is a poor proxy for devil abundance. Alternatively, it is also possible that the devil does not regulate abundance of the spotted-tailed quoll. Support for this idea comes from the lack of evidence for increased quoll abundance in areas where devil disease has been present for >10 years (Figure 2.2). We speculate that any benefits that to the spotted-tailed quoll from devil decline could be offset by increased occurrence of the feral cat (Hollings *et al.* 2014), which may compete with the spotted-tailed quoll for food and den resources (Glen and Dickman 2013; Glen and Dickman 2005; Molsher 1999). In summary, to date, there is no evidence for numerical suppression of the spotted-tailed quoll by the devil, or for mesopredator release of the spotted-tailed quoll following devil decline. Our results indicate that Tasmanian spotted-tailed quoll abundance is primarily driven by bottom-up environmental factors, rather than top-down competition from the Tasmanian devil, but hypothesise that habitat preferences of the mainland spotted-tailed quoll are strongly influenced by top-down

competition from the red fox.

2.5.3 *Spatial distribution of potential threats*

Clearly, the recent introduction of the European red fox to Tasmania poses a serious threat to both the spotted-tailed quoll and its prey. State-wide, optimal fox habitat overlapped with 42 % of optimal quoll habitat. The most extensive overlap and thus the greatest risk of future decline is in the Northern Midlands and Flinders bioregions, both of which also contain a high proportion of predicted quoll core habitat. As is the case on mainland Australia, in Tasmania the red fox is predicted to reach highest abundance in open forest or cleared agricultural landscapes with lower annual mean precipitation (Sarre *et al.* 2013), the same environmental conditions currently preferred by the Tasmanian spotted-tailed quoll. Based on the current distribution and habitat associations of the south-eastern mainland spotted-tailed quoll, if red fox populations were to establish in Tasmania, we expect that the distribution of the Tasmanian spotted-tailed quoll would contract to cooler, higher elevation and rainfall, extensively forested and topographically rugged areas of the West, Southern Ranges and Central Highlands bioregions, where overlap with optimal fox habitat is lowest. In this scenario, Tasmanian quolls would inhabit environmental conditions which would more closely resemble much of the current distribution of mainland quolls. Although these habitats are not currently preferred, they could be critical in providing refuge in the face of future fox establishment.

Our finding that spotted-tailed quoll abundance is positively associated with environmental drivers of productivity puts the quoll at an overall high risk of population decline from land use change. In Tasmania, as in other parts of the world, the most productive arable land has been preferentially selected for settlement and agricultural development, while

reserved land tends to be in less productive, high elevation, rugged terrain (Margules and Pressey 2000). The land tenure and reservation status of predicted quoll core distribution simply reflects their environmental preferences for productive landscapes, which are in turn correlated with human land uses. That 87% of the predicted core distribution of the Tasmanian spotted-tailed quoll lies outside of the formal reserve system, and 53% is on private land further highlights the precarious security of quoll habitat. Habitat on unreserved land carries a higher risk of future disturbance, which in Tasmania could include expansion or intensification of agriculture, production forestry, mining, road development, dam development for agriculture, or urban and peri-urban subdivision. Furthermore, the relatively high proportion of core habitat on private land means that there are limited options for expansion of the formal reserve system to encompass preferred habitat. Future conversion of public land to reserve is a more likely prospect, but our results suggest that only a moderate amount of habitat on this land tenure reflects the current habitat preferences of the Tasmanian spotted-tailed quoll.

2.5.4 Recovery and restoration

Modelled spatial predictions of abundance and habitat suitability are useful to identify threats within a species' current distribution, and also where future reintroductions could occur. (Cianfrani *et al.* 2010). Our model predicts that King and Flinders Islands in the Bass Strait to the north of Tasmania, where the spotted-tailed quoll has become extinct since European settlement, still contains highly suitable quoll habitat. This combined with the absence of foxes and high abundance of medium-sized prey (Anon 2013) makes these islands prime candidates for future reintroductions should physical isolation from threatening processes on mainland Tasmania be required.

If we are correct in supposing that both the niche and distribution of the south-eastern

mainland spotted-tailed quoll have contracted since European settlement, management actions such as fox control, habitat restoration, and reintroductions should be conducted not only in their current distribution and preferred habitat, but also in the lower elevation, lower rainfall, less densely forested, coastal areas of its former distribution, which our models suggest may once have represented preferred habitat. Indeed, quolls do persist in these habitats in north-eastern New South Wales (Andrew 2005; Lunney and Matthews 2001), and management to connect habitat and suppress foxes on disturbed farmland between remnant coastal populations and higher density populations on the plateau and tablelands (Glen and Dickman 2011) may improve population persistence. Similarly, it is possible that tracts of vacant habitat intervening disjunct spotted-tailed quoll populations in Victoria, including farmland, that might provide suitable abiotic conditions for the spotted-tailed quoll but are not occupied because they support a high abundance of foxes may support quoll populations if fox control and recovery of critical weight range prey could be achieved.

2.5.5 Limitations and future improvements

Habitat suitability maps are typically used by conservation managers as if they represent certainty (Wintle *et al.* 2004). In reality, species distribution models and their resulting predictive maps contain numerous sources of uncertainty, including measurement error in predictor variables, model structure, accuracy of predictions, and representativeness of species records used in model building (Burgman *et al.* 2005).

To account for some of the uncertainty associated with model structure we used model averaging. While both the low correlation between training and test data from cross-validation and the high error around predicted values showed that model predictions were not precise, the model was extremely well calibrated. This indicates that, overall, the model is correctly

predicting areas of high and low abundance, but that the actual abundance value predicted at a cell is not reliable. Therefore, while our model can be reliably used by conservation managers to identify relative habitat suitability at a given location, it cannot be used to quantify absolute abundance at a location, or to directly estimate Tasmanian spotted-tailed quoll population size.

An important potential source of uncertainty that we were not able to account for was imperfect detection in the quoll abundance data (MacKenzie *et al.* 2002). Where detection is related to environmental characteristics, the importance of environmental covariates positively related to detection probability will be inflated leading to biased coefficient estimates (Gu and Swihart 2004). Here, it is possible that the proportion of forest cover could be related to detectability (MacKenzie *et al.* 2002), in that quolls inhabiting fragmented environments with low mean forest cover may encounter traps more rapidly than those in continuous habitats. However, our knowledge of persistent high density spotted-tailed quoll populations in localities with low forest cover suggests this is not the case (E.g. Narawntapu and Woolnorth, Figure 2.2). The low trap success in our study meant that even simple models built using an occupancy modelling framework could not converge. Given the high trap effort that was employed during data collection, trap success is unlikely to be exceeded in the future, and building occupancy models for quolls using trapping data is not feasible. Thus, future quoll distribution models that account for imperfect detection will need to be built using survey methods with higher detection probability, such as camera traps.

Despite the fact that the model was comprised of environmental variables that are thought to be important drivers of quoll distribution, our model explained less than 20% of the variation in quoll abundance. Improvement to model fit could be made through the use of proximal predictor variables that are more directly related to quoll resource requirements, for example the presence of suitable den habitat or the abundance of prey. However, as these variables are

not likely to be mapped at the scale or extent required for predictive purposes, their utility in species distribution modelling is limited. Further research on the environmental correlates of spotted-tailed quoll prey density and den habitat are required to build spatial layers of these factors for predictive purposes.

2.5.6 Conservation management implications

Our results have important implications for the management, recovery, and restoration of spotted-tailed quolls, both in south-eastern mainland Australia and Tasmania. First, it is clear that information on the mainland spotted-tailed quoll should not be used to inform conservation management actions for the Tasmanian subspecies, or vice-versa, without explicit consideration of differences in predator assemblages and prey availability in the two locations. Second, the absence of a relationship between quoll abundance and any broad vegetation community means that efforts to manage quoll habitat on this basis are unlikely to conserve important habitat. Rather, all native vegetation communities within the core distribution should be considered of equal high importance, and priority areas for management actions should be considered spatially, guided by our maps of predictive habitat suitability. Third, given the wide-ranging nature of quolls, and given that a large proportion of predicted core distribution occurs outside of reserves on private land, the reserve system alone is unlikely to secure sufficient habitat for viable populations. In any case, the wide-ranging behaviour of many mammalian predators, including the spotted-tailed quoll, means that reserves alone will not provide inherent protection from all threats, or sufficient area to support viable populations. Therefore, managing threats on non-reserved land subject to a variety of land-use activities is key to their conservation management. Finally, given that a large proportion of core habitat occurs off reserve on private land, where it is subject to increasing pressure from land use change and

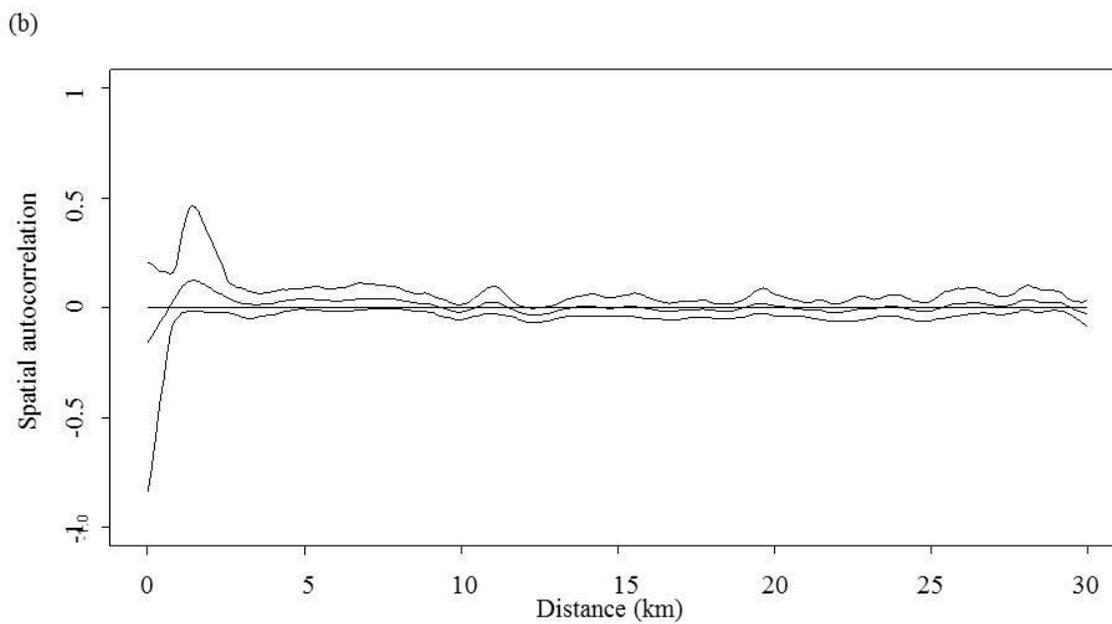
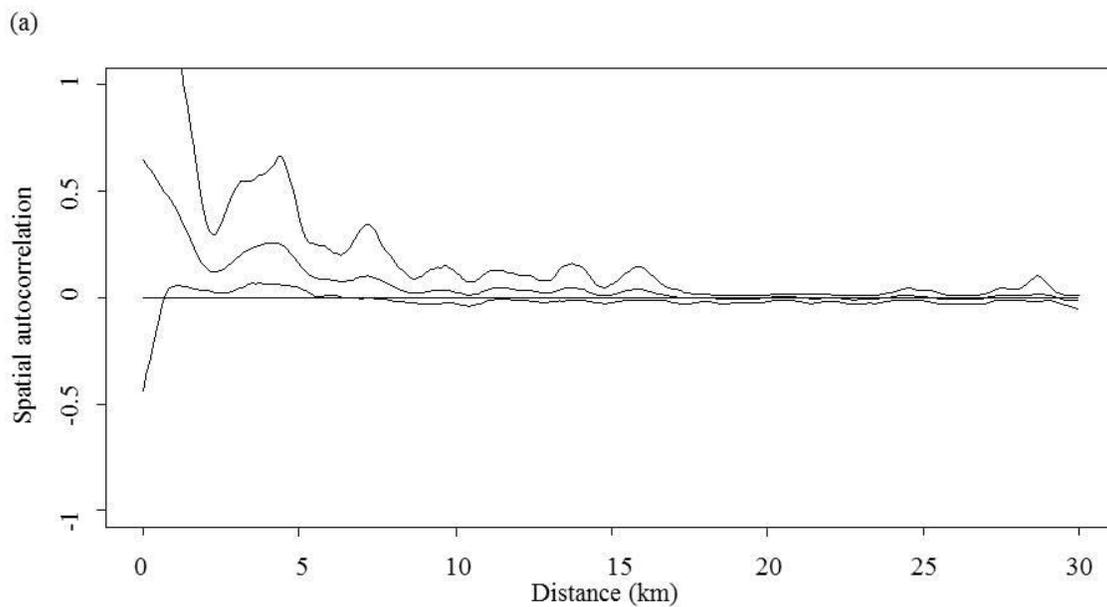
agricultural intensification, it is vital that management strategies and recovery actions involve and engage private landholders as well as public land managers.

Appendix 2.1: Coefficient estimates, AICc, and Akaike weights for 95% confidence model set of spotted-tailed quoll abundance in Tasmania, Australia.

MODEL	AG	AMPREC	AMTEMP	DEVIL	EFFORT	EFFORT^2	FOR	PRECCV	TOPRUG	WEF	DF	Δ AIC	WEIGHT
245			0.457		0.070	-0.001	-0.519	0.026			7	0.00	0.047
182	0.675		0.432		0.071	-0.001		0.028			7	0.02	0.047
694	0.518		0.425		0.070	-0.001		0.032		-0.455	8	0.25	0.042
190	0.653		0.438	-0.733	0.071	-0.001		0.031			8	0.39	0.039
693			0.457		0.070	-0.001		0.034		-0.626	7	0.52	0.037
246	0.441		0.432		0.071	-0.001	-0.346	0.026			8	0.64	0.034
702	0.503		0.431	-0.699	0.070	-0.001		0.035		-0.438	9	0.75	0.033
701			0.464	-0.728	0.070	-0.001		0.038		-0.603	8	0.87	0.031
253			0.464	-0.596	0.070	-0.001	-0.471	0.029			8	0.94	0.030
757			0.450		0.070	-0.001	-0.357	0.030		-0.370	8	1.11	0.027
254	0.461		0.437	-0.632	0.071	-0.001	-0.289	0.029			9	1.46	0.023
184	0.708	0.016	0.470		0.072	-0.001		0.026			8	1.48	0.023
696	0.549	0.017	0.464		0.071	-0.001		0.030		-0.462	9	1.67	0.021
438	0.647		0.418		0.071	-0.001		0.026	-0.003		8	1.80	0.019
247		0.008	0.478		0.071	-0.001	-0.515	0.025			8	1.87	0.019
758	0.419		0.427		0.070	-0.001	-0.205	0.030		-0.341	9	1.89	0.018
765			0.457	-0.628	0.070	-0.001	-0.297	0.033		-0.394	9	1.93	0.018
501			0.452		0.070	-0.001	-0.504	0.025	-0.001		8	1.99	0.018
192	0.593	-0.022	0.389	-1.232	0.071	-0.001		0.037			9	2.07	0.017
950	0.503		0.416		0.070	-0.001		0.031	-0.002	-0.442	9	2.16	0.016
695		0.013	0.490		0.071	-0.001		0.033		-0.639	8	2.17	0.016
703		-0.030	0.394	-1.395	0.070	-0.001		0.044		-0.551	9	2.23	0.016
949			0.442		0.070	-0.001		0.032	-0.003	-0.598	8	2.25	0.015
181			0.482		0.072	-0.001		0.029			6	2.27	0.015
446	0.633		0.428	-0.715	0.071	-0.001		0.030	-0.002		9	2.28	0.015
255		-0.031	0.391	-1.286	0.070	-0.001	-0.432	0.036			9	2.29	0.015
248	0.483	0.013	0.463		0.071	-0.001	-0.324	0.024			9	2.29	0.015
189			0.488	-0.793	0.072	-0.001		0.033			7	2.34	0.015
704	0.461	-0.018	0.393	-1.094	0.070	-0.001		0.039		-0.421	10	2.57	0.013

766	0.437		0.432	-0.657	0.070	-0.001	-0.139	0.033		-0.362	10	2.60	0.013
502	0.441		0.427		0.071	-0.001	-0.332	0.026	-0.001		9	2.63	0.013
957			0.451	-0.709	0.070	-0.001		0.036	-0.003	-0.583	9	2.72	0.012
958	0.492		0.425	-0.688	0.070	-0.001		0.034	-0.001	-0.430	10	2.73	0.012
759		0.011	0.477		0.070	-0.001	-0.343	0.029		-0.391	9	2.89	0.011
509			0.460	-0.593	0.070	-0.001	-0.461	0.028	-0.001		9	2.95	0.011
191		-0.042	0.388	-1.713	0.070	-0.001		0.043			8	3.06	0.010
1013			0.444		0.070	-0.001	-0.339	0.029	-0.001	-0.372	9	3.10	0.010
256	0.410	-0.021	0.391	-1.102	0.070	-0.001	-0.282	0.034			10	3.18	0.010
440	0.679	0.017	0.457		0.072	-0.001		0.024	-0.003		9	3.24	0.009
767		-0.027	0.394	-1.232	0.069	-0.001	-0.276	0.040		-0.363	10	3.43	0.009
760	0.464	0.015	0.462		0.071	-0.001	-0.171	0.028		-0.366	10	3.43	0.009
510	0.461		0.434	-0.630	0.071	-0.001	-0.280	0.029	-0.001		10	3.47	0.008
952	0.533	0.017	0.455		0.071	-0.001		0.028	-0.002	-0.448	10	3.56	0.008
437			0.456		0.071	-0.001		0.026	-0.005		7	3.60	0.008
503		0.009	0.474		0.071	-0.001	-0.497	0.024	-0.001		9	3.85	0.007
951		0.014	0.475		0.070	-0.001		0.030	-0.004	-0.611	9	3.87	0.007
1014	0.418		0.421		0.070	-0.001	-0.189	0.029	-0.001	-0.343	10	3.88	0.007
445			0.466	-0.756	0.071	-0.001		0.030	-0.004		8	3.90	0.007
1021			0.452	-0.625	0.070	-0.001	-0.284	0.033	-0.001	-0.395	10	3.93	0.007
448	0.585	-0.020	0.387	-1.174	0.071	-0.001		0.035	-0.001		10	4.04	0.006
183		0.011	0.509		0.072	-0.001		0.028			7	4.05	0.006
959		-0.028	0.392	-1.337	0.069	-0.001		0.043	-0.001	-0.543	10	4.21	0.006
504	0.483	0.014	0.458		0.071	-0.001	-0.306	0.024	-0.001		10	4.27	0.006
511		-0.031	0.392	-1.298	0.070	-0.001	-0.436	0.037	0.000		10	4.31	0.006
768	0.394	-0.018	0.393	-1.055	0.070	-0.001	-0.140	0.038		-0.345	11	4.41	0.005
960	0.457	-0.017	0.392	-1.062	0.070	-0.001		0.038	-0.001	-0.418	11	4.57	0.005
1022	0.436		0.429	-0.654	0.070	-0.001	-0.128	0.033	-0.001	-0.364	11	4.61	0.005
1015		0.011	0.471		0.070	-0.001	-0.321	0.028	-0.002	-0.394	10	4.85	0.004
117			0.444		0.070	-0.001	-0.642				6	4.90	0.004
447		-0.038	0.384	-1.603	0.070	-0.001		0.040	-0.003		9	4.93	0.004
512	0.409	-0.021	0.391	-1.105	0.070	-0.001	-0.283	0.035	0.000		11	5.21	0.004
439		0.012	0.484		0.072	-0.001		0.024	-0.005		8	5.34	0.003

Appendix 2.2: Spline correlograms with 95% bootstrap confidence intervals of (a) spotted-tailed quoll abundance response data and (b) Pearson's residuals from global model. Y-axis shows value of *Morans I* at intercept. X axis shows distance between observations (km).



**Chapter 3: The influence of environmental factors and
co-occurring predators and prey on the abundance of
Tasmania's mammalian predators**



3.1 Abstract

The loss of top predators is causing changes to lower trophic levels in diverse ecosystems globally. Understanding the role of top-down and bottom-up processes on predator abundance and co-occurrence is essential to predicting potential future changes to ecosystems following the decline or loss of apex predators.

The island of Tasmania retains an almost intact suite of Australian predators, but is at risk of change due to decline of the top predator, the Tasmanian devil, and predicted increases in mesopredators, including the introduced feral cat and the native spotted-tailed quoll. Currently, the factors driving the abundance and co-occurrence of these species are not well understood.

We conducted a large-scale remote camera survey to quantify the role of bottom-up environmental processes and potential for top-down interspecific interactions in determining the abundance of three mammalian predator species and their common prey. In a multi-stage approach, we first used Royle–Nichols(RN) models to develop single-species models of the effect of environment on abundance. Abundance estimates from these models were then used in simple correlation analysis, as predictor variables in RN models, and in quantile regression to investigate limiting effects of predators and prey on one another. The environmental factors driving predator and prey abundance differed among species. We found no evidence to suggest that any predator behaviourally or numerically suppressed any other. Similarly, we found no support for the idea that the abundance of any predator increases with or is limited by prey abundance.

Given the variability in results between our study and previous studies of Tasmanian predator co-occurrence, we suggest that further research on fitness outcomes of fine scale interspecific interactions and niche overlap is required to better understand broad scale patterns of co-occurrence in Tasmanian predators, and to predict the potential effect of top predator

decline.

3.2 Introduction

Through their trophic position as apex consumers, carnivores play a vital role in regulating the structure, function and resilience of ecosystems (Ripple *et al.* 2014; Ritchie and Johnson 2009; Terborgh *et al.* 2001). Terrestrial carnivores are currently experiencing high rates of decline due to habitat loss and modification, human persecution, and loss of prey (Ripple *et al.* 2014). Top predators can have a strong influence on ecosystem structure and function (Paine 1980), and their decline can have profound effects on the abundance and distribution of other species at lower trophic levels and whole ecosystems (Estes *et al.* 2011; Ripple *et al.* 2014). For example, top predator decline can result in numerical or behavioural release of smaller predators (e.g. mesopredator release, Soulé *et al.* 1988). Increased predation by mesopredators can lead to declines in prey abundance (Crooks and Soule 1999; Johnson *et al.* 2007), or altered prey behaviour, with resultant detrimental effects on the vegetation community (Fortin *et al.* 2005; Hebblewhite *et al.* 2005).

In addition to the top-down effects of species at high trophic levels, bottom-up processes such as productivity and anthropogenic disturbance also determine the strength of top-down effects of apex predators on mesopredators (Creel *et al.* 2001; Oksanen and Oksanen 2000). For example, in Sweden, the magnitude of mesopredator release of red fox (*Vulpes vulpes*) from wolf (*Canis lupus*) and Eurasian lynx (*Lynx lynx*) competition was greatest in high productivity human-modified agricultural environments where prey were abundant, and least in unproductive boreal regions where low resource availability limited prey and thus mesopredator abundance even in the absence of top predators (Elmhagen and Rushton 2007). The abundance of some mesopredators and their ecological effects on lower trophic levels has

also been shown to be highest in fragmented vegetation (Crooks and Soule 1999; Irwin *et al.* 2009; Terborgh *et al.* 2001). Thus, both top-down and bottom-up forces play an important role in determining the abundance of mesopredators and their role in regulating lower trophic levels.

On the island of Tasmania, Australia, the native mammalian carnivore community is almost intact. Following the extinction of the thylacine (*Thylacine cynocephalus*) in the 1930s, the Tasmanian devil (*Sarcophilus harrisii*) became the largest (7 - 9 kg, Menkhorst and Knight 2010) extant marsupial carnivore, and the apex terrestrial mammalian predator in the Tasmanian system. The devil shares a sympatric island-wide distribution with two smaller mammalian mesopredators: the endemic marsupial spotted-tailed quoll (*Dasyurus maculatus*) (1.5 – 7 kg); and the introduced eutherian feral cat (*Felis catus*) (2.5 – 6.5 kg) (Menkhorst and Knight 2010).

The similar body size and ecological requirements of the devil, spotted-tailed quoll and cat indicates high potential for exploitation and interference competition among them (Hollings *et al.* 2014; Jones and Barmuta 1998; Jones and Barmuta 2000). All three species are hypercarnivores with a preference for mammalian prey (Buckmaster 2012; Glen and Dickman 2006a; Glen *et al.* 2011; Jones and Barmuta 1998; Lazenby 2012), use similar den structures (Glen and Dickman 2008; Smith 2012), and have been recorded from a wide range of habitats (Chapter 2, Green and Scarborough 1990). As the largest carnivore, devils are likely to experience lower predation pressure than the other two species. Devils are competitively dominant at carcasses, so larger kills that cannot be quickly consumed by spotted-tailed quolls or cats may be lost to devils (Jones and Barmuta 2000). Incidences of cats killing spotted-tailed quolls (Museum of Victoria record cited in Long and Nelson 2008) and population viability analyses both suggest that the spotted-tailed quoll is vulnerable to competition from cats (Burnett and Marsh 2004; Glen and Dickman 2013).

The Tasmanian devil is now threatened with extinction by an invariably fatal transmissible cancer, Devil Facial Tumour Disease (DFTD) (Hawkins *et al.* 2006). First observed in 1996, DFTD has now spread to over 80% of the devil's distribution, and has resulted in population declines of up to 95% (Save the Tasmanian Devil Program 2013). It has been hypothesised that the reduced abundance of the devil will result in mesopredator release of the spotted-tailed quoll and cat (Hollings *et al.* 2014; Jones *et al.* 2007). Three recent studies addressed the relationship between the co-occurrence of these species. Lazenby and Dickman (2013) found that feral cats were detected less frequently at cameras where devils were present, potentially indicating behavioural avoidance; however, the probability of occupancy by cats was independent of devils (Lazenby 2012). In contrast, a camera trapping study in northwest Tasmania found significant positive associations between occurrence of devils and cats, and occurrence of devils and spotted-tailed quolls (Saunders 2011). Finally, Hollings *et al.* (2014) found an inverse relationship between devil and cat occurrence. Hollings *et al.* (2014) also found a significant increase in cat occurrence where DFTD was present the longest (>10 years), but only where productivity was low, highlighting the importance of considering bottom-up and top-down influences on changes in abundance.

Given that localised extinctions of the devil are predicted to occur in the next ten years (McCallum *et al.* 2007), and the potential for mesopredator release and trophic cascades in the Tasmania system, the need to understand correlates of apex predator and mesopredator abundance is urgent. Although niche partitioning between the devil and the spotted-tailed quoll has been demonstrated at fine spatial scales (Jones and Barmuta 2000), landscape scale drivers of the abundance and co-occurrence of devils, cats and spotted-tailed quolls, including bottom-up and top-down effects, are not well understood. The inconsistent results from studies to date suggest that reliable generalisations of the relationship among Tasmanian predators cannot yet

be made.

The purpose of this study is to investigate the influence of bottom-up environmental variables and top-down abundance of other predators on the abundance of predators and mammalian prey in Tasmania. Our predictions on environmental effects on abundance are:

1. Productivity has a positive effect on the abundance of predators and prey.

Productivity has been shown to increase carrying capacity for prey, supporting higher abundance and diversity of predators (Oksanen *et al.* 1981; Oksanen and Oksanen 2000).

2. Forest cover has a positive effect on spotted-tailed quoll abundance, and no effect for the devil and the cat.

The spotted-tailed quoll is regarded as a forest specialist (Belcher 2004; Belcher and Darrant 2006b; Jones and Rose 1996) and should therefore reach highest abundance in contiguous forest, while the devil and cat are habitat generalists (Denny and Dickman 2010; Rounsevell *et al.* 1991) and should be insensitive to the amount of forest cover and degree of fragmentation.

3. Forest fragmentation has a negative effect on spotted-tailed quoll abundance, and either a positive effect or no effect for the devil and the cat.

Reasoning as 2 above.

Our predictions for the effects of co-occurrence on abundance are:

1. The Tasmanian devil behaviourally and numerically suppresses the cat and the spotted-tailed quoll. In the Tasmanian environment it has been predicted that the feral cat and spotted-tailed quoll will increase in abundance and reduce their avoidance behaviours when released from competition with the devil (Hollings *et al.* 2014; Jones *et al.* 2007). If this is the case, we would expect an inverse relationship between spotted-tailed quoll abundance and

detection, and that of the cat and the devil.

2. The cat behaviourally and numerically suppresses the spotted-tailed quoll. The two species have similar resource requirements, but the higher reproductive rate, less specialised habitat requirements, and larger body size of the cat (reviewed in Denny and Dickman 2010) relative to the spotted-tailed quoll (reviewed in Long and Nelson 2008) mean that the cat is able to reach higher densities in the landscape and is likely to dominate in direct aggressive encounters.

3. Predator abundance increases with and is limited by prey abundance. If the abundance of food resources is a limiting factor for Tasmanian predators (e.g. a determinant of probability of population density), we would expect higher abundance of predators where prey abundance is greatest (Karanth *et al.* 2004; Mittelbach 2012).

In this study, we define evidence for behavioural suppression as lower detection probability of a species where another predator was recorded, and evidence for numerical suppression as an inverse relationship between abundance of different predators.

3.3 Methods

3.3.1 Study region

Our sites spanned three broad regions of Tasmania, covering a combined 1,400 km² (Figure 3.1). The sampling area in the northwest region was larger than that in the south or the north-east; as a result, sites in the north-west spanned a broader range of climatic conditions than those in the warmer and wetter north-east and south regions (Appendix 3.1).

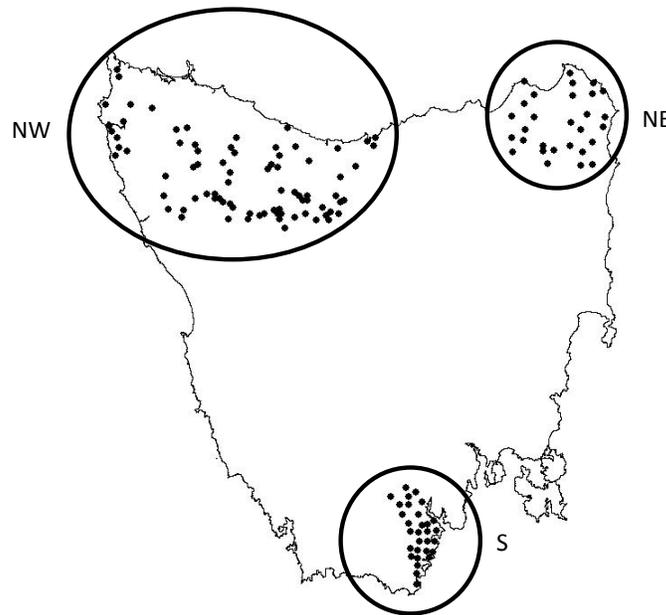


Figure 3.1: Map of Tasmania, Australia, showing study regions (large open circles: NW = north-west; S = south; NE = north-east) and locations of cameras within regions (small closed circles within regions).

3.3.2 Site selection

Site selection was undertaken using ArcGIS 9.2 (ESRI, Redlands, California, USA). Sites were chosen to be a minimum of 3 km apart, outside of towns, and to be accessible by road. We expected that devil abundance would be highest in the north-west region and lowest in the north-east region (Hawkins *et al.* 2006) and that quoll abundance would be lower in the south region than in the north-west or north-east regions (Chapter 2), but we had no prior knowledge of the abundance of any species at any given camera site.

3.3.3 Predictor variables

Environmental and spatial predictor variables were defined using ArcGIS 9.2 (ESRI, Redlands, California, USA). We used three variables to measure the influence of environment

on the abundance of predators and prey: productivity, (MANPP); forest cover (FOR); and edge density (EDGE). We first used ArcGIS to generate 1 km² circular buffers around each camera site and then extracted the value for each predictor variable within the buffer. We chose a 1 km² buffer as it represents among the smallest home ranges recorded by both the spotted-tailed quoll and the cat (Buckmaster 2012; Glen and Dickman 2006b; Molsher *et al.* 2005).

Productivity was derived from a model of annual net primary production (CSIRO 2001), a standard measure of productivity that has been associated with vegetation growth, herbivore abundance and carnivore abundance (Oksanen and Oksanen 2000). Forest cover and edge density were estimated using the Tasmanian vegetation mapping spatial database TasVeg 2.0 (TASVEG 2009). Forest cover was defined as the proportion of rainforest, eucalypt forest, and non-eucalypt forest in the 1 km² buffer. Edge density was calculated as the length (km) of the interface between closed vegetation (forest and scrub) and open vegetation (native grassland and pasture) within the 1 km² buffer. We used an analysis of variance (ANOVA) to check that the distribution of these three predictor variables was consistent among study regions.

We included study region as a predictor variable to account for spatial variation in unmeasured factors that vary geographically across Tasmania (REGION). Finally, for devils, we also included a variable indicating the estimated year of outbreak of Devil Facial Tumour Disease (DFTD) at the site. Because our study regions coincide with timing of DFTD arrival (i.e. DFTD arrival <1999 in all north-east region sites; DFTD absent in >90% of north-west region sites), REGION and DFTD cannot be distinguished as predictor variables. Thus, DFTD was included as a variable in the devil abundance model, and REGION was included as a predictor variable in the cat, spotted-tailed quoll, and prey abundance models. Prior to model fitting I standardised all continuous candidate predictor variables and assessed them for collinearity. Predictor variables are summarised in Table 3.1.

MODEL	VARIABLE	DESCRIPTION	STATE
ENVIRONMENT	BAIT	Bait age, days since camera was baited. Range 0 - 13.	p
	SURVEY	Camera trapping protocol. Protocol A = north-west region Protocol B = north-east and south regions	p
	FOR	Proportion of native forest cover in surrounding 1 km ²	p, λ
	EDGE	Density of closed-open vegetation edge (km / km ²)	λ
	MANPP	Mean annual net primary production (kg C / m ² / year)	λ
	REGION	Region camera site is within (see Figure 1) NE = north-east Tasmania; NW = north-west Tasmania S = south Tasmania	λ
	DFTD	Year of Devil Facial Tumour Disease (DFTD) arrival A = DFTD absent B = DFTD present, outbreak 2004 - 2007 C = DFTD present, outbreak <1999	λ
CO-OCCURRENCE	STQP	Night-specific occurrence of the spotted-tailed quoll A = STQ absent; P = STQ present	p
	TDP	Night-specific occurrence of the Tasmanian devil A = TD absent; P = TD present	p
	CATP	Night-specific occurrence of the cat A = CAT absent; P = CAT present	p
	SQ	Empirical Bayes estimate of spotted-tailed quoll mean abundance at each site. Range = 0.029– 6.469	λ
	TD	Empirical Bayes estimate of devil mean abundance at each site. Range = 0.034 – 9.41	λ
	CAT	Empirical Bayes estimate of cat mean abundance at each site. Range = 0.083 – 3.324	λ
	PREY	Empirical Bayes estimate of potential prey mean abundance at each site. Range = 0.006 – 8.164	λ

Table 3.1: Predictor variables used in Royle-Nichols models investigating the effect of environmental factors and co-occurring species on spotted-tailed quoll (STQ or SQ), Tasmanian devil (TD), cat, and prey abundance in Tasmania, Australia. State: p = covariate on detection probability; λ = covariate on abundance.

3.3.4 Camera survey protocols

I used two different protocols for camera trapping. Protocol A was used for surveys in the north-west region from June to September 2010. At each site, two Scoutguard SG550V remote cameras spaced between 200 and 300 m apart were set for 7 - 21 nights. Cameras were set 10 – 20 m away from roads and tracks, and mounted with straps to either a tree trunk or a 1 m stake at a height of 30 – 50 cm from the ground and facing a bait station. Cameras were baited with a mixture of wallaby mince and beef liver, placed in a 15 mm gauge galvanised wire cage fixed to the top of a 1.8 m wooden stake that was driven into the ground 2.5 – 3 m away. Vegetation was cleared between the camera and the bait station to avoid false triggers of the cameras. Approximately 50 mL of muttonbird oil was poured on the bait cage and between the camera and bait station. Cameras were programmed for 24-hour operation to take one minute of video with a forty-second pause between successive videos. The date and time of each video was recorded. Protocol B was used for surveys in the north-east region in February 2011 and in the south region in May 2011. At each site, one Pixcontroller Trailmaster Digital Eye 12.1 camera was set for 20 nights. Cameras were set 10 – 20 m from access roads and tracks, and mounted with straps to a tree trunk at a height of 30 – 50 cm from the ground and facing a bait station. Cameras were baited with a scent lure of tinned sardines, muttonbird or fish oil, dried liver, and rolled oats placed in a perforated PVC pipe tube suspended from a tree at approximately 1.5 m above the ground, and a food reward lure of approximately 250 g of road-killed wallaby placed on the ground secured with tent pegs. Cameras were programmed for 24-hour operation. The date and time of each video was recorded. To control for differences in detection probability resulting from the use of two different survey methods, I included a two level categorical covariate, SURVEY, in the detection probability component of the environment models (Table 3.1)

3.3.5 *Species data handling*

A trap night was defined as the 24-hour period beginning and ending at 12 noon. The number of detections of each mammal species was recorded for each camera trap night. For the north-west region where two cameras were used, nightly data from both cameras were aggregated into one detection history, with the maximum number of detections per night per camera retained as the value for the site. Data were excluded for nights that cameras were not operational e.g. due to battery failure or cameras being removed from tree trunks by devils.

We used the camera data to generate a detection history consisting of a 1 (detected) or 0 (not detected) for each trap night and each site separately for the spotted-tailed quoll, Tasmanian devil, and feral cat. While our camera trapping protocols were designed primarily to detect terrestrial carnivores, the presence of other mammals was also recorded. We also created a fourth detection history for mammalian prey by aggregating data for all small- and medium-sized mammals that fall within the size range of prey species taken by the devil, spotted-tailed quoll and cat (Appendix 2; Glen and Dickman 2006a; Glen *et al.* 2011; Jones and Barmuta 1998).

3.3.6 *Data analysis - modelling strategy*

We estimated spotted-tailed quoll, Tasmanian devil, cat, and prey abundance at each site with a single-species single-season Royle-Nichols abundance induced heterogeneity model (RN model, Royle and Nichols 2003) in R 3.0 (R Core Team 2013) using the package ‘unmarked’ (Fiske and Chandler 2011). The RN model is an extension of the standard site occupancy model (MacKenzie *et al.* 2002), in which a species’ detection history is used to estimate the probability of detecting a species given that it is present (p), which is in turn used to estimate

the probability of occupancy (ψ) in sites where the species was not detected. Standard site occupancy models assume that detection probability is either identical among sample units or varies only with measured predictor variables. However, animal abundance is an important source of heterogeneity in detection probability; where abundance is high, the number of individuals available to be detected is also high, thus increasing the probability of detection. The RN model extends the standard site occupancy model by accounting for heterogeneous detection probabilities resulting from variation in abundance among sites, and in fact exploits this variation in detection probability to produce an estimation of abundance from the latent detection probability distribution. Thus, in the RN model, a species' detection history is used to estimate the probability of detection given that it is present (p), which is in turn used to estimate abundance (λ). Both of these processes can be modelled with covariates. This model is well suited to our data because the high rates of occupancy for Tasmanian devils (84% of sites occupied) and prey (72% of sites occupied) meant that modelling the factors that influenced probability of occupancy was uninformative; however, the vast differences in site-specific detection histories allowed us to distinguish the importance of predictor variables and estimated abundance in occupied sites. Furthermore, this approach allowed us to estimate site-specific abundance without requiring unique identification of individuals.

We used a two-stage approach to model selection. First, we identified the variables that influenced detection probability by holding abundance constant and modelling all possible combinations of the detectability variables including a null model. Models were ranked according to differences (Δ) in their AICc scores. Models with: $\Delta\text{AICc} < 2$ were considered equivalent; $\Delta\text{AICc} 2 - 7$ provide little support that models differ; $\Delta\text{AICc} = 7-10$ provide some support that models differ; while models with $\Delta\text{AICc} > 10$ gave substantial support that models differ (Burnham and Anderson 2002).

Because the goal of modelling detection probability is to account for detection bias, we considered any variable included in the equivalent top model set (i.e. with $\Delta AICc < 2$) to have a potential influence on detection, and these variables were retained in the detection probability model. Second, we held constant the detection model selected in stage one and modelled all possible combinations of the abundance variables. Variable combinations were generated using the dredge function in the R package MuMIn (Bartoń 2013). AICc was again used to rank candidate models, and the relative support for each model was also assessed with AIC weights. In the case of equivalent models with $\Delta AICc < 2$, model averaging was used to estimate variable coefficients, standard errors, z scores and P-values as well as variable relative importance (Burnham and Anderson 2002). Generation of candidate model sets and model averaging were conducted using the R package MuMIn (Bartoń 2013).

Adequacy of model fit was assessed on the basis of R^2 and checked using the parametric bootstrap in the unmarked package. Prior to analysis, all continuous variables were standardised to have a mean = 0 and variance = 1, allowing us to assess the comparative influence of continuous variables by their model averaged effect sizes. The effect of categorical variables was assessed relative to a baseline level (Table 3.1). We interpreted confidence intervals that did not overlap zero as indicating a statistically significant effect of that variable on abundance.

3.3.7 Environment models

To investigate the effect of environment on predator and prey abundance, we fit separate RN models to the detection histories of each of the three predator species and to prey. Time since baiting, forest cover, and survey protocol were included as covariates on the detection component of the model. Forest cover, forest fragmentation, mean annual net primary

production, and region (quoll, cat, prey models) or DFTD (devil model) were included as covariates on the abundance component of the model (Table 3.1). Following model selection, as outlined in 3.3.6, we derived site-specific abundance from empirical Bayes estimates of the mean of the posterior distribution of latent abundance using the `ranef` function in `unmarked` (Fiske and Chandler 2011). Because `ranef` cannot estimate abundance from model averaged parameters, abundance estimates were based on a model that included all variables in the top model set that had $AICc < 2$.

3.3.8 Co-occurrence models

We initially aimed to investigate co-occurrence using two-species, single-season occupancy models (MacKenzie *et al.* 2004). However, these models failed to converge when variables were added to either detection probability or occupancy. We therefore used the predicted abundance estimates from the environment models to investigate patterns of co-occurrence among predators and prey. In the first instance, we visualised the relationship among predators and prey with pairwise scatterplots of their predicted abundances. We also estimated Pearson correlation coefficients and Spearman rank correlation coefficients for each pairwise combination of predator and prey to investigate the strength of their linear and non-linear associations. We then fit separate RN models to the detection histories of the three predators and prey. The predicted abundances of other predators and prey obtained from the environment models were included as covariates on the abundance component of the model. The observed presence or absence of non-response predator species on each survey night was included as a covariate in the detection component of the model. To determine the relative role of bottom-up and top-down factors in driving predator abundance, the relative fit and support for the top environment and co-occurrence models were compared via their $AICc$ scores.

We examined the potential for limiting effects of: (i) predators on one another; (ii) predators on prey; or (iii) prey on predators with quantile regression (Koenker and Bassett Jr 1978) using the `quantreg` package (Koenker 2013) in R 3.0. If the abundance of a predator or prey acts as a limiting factor constraining the abundance of another predator or prey, we expected that the upper limits of the abundance distribution of one predator would constrain that of the other. Thus, we were interested in estimating the upper quantiles of the response distributions rather than the mean of the response distribution. Estimates of variance for quantile regression coefficients may not be dependable for extreme quantiles when data are limited, so we used the $n > 10/(1-q)$ rule of thumb of Scharf et al (1998) to determine the maximum regression quantile that could reliably be estimated from our sample size ($n=141$). We calculated 90th quantile regression to investigate the potential for limiting effects of (i) the abundance of predators on one another, (ii) predator abundance on prey abundance (iii) prey abundance on predator abundance, (iv) endemic predators on prey (i.e. sum abundance of Tasmanian devil and spotted-tailed quoll) and (v) all predators on prey (i.e. sum abundance of Tasmanian devil, spotted-tailed quoll, and cat), (vi) prey on endemic predators, and (vii) prey on all predators. Standard errors of regression coefficients were estimated using a parametric bootstrap.

3.4 Results

3.4.1 Detections and trap nights

We surveyed 141 sites for a total of 3,666 camera trap nights, which resulted in 157 spotted-tailed quoll detections, 565 Tasmanian devil detections, 79 cat detections, and 425 small- or medium-sized mammal prey detections. Naïve site occupancy (e.g. percentage of sites

with ≥ 1 detection unadjusted for detection probability) was 48% for spotted-tailed quolls, 83% for devils, 30% for cats, and 72% for prey. Spotted-tailed quolls and devils were recorded at 38% of sites, spotted-tailed quolls and cats were recorded at 18% of sites, devils and cats were recorded at 23% of sites, and all three predators were recorded at 13% of sites. At 6% of sites no predators were detected.

3.4.2 Environmental models

Although there was a single best model for devil detection probability, the top model set ($\Delta\text{AICc} < 2$) of detection probability p for the quoll, cat and prey consisted of multiple possible models indicating some model uncertainty (Table 3.2). The top model set always included variables for bait age (BAIT) and survey protocol (SURVEY) (Table 3.2). Detection probability declined with bait age for all predators and prey (Figure 3.2), but this effect was statistically significant for the Tasmanian devil only (Figure 3.3). For data from Protocol A in northwest Tasmania, with forest cover held at a mean level, model averaged nightly detection probability estimates ranged from (mean \pm se) 0.051 ± 0.019 to 0.101 ± 0.023 for the spotted-tailed quoll, 0.102 ± 0.024 to 0.197 ± 0.032 for the devil, 0.034 ± 0.019 to 0.074 ± 0.024 for cat, and 0.112 ± 0.024 to 0.147 ± 0.019 for prey (Figure 3.2). For data from Protocol B in southern and north-eastern Tasmania, with forest cover held at a mean level, model averaged nightly detection probability estimates ranged from (mean \pm se) 0.003 ± 0.011 to 0.060 ± 0.016 for the spotted-tailed quoll, 0.072 ± 0.015 to 0.144 ± 0.022 for the devil, 0.026 ± 0.013 to 0.057 ± 0.020 for cat, and 0.117 ± 0.022 to 0.159 ± 0.020 for prey (Figure 3.2).

The environmental variables associated with abundance differed among predator species (Table 3.2, Figure 3.3). The spotted-tailed quoll top model set (with $\Delta\text{AICc} < 2$) carried 66% of model weight, and R^2 values indicated that individual models explained approximately 11% of

variation in abundance (Table 3.2). Spotted-tailed quoll abundance was best explained by mean annual net primary production (MANPP), which was included as a predictor in all three top models (Table 3.2), and had a statistically significant positive effect on abundance (Figure 3.3).

The devil top model set carried 71% of model weight, and individual models explained approximately 46% of variance in devil abundance. Devil abundance was best explained by DFTD arrival time, proportion of forest cover (FOR) and edge density (EDGE) (Table 3.2). Devil abundance was significantly higher in disease free sites (DFTD A) than where DFTD arrived prior to 1999 (DFTD C) (Figure 3.3). Devil abundance also increased significantly as the proportion of forest cover decreased and as edge density increased (Figure 3.3). Testing the effect of environmental influences on devil abundance is limited due to the strong effect of DFTD on abundance across two thirds of the sites, which may confound attempts to link abundance to other factors. Repeating the analysis with disease-free sites only and DFTD and SURVEY excluded as predictor variables still indicated effects of productivity ($\beta = -0.123$, 95% CI = $-0.273 - 0.027$), forest cover ($\beta = -0.307$, 95% CI = $-0.514 - 0.100$) and edge ($\beta = 0.237$, 95% CI = $-0.034 - 0.440$) on devil abundance that were similar in strength and magnitude to that in the state-wide model.

Cat abundance was not well explained by our environmental predictor variables. Although the top model set for the cat carried 45% of model weight, individual models explained only ~ 4% of variation in cat abundance (Table 3.2). Only the intercept model and a model with proportion of forest cover were included in the cat abundance top model set, and the effect of forest cover was not statistically significant (Table 3.2, Figure 3.3).

RESPONSE	STATE	MODEL CONSTANT	MODEL VARIED	R ²	DF	AICc	ΔAICc	w
STQ	<i>p</i>	λ(EDGE, MANPP, FOR, REGION)	<i>p</i> (BAIT)	0.107	8	1048.00	0.00	0.248
			<i>p</i> (.)	0.086	7	1048.96	0.96	0.153
			<i>p</i> (BAIT, SURVEY)	0.113	9	1049.22	1.22	0.135
			<i>p</i> (BAIT, FOR, SURVEY)	0.127	10	1049.36	1.36	0.126
			<i>p</i> (BAIT, FOR)	0.109	9	1049.90	1.85	0.098
	<i>λ</i>	<i>p</i> (BAIT, FOR, SURVEY)	λ(MANPP)	0.108	6	1043.30	0.00	0.289
			λ(MANPP, FOR)	0.118	7	1043.94	0.64	0.21
			λ(EDGE, MANPP)	0.115	7	1044.47	1.17	0.162
TD	<i>p</i>	λ(EDGE, MANPP, FOR, REGION)	<i>p</i> (BAIT, SURVEY)	0.466	9	2111.60	0.00	0.558
	<i>λ</i>	<i>p</i> (BAIT, SURVEY)	λ(EDGE, FOR, DFTD)	0.461	8	2110.50	0.00	0.452
			λ(EDGE, MANPP, FOR, DFTD)	0.466	9	2111.56	1.06	0.267
CAT	<i>p</i>	λ(EDGE, MANPP, FOR, REGION)	<i>p</i> (FOR)	0.036	8	642.60	0.00	0.189
			<i>p</i> (BAIT, FOR)	0.051	9	642.72	0.12	0.178
			<i>p</i> (SURVEY)	0.031	8	643.35	0.75	0.13
			<i>p</i> (.)	0.013	7	643.67	1.07	0.111
			<i>p</i> (BAIT)	0.028	8	643.69	1.09	0.11
			<i>p</i> (FOR, SURVEY)	0.043	9	643.84	1.24	0.101
			<i>p</i> (BAIT, SURVEY)	0.043	9	643.86	1.26	0.101
			<i>p</i> (BAIT, FOR, SURVEY)	0.056	10	644.29	1.69	0.081
	<i>λ</i>	<i>p</i> (BAIT, FOR, SURVEY)	λ(.)	0.035	5	636.00	0.00	0.302
			λ(FOR)	0.041	6	637.36	1.36	0.153
PREY	<i>p</i>	λ(EDGE, MANPP, FOR, REGION)	<i>p</i> (.)	0.087	7	1848.20	0.00	0.317
			<i>p</i> (BAIT)	0.096	8	1848.98	0.78	0.215
			<i>p</i> (SURVEY)	0.089	8	1850.11	1.91	0.122
	<i>λ</i>	<i>p</i> (BAIT, SURVEY)	λ(MANPP, FOR, REGION)	0.098	8	1848.80	0.00	0.249
			λ(FOR, REGION)	0.079	7	1849.46	0.66	0.179
			λ(.)	0.062	6	1849.86	1.06	0.146

Table 3.2: Comparison of models exploring the influence of environmental and regional factors on detection probability (p) and abundance (λ) of the spotted-tailed quoll (STQ), feral cat (CAT), Tasmanian devil (TD) and mammalian prey (PREY) in Tasmania. R² is the proportion of variance explained by the model; DF is the number of parameters in the model; ΔAICc is the difference in AICc values between each model and the lowest ranked model; w is AIC weight. Only top ranked models with ΔAICc < 2 are presented

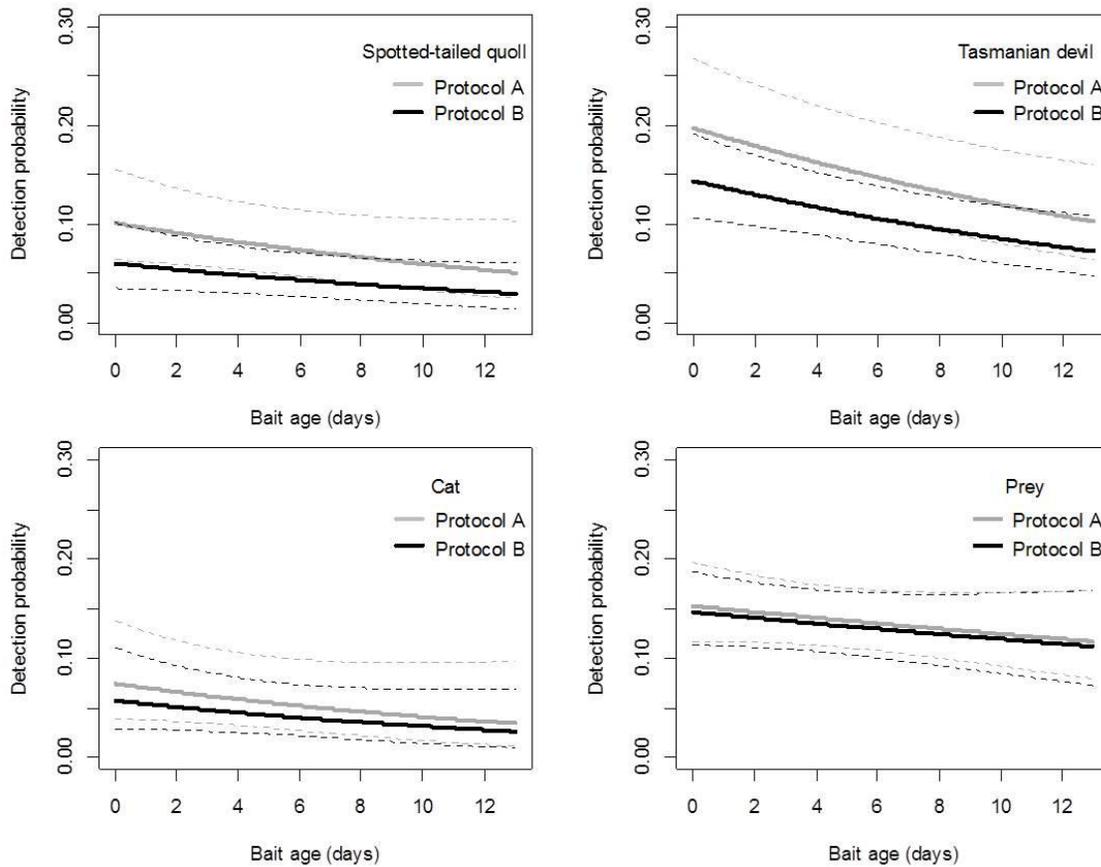


Figure 3.2: Nightly detection probability as a function of time since bait was set (BAIT) conditional on survey protocol (SURVEY Protocol A or B) for the spotted-tailed quoll, Tasmanian devil, cat, and prey. Dark lines indicated mean predicted detection probability given time since bait was set and survey protocol, light dashed lines indicate upper and lower 95% confidence intervals of predictions.

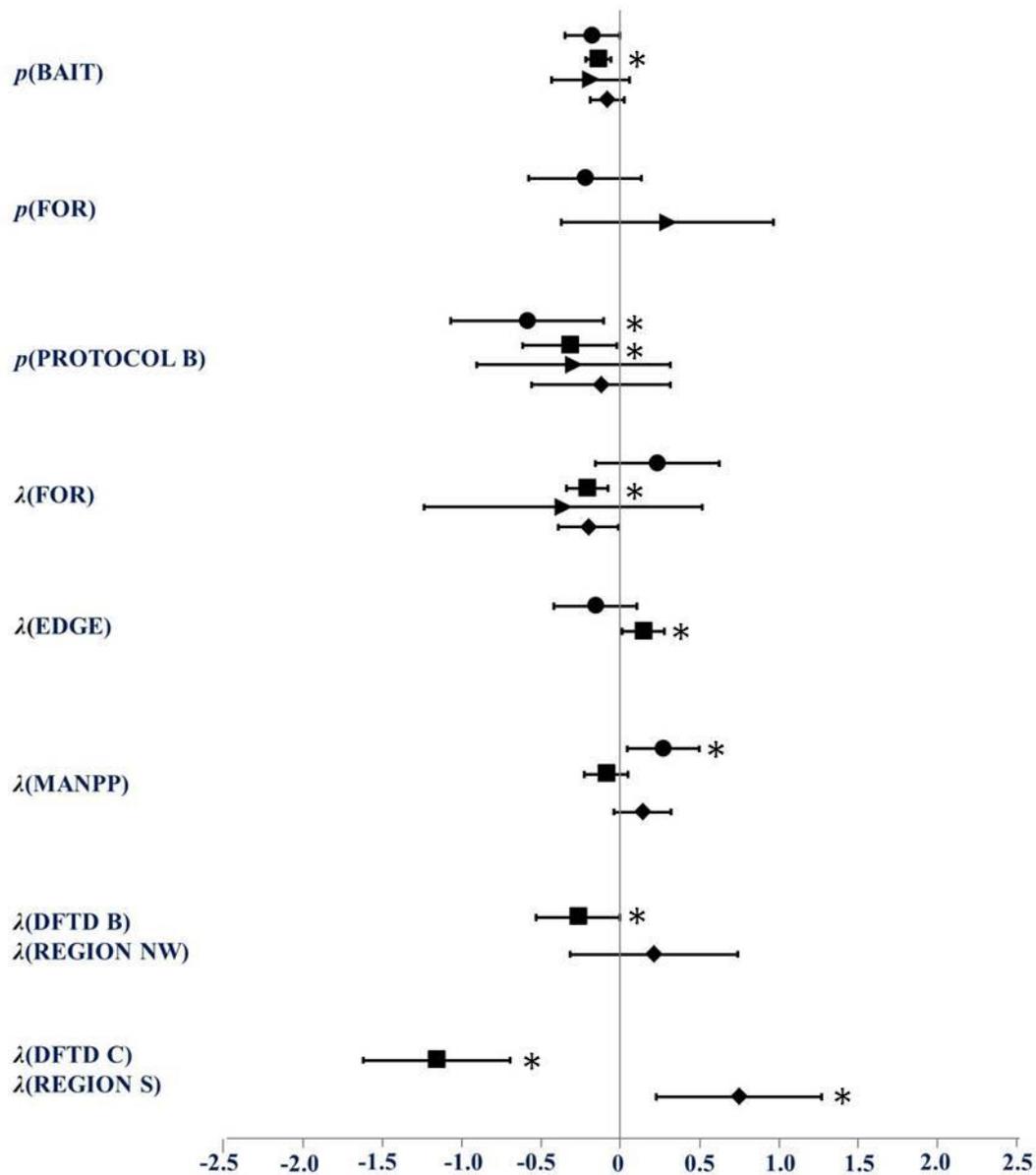


Figure 3.3: Model averaged coefficient estimates and 95% confidence intervals from the highest ranked models ($\Delta\text{AICc} < 2$) estimating the effect of environmental and regional variables on the detection probability (p) and abundance (λ) of the spotted-tailed quoll (circles), Tasmanian devil (squares), cat (triangles) and prey (diamonds). Y-axis shows predictor variables. X-axis indicates effect sizes on standardized scale. Stars denote statistical significant effects i.e. confidence interval does not span zero.

The prey top model set carried 57% of model weight, and individual models explained approximately 6 - 10% of variance in abundance (Table 3.2). Models containing environmental predictor variables provided equivalent or less support than the intercept-only model for abundance. However, there was a significant effect of proportion of forest cover: prey abundance declined as the proportion of forest cover increased (Table 3.2, Figure 3.3).

3.4.3 Co-occurrence models

Low Pearson and Spearman rank correlation coefficients indicated a lack of simple linear or monotonic relationships among predicted abundances of predator species and prey (Figure 3.4). For all three predator species and prey, the top model set ($\Delta AICc < 2$) for detection probability consisted of multiple possible models. The intercept-only detection model provided equivalent or better fit than models that included the presence of other predators (Table 3.3). Cat presence on the same trap night had a positive effect on both spotted-tailed quoll and devil detection probability, and similarly, devil and spotted-tailed quoll presence had a marked positive effect on cat detection probability, however, these effects were not statistically significant (Figure 3.5).

The intercept-only model was included in the top model set for both the spotted-tailed quoll and the devil, indicating that for these two species, inclusion of the predicted abundance of co-occurring predators and prey did not significantly improve model fit relative to an abundance model with no variables (Table 3.3). However, the cat model did not include the intercept-only model, indicating that inclusion of the abundance of other predators and prey improved the fit of this model (Table 3.3). The spotted-tailed quoll top model set carried approximately 71% of model weight, and individual models explained approximately 2 - 4% of variation in abundance (Table 3.3).

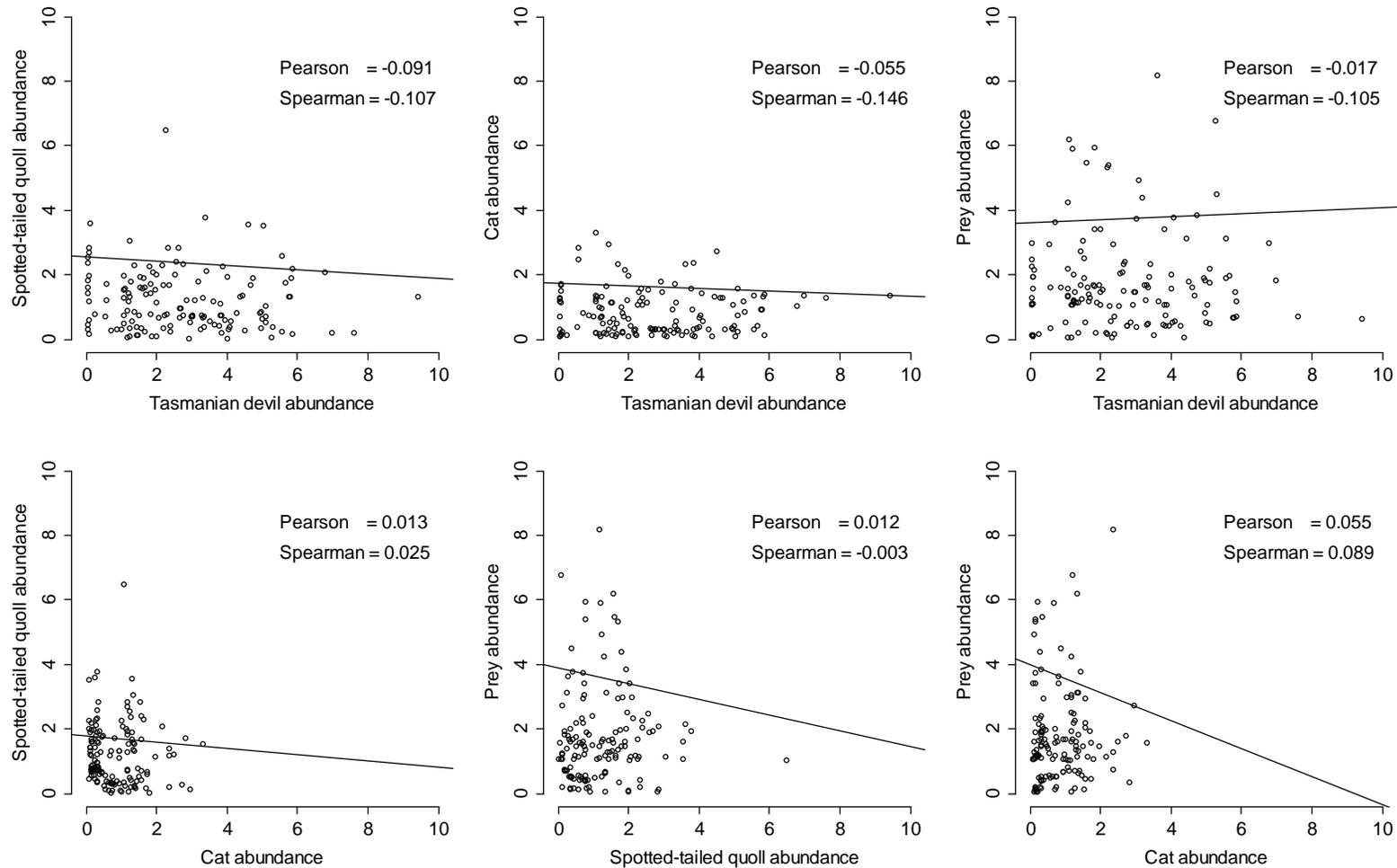


Figure 3.4: Relationship between all pairwise combinations of mean predicted abundances for the spotted-tailed quoll, Tasmanian devil, cat, and prey generated from Royle-Nichol models of environmental effects on abundance across Tasmania, Australia. Pearson = Pearson correlation coefficient value; Spearman = Spearman rank correlation coefficient values. Lines indicate the regression line for the 90th quantile.

RESPONSE	REGION	STATE	MODEL CONSTANT	MODEL VARIED	R ²	df	AICc	ΔAICc	w		
SQ	ALL	p	λ(CAT*TD*PREY)	p(.)	0.045	9	1059.60	0.00	0.416		
				p(CATP)	0.058	10	1060.10	0.50	0.324		
				λ	p(CATP)	λ(PREY)	0.033	4	1050.50	0.00	0.193
				λ(.)		0.017	3	1050.70	0.2	0.175	
		λ	p(CATP)	λ(PREY, TD)	0.037	5	1051.90	1.44	0.094		
				λ(CAT)	0.022	4	1052.08	1.58	0.088		
				λ(CAT, PREY)	0.036	5	1052.16	1.66	0.084		
				λ(TD)	0.020	4	1052.26	1.76	0.080		
TD	ALL	p	λ(SQ*CAT*PREY)	p(.)	0.056	9	2192.20	0.00	0.384		
				p(CATP)	0.071	10	2192.33	0.13	0.361		
		λ	p(CATP)	λ(CAT, SQ)	0.060	6	2184.90	0.00	0.239		
				λ(.)	0.011	3	2185.65	0.75	0.164		
				λ(CAT)	0.022	4	2186.20	1.30	0.125		
CAT	ALL	p	λ(TD*SQ*PREY)	p(.)	0.067	9	640.30	0.00	0.353		
				p(STQP)	0.078	10	640.93	0.63	0.257		
				p(TDP)	0.076	10	641.17	0.87	0.229		
				p(STQP, TDP)	0.087	11	641.87	1.57	0.161		
				λ	p(TDP, STQP)	λ(TD, PREY)	0.067	6	633.50	0.00	0.163
		λ(TD, SQ, PREY)	0.076	7		634.33	0.83	0.107			
		λ(PREY)	0.044	5		634.69	1.19	0.090			
		λ(TD)	0.044	5		634.76	1.26	0.087			
		λ(TD, SQ)	0.056	6		635.13	1.63	0.072			
		λ(TD, PREY, TD*PREY)	0.070	7		635.17	1.67	0.071			
		λ(SQ, PREY)	0.055	6	635.26	1.76	0.068				

Table 3.3: Comparison of models exploring the influence of co-occurring predators and prey on detection probability (p) and abundance (λ) of each predator species: spotted-tailed quoll (SQ), Tasmanian devil (TD), and cat (CAT). Models with interactions also included all lower order terms i.e. main effects and two-way interactions. R^2 is the proportion of variance explained by the model; DF is the number of parameters in the model; $\Delta AICc$ is the difference in AICc values between each model and the lowest ranked model; w is AIC weight. Only top ranked models with $\Delta AICc < 2$ are presented.

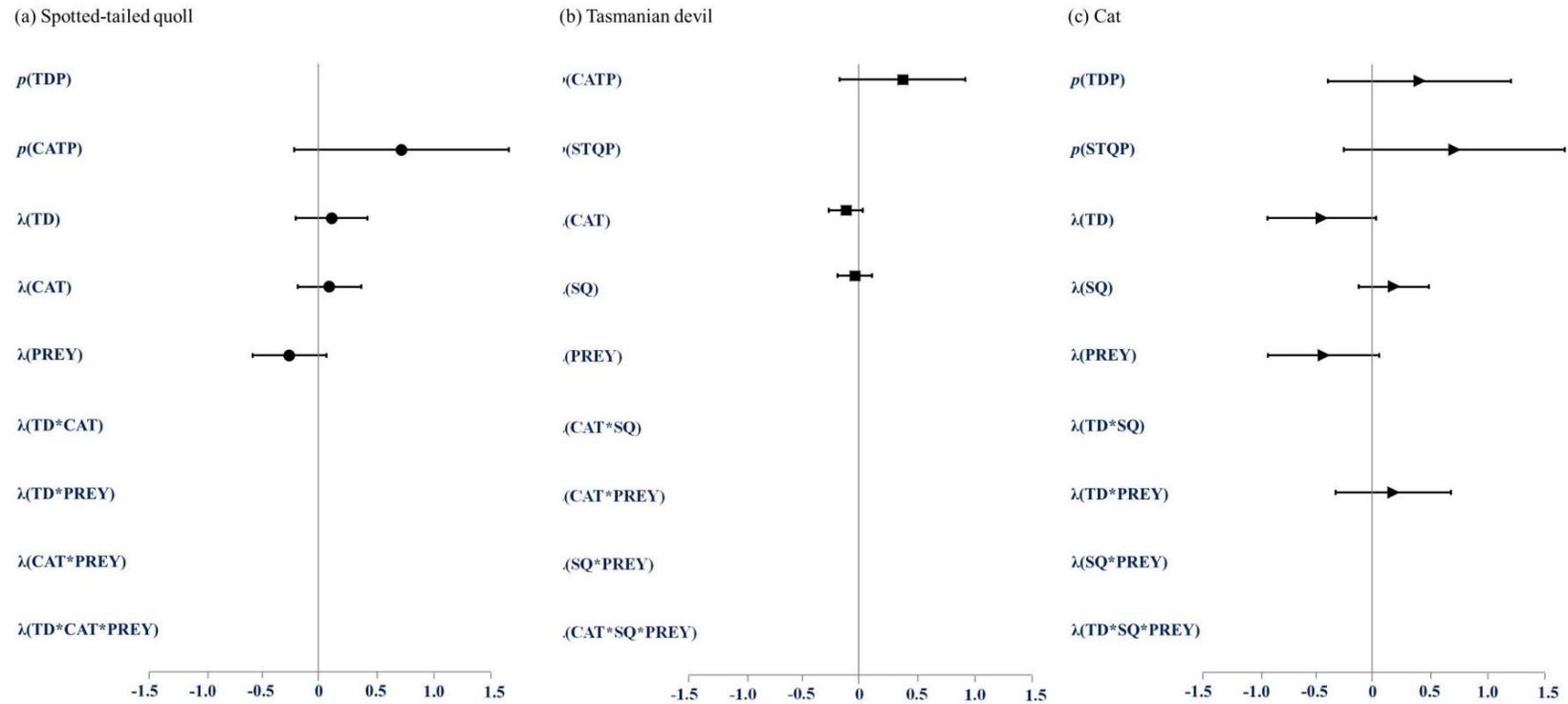


Figure 3.5: Model averaged coefficient estimates and 95% confidence intervals from the highest ranked models ($\Delta\text{AICc} < 2$) estimating the effect of the abundance of co-occurring predators and prey on the detection probability (p) and abundance (λ) of the (a) spotted-tailed quoll, (b) Tasmanian devil, and (c) feral cat across Tasmania. Y-axis shows predictor variables. X-axis indicates effect sizes on standardized scale. As all 95% confidence intervals overlapped zero, no predictors of co-occurrence were statistically significant.

The Tasmanian devil top model set carried approximately 53% of model weight, and individual models explained approximately 1 - 6% of variation in abundance (Table 3.3). The cat top model set carried approximately 65% of model weight and explained 4 - 8% of variation in cat abundance (Table 3.3).

The abundance of other predators was included as a variable in the top model set for each predator species (Table 3.3) but their effects on the focal predator's abundance were never statistically significant (Figure 3.5). Interactive effects of other predators were not included in the top model set of any predator species or of prey (Table 3.3). Prey abundance was included as a predictor variable in the top model set for the spotted-tailed quoll and cat (Table 3.3) but it did not have a significant effect on either species' abundance (Figure 3.5).

All environment and co-occurrence models fit the data (all parametric bootstrap p -values > 0.099). Co-occurrence models did not provide better model fit to the data than environment models. For the spotted-tailed quoll, there was some support that the environment models (AICc range = 1043.3 - 1044.5) better explained quoll abundance than the co-occurrence models (AICc range = 1050.5 - 1052.3). For the Tasmanian devil, there was substantial support that the environment model (AICc range = 2110.50 - 2110.6) fit better than the co-occurrence model (AICc range = 2184.9 - 2186.2). The cat environment model provided similar fit to the co-occurrence model, with environment model AICc equivalent to or slightly lower than co-occurrence model AICc (Cat AICc: environment model range = 636.0 - 637.4; co-occurrence model range = 633.5 - 635.3)

We found no evidence for a limiting effect of any predators on one another, or prey on any predator (Table 3.4, Figure 3.4). Furthermore, we found no evidence to suggest a limiting effect of any predators (either species or groups) on prey (Table 3.4).

MODEL	SLOPE (\pm SE)
SQ ~ TD	-0.068 (0.080)
CAT ~ TD	0.062 (0.272)
SQ ~ CAT	-0.038 (0.047)
CAT ~ SQ	-0.094 (0.085)
PREY ~ TD	0.09 (0.236)
PREY ~ SQ	-0.51 (0.328)
PREY ~ CAT	-0.626 (0.594)
PREY ~ ENDEMIC	-0.037 (0.221)
PREY ~ ALL	-0.133 (0.193)
TD ~ PREY	-0.025 (0.207)
SQ ~ PREY	-0.148 (0.094)
CAT ~ PREY	-0.085 (0.118)
ENDEMIC ~ PREY	-0.129 (0.300)
ALL ~ PREY	-0.087 (0.258)

Table 3.4: Slope coefficients (\pm standard error) from quantile regression analyses investigating limiting effects of predators and prey on one another's abundance in Tasmania, Australia. Regressions were conducted on 80th quantile. SQ = spotted-tailed quoll; TD = Tasmanian devil; CAT = feral cat; PREY = small- and medium-sized mammalian prey; ENDEMIC = predator species endemic to Tasmania (e.g. sum of quoll and devil abundance); ALL = all predators (e.g. sum of quoll, devil, and cat abundance). * denotes statistically significant at $\alpha=0.05$ (none significant).

3.5 Discussion

Our research provides novel insight into the bottom-up and top-down determinants of Tasmanian predator distribution. Although we found a positive relationship between spotted-tailed quoll abundance and productivity, there was no effect of productivity on devils, cats or mammalian prey. As expected, we did not find a significant relationship between cat abundance and forest cover or fragmentation. Contrary to our predictions, we did not find a relationship between spotted-tailed quoll abundance and forest cover and fragmentation, and devil abundance increased with decreasing forest cover and increasing fragmentation. We found no evidence to suggest that any predator behaviourally or numerically suppresses any other predator or mammalian prey. Similarly, we found no support for the idea that the abundance of any predator increases with or is limited by mammalian prey abundance. Models that included

bottom-up environmental variables had more support than those that included the abundance of other predators or mammalian prey, suggesting that top-down competition may not play a major role in determining the abundance and distribution of Tasmanian predators.

3.5.1 Environmental factors

Although spotted-tailed quoll abundance increased with increasing productivity, this was not through an effect of productivity increasing mammalian prey abundance. Likewise, we did not find a relationship between productivity and devil or cat abundance. The reason for the relationship between productivity and spotted-tailed quoll abundance is not clear, and it may be that net primary production is correlated with some other unmeasured environmental variable that is linked with that species' prey abundance. At face value, our results appear to differ from the Hollings *et al.* (2014) finding that cat occurrence and top-down control of cats by devils was positively associated with factors they believed to be associated with productivity such as rainfall, vegetation type, prey abundance, and human settlement. However, productivity was not directly measured in that study, making direct comparison difficult.

There are at least three potential explanations for the lack of effect of productivity found here. Theory (Oksanen *et al.* 1981; Oksanen and Oksanen 2000) and empirical studies (Elmhagen *et al.* 2010; Elmhagen and Rushton 2007) show that in cold, unproductive areas, intense winter grazing pressure prevents the accumulation of above ground biomass and woody vegetation, which limits prey abundance and therefore the abundance and diversity of predators. However, those studies considered the unproductive tundra and boreal forests of Finland and Scandinavia (primary production < 2 kg C yr) (Oksanen and Oksanen 2000). In contrast, the low latitude, maritime climate in Tasmania results in restricted snow cover, a long growing season and relatively high primary production, with over 99% of the state having mean

net primary production $> 2 \text{ kg C yr}^{-1}$. The high productivity and relatively constant availability of forage in the Tasmanian system may mean that productivity is not the primary factor limiting mammalian prey abundance, and therefore productivity is also not strongly linked to predator abundance. A second non-exclusive explanation for our results is that broad-scale anthropogenic disturbance of landscapes in Tasmania has decoupled the relationship between net primary production and the abundance of mammalian prey and predators. Finally, it is also possible that the limited number of sites used in this study resulted in insufficient statistical power to resolve relationships between predator species and the environment, or among predator species.

The positive effect of edges and open vegetation on devil abundance may reflect selection for the portion of mammalian prey that is using those habitats. Edge density was not included in the top prey models, perhaps because we included both anthropogenic (forest - pasture) and natural (forest – native grassland or heath) edges; devil prey is less abundant in the latter. Previous studies that found a positive effect of edge on devil density considered only anthropogenic edges (Baynes 2007; Pukk 2005). The devil prefers medium- to large-sized mammalian prey such as the pademelon and Bennett's wallaby (Jones and Barmuta 1998; Pemberton *et al.* 2008) which reach highest abundance in heterogeneous landscapes and along edges in agricultural landscapes, because of the proximity of foraging habitat in pasture or plantation that is adjacent to forest for shelter (Le Mar and McArthur 2005). Furthermore, this finding may indicate that a relationship between abundance and edge density is negative or absent for others of the more than 14 mammalian prey species that we recorded.

The lack of effect of forest cover and edge density on quoll and cat abundance may indicate either prey selection from a range of habitats, or competition from devils in fragmented open landscapes. While cat abundance has been found to be higher in open habitat than closed

forest (Dickman 1996), the species is capable of persisting in forested landscapes at moderate to high densities (Buckmaster 2012). Similarly, our results support the idea that the spotted-tailed quoll is not restricted to completely forested landscapes (Chapter 2). On average, both of these mesopredators take smaller prey than the devil (Jones and Barmuta 1998; Lazenby 2012; Taylor 1986), and are generalist predators capable of switching among prey species to exploit locally abundant resources (Dawson *et al.* 2007; Molsher 1999; Risbey *et al.* 1999).

3.5.2 Co-occurrence – behavioural suppression

We did not find clear evidence for an effect of the presence of any predator on the detection probability of any predator or mammalian prey. Therefore, our data do not support the hypothesis that the devil behaviourally suppresses the activity of the cat or the spotted-tailed quoll, or that the cat behaviourally suppresses the activity of spotted-tailed quolls. However our evidence is not sufficient to reject this hypothesis entirely. Our finding of a trend toward a positive association between the detection probability of a predator and the presence of other predator(s) indicates that predators tended to be active on the same night at the same site, perhaps as a common response to prey activity or favourable conditions for hunting. Our results differ from those of Lazenby and Dickman (2013), where the probability of detecting a feral cat at a camera was found to be consistently lower at sites where devils were detected. There are, however, large and overlapping confidence intervals in both our study and that of Lazenby and Dickman (2013), which may simply mean that the true effect of devil presence on cat detection probability is intermediate between both estimates. While our results differ, we echo the conclusion of Lazenby and Dickman (2013) that future analysis of camera trapping data should address potential bias in detection probability resulting from the presence of other species, and suggest that these relationships still need to be resolved in the Tasmania context.

3.5.3 Co-occurrence –abundance relationships among predators

Our finding that cat abundance was not related to or limited by devil abundance concurs with that of a study on probability of cat occupancy in southern Tasmania (Lazenby 2012), but differs from two other empirical studies. The first of these interpreted an increase in cat occurrence in north-eastern Tasmania, where DFTD has been longest established, as a result of devil population decline (Hollings *et al.* 2014). Conversely, the second found a strong positive association between devil and cat abundance in north-western Tasmania (Saunders 2011).

One potential explanation for the differing results is that the apparent relationships between devil and cat occurrence may instead reflect coincidental unmeasured environmental variables affecting mesopredator abundance or detection probability. For example, between 1996 and 2008 (the same period that devils were declining from DFTD), rates of forest clearance in the Ben Lomond bioregion, where 80% of the early disease arrival (i.e. decreasing devil abundance) sites from Hollings *et al.* (2014) were located, were 2.5 - 12 times that of the Midlands, South-East and Central Highlands bioregions (FPA 2008). Such disturbances could increase food resources and thereby cat occurrence (Liberg *et al.* 2000). Additionally, an increase in open areas, in improving visibility, could result in an increase in cat detection probability along spotlighting transects (Hayward and Marlow 2014). It is possible that rather than cat occurrence increasing as a result of devil decline, the observed mesopredator release of cats could result from an increase in probability of detecting cats along spotlighting transects due to better visibility of open areas vs forest (Denny and Dickman 2010; Hayward and Marlow 2014).

3.5.4 Co-occurrence – abundance relationships between predators and prey

The lack of positive or limiting relationship of prey abundance on predator abundance may relate to insufficiently comprehensive measurements of prey abundance. Further dividing prey into size categories or modelling the occurrence of a few indicator species relevant to each predator may reveal an influence of prey on predators. Alternatively, abundance of additional prey taxa may be important. For example, in Tasmania, birds have been shown to be a component of the diet of the cat (Lazenby 2012; Taylor 1986), spotted-tailed quoll (Jones and Barmuta 1998) and devil (Jones and Barmuta 1998; Pemberton *et al.* 2008). Finally, strong relationships between predator and prey abundance may only become apparent during times of resource limitation such as drought. Resources were abundant during our study period.

Competition theory predicts that sympatric competing species can coexist via resource partitioning; if different species prefer different microhabitats, prey, or activity times, or have different hunting strategies, their interactions will be low even where there is high spatial overlap (Davies *et al.* 2007; Rosenzweig 1966). In this study, we measured only spatial overlap in detection and abundance, and found no evidence that the devil regulates the abundance of the two mesopredators, the spotted-tailed quoll or the cat, or that the cat regulates abundance of the spotted-tailed quoll. Importantly, this result does not preclude the possibility that animals avoid potential competitive interactions at finer scales than those measured here. The use of smaller prey and arboreal forest habitat by the spotted-tailed quoll has been suggested as a mechanism to avoid competition from the devil (Jones and Barmuta 2000). In addition, there is evidence of “the ghost of competition past” structuring the Tasmanian marsupial carnivore guild on an evolutionary time scale, with character displacement resulting in equal spacing in prey size distribution in Tasmania and thus minimisation of competition in the guild now (Jones 1997). Similarly, dietary studies indicate that the feral cat consumes smaller prey than the devil (Jones and Barmuta 1998; Lazenby 2012; Pemberton *et al.* 2008; Taylor 1986) and that two species

have different hunting styles (Attard *et al.* 2011), indicating some amount of separation in their ecological requirements that may facilitate co-occurrence. Although overlapping spatially, it is also possible that the devil, cat and spotted-tailed quoll are active at different times of day. Our results suggest that any competitive interactions or temporal avoidance among these predators occurring at fine spatial scales do not translate into a numerical relationship at the distribution scale.

3.5.5 Limitations

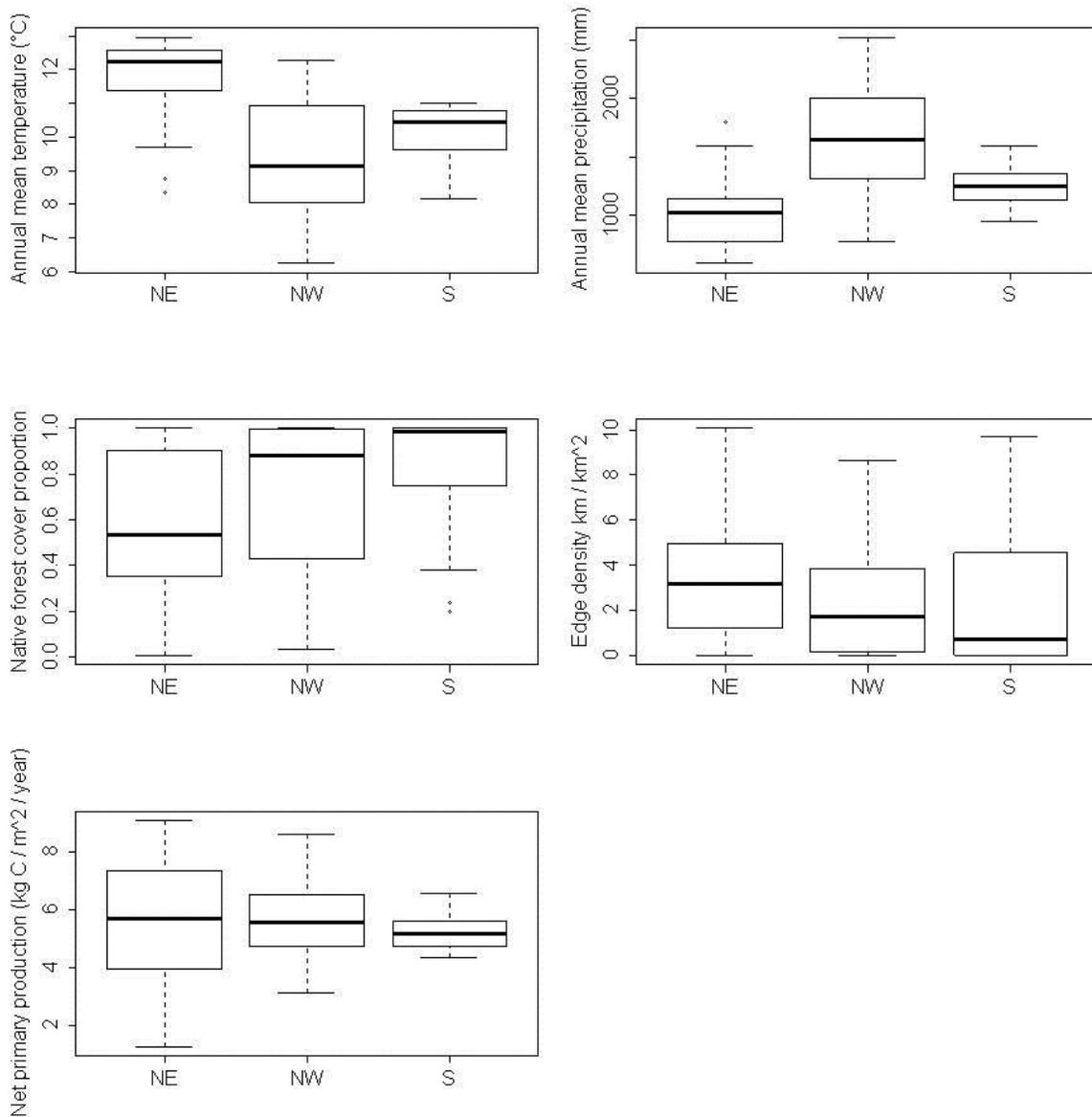
Our estimates are relatively imprecise (Appendix 3.3) due to the low detection probability of predators; however, our choice of methods means that they are also unbiased, and should accurately reflect interspecific patterns in abundance. Uncertainty around the estimates of predator abundance could not be accounted for when they were used as predictor variables in the co-occurrence models. Low detection probability is a common problem in surveys of wide-ranging predators (O'Connell Jr *et al.* 2006); even when a site is occupied, the frequency of detections is often low because cameras sample only a small proportion of an individual animals home range, and may therefore only be encountered when the animal is nearby, which may be as infrequently as once or twice a week. Although low, our detection probability estimates are within the range of those previously reported from camera trapping surveys for these study species (Nelson *et al.* 2010; Saunders 2011) and for ecologically similar predators in other ecosystems (O'Connell Jr *et al.* 2006), and thus reflect challenges in surveying carnivores, rather than inherent problems in our survey method. Uncertainty in predicted abundance estimates could propagate in the co-occurrence models, making interspecific effects even more difficult to detect. Raw counts or an abundance index would provide more precise estimates of the effects of covariates than predicted abundance, but they

could be biased (Gu and Swihart 2004) or underestimate abundance by an unknown amount (MacKenzie *et al.* 2002).

3.5.6 Conclusions

In summary, although we found effects of productivity, forest cover and fragmentation on abundance and distribution of predators, there was little evidence for behavioural or numerical suppression of mesopredators by the top predator, or mesopredators by one another at our study sites. Thus, our results do not support the hypothesis that decline of the top predator, the devil, will lead to mesopredator release, or density- or behaviourally-mediated trophic cascades in the Tasmanian system, at least with respect to the carnivore species studied. However, given the variability in results between our study and others (Hollings *et al.* 2014; Lazenby and Dickman 2013; Saunders 2011), we emphasise the need for detailed study of the basic ecology of Tasmanian predators, including prey resource preferences, microhabitat selection, activity times, hunting strategies, and frequency of interspecific interactions to better understand the mechanisms of interspecific relations. Ideally future approaches would include manipulative experiments (Schoener 1983) through predator reintroduction or removal, but such experiments may not be viable given the need to avoid additional impacts on these threatened species. Space-for-time and mechanistic field studies in multiple landscape contexts and seasons could also strengthen inference from correlative studies such as ours. Importantly, the fitness outcomes resulting from niche overlap or partitioning are required before spatial overlap or correlations in abundance can be definitely attributed to asymmetric competition, and to predict ecosystem impacts of Tasmanian devil decline, or decline of top predators more broadly.

Appendix 3.1: Sampling of rainfall, temperature and environmental predictor variables among study regions.



Appendix 3.2: Small- and medium-sized mammals considered as potential prey for the spotted-tailed quoll, Tasmanian devil, and / or cat. Not all species listed were recorded on our cameras, and not all camera records could be identified to species level, particularly small mammals. Weights are minimum and maximum for species as per Menkhort and Knight (2004).

COMMON NAME	SPECIES NAME	BODY WEIGHT (g)
Bennett's wallaby	<i>Macropus rufogriseus</i>	16,000 – 27,000
Black rat	<i>Rattus rattus</i>	95 - 300
Broad-toothed mouse	<i>Pseudomys fuscus</i>	95 - 145
Brown rat	<i>Rattus norvegicus</i>	280 - 500
Common ringtail possum	<i>Pseudocheirus peregrinus</i>	660 - 900
Common brushtail possum	<i>Trichosurus vulpecular</i>	1500 - 4000
Dusky antechinus	<i>Antechinus swainsonii</i>	38 - 170
Eastern barred bandicoot	<i>Perameles gunnii</i>	500 - 1100
Eastern pygmy-possum	<i>Cercartetus nanus</i>	15 - 38
European hare	<i>Lepus europeaus</i>	2,500 – 6,500
European rabbit	<i>Oryctolagus cuniculus</i>	1,000 – 2,400
House mouse	<i>Mus musculus</i>	10 - 25
Little pygmy-possum	<i>Cercartetus lepidus</i>	25 - 40
Long-nosed potoroo	<i>Potorous tridactylus</i>	660 – 1,600
Long-tailed mouse	<i>Pseudomys higginsii</i>	50 - 90
New Holland mouse	<i>Pseudomys novaehollandiae</i>	15 - 25
Southern brown bandicoot	<i>Isodon obesulus</i>	400 - 1000
Sugar glider	<i>Petaurus breviceps</i>	90 - 150
Swamp antechinus	<i>Antechinus minimus</i>	28 - 100
Swamp rat	<i>Rattus lutreolus</i>	55 - 160
Tasmanian pademelon	<i>Thylogale billardierii</i>	5,800 – 9,000
Water rat	<i>Hydromys chrysogaster</i>	620 – 1,200

Appendix 3.3: Mean and upper and lower 95% confidence interval from posterior distribution of predicted predator and prey abundance in Tasmania, Australia. These values were used in co-occurrence models.

Site	Quoll			Devil			Cat			Prey		
	Mean	UCI	LCI									
1	0.320	0	2	4.045	2	7	0.742	0	3	0.524	0	2
2	0.742	0	3	3.852	2	7	0.303	0	2	0.416	0	2
3	0.173	0	1	5.856	3	10	1.389	0	4	0.719	0	3
4	0.641	0	3	4.998	2	9	0.431	0	2	0.546	0	2
5	0.379	0	2	3.353	1	6	0.584	0	2	0.492	0	2
6	0.757	0	3	3.031	1	6	0.303	0	2	0.404	0	2
7	0.366	0	2	1.555	1	3	0.635	0	3	0.546	0	2
8	0.436	0	2	3.778	1	7	1.567	1	3	0.471	0	2
9	0.240	0	1	2.393	1	5	1.090	0	3	0.711	0	3
10	0.356	0	2	1.241	0	4	0.712	0	3	1.994	1	4
11	0.204	0	1	7.616	4	12	1.283	0	4	0.720	0	3
12	0.191	0	1	6.987	3	11	1.379	0	4	1.814	1	4
13	0.314	0	2	3.235	1	6	0.923	0	3	1.689	1	4
14	0.374	0	2	5.300	3	9	0.860	0	3	4.510	2	7
15	1.235	0	4	2.847	1	5	0.310	0	2	0.541	0	2
16	0.330	0	2	0.994	0	3	0.725	0	3	0.538	0	2
17	0.335	0	2	0.877	0	3	0.764	0	3	1.632	1	4
18	0.723	0	3	2.980	1	6	0.303	0	2	1.459	1	3
19	0.192	0	1	3.831	1	7	2.359	1	5	0.733	0	3
20	0.808	0	3	4.918	2	8	0.349	0	2	1.896	1	4
21	0.767	0	3	2.767	1	5	0.305	0	2	0.408	0	2
22	0.823	0	3	4.277	2	7	0.303	0	2	0.421	0	2
23	0.856	0	3	4.968	2	8	0.303	0	2	1.840	1	4
24	0.519	0	2	2.954	1	6	1.486	1	3	1.487	1	3
25	1.890	1	4	5.805	3	9	1.317	1	3	1.469	1	3
26	2.402	1	5	2.537	1	5	1.559	1	3	2.058	1	4
27	0.623	0	3	3.923	2	7	0.365	0	2	0.433	0	2
28	0.662	0	3	3.313	1	6	1.721	1	4	0.461	0	2
29	2.307	1	4	2.168	1	4	0.266	0	2	0.197	0	1
30	0.961	0	3	2.668	1	5	0.303	0	2	1.501	1	3
31	0.524	0	2	5.096	2	9	0.756	0	3	1.759	1	4
32	1.749	1	4	5.651	3	9	0.443	0	2	1.994	1	4
33	0.281	0	2	4.496	2	8	2.728	1	5	1.807	1	4

34	0.337	0	2	4.958	2	8	1.076	0	3	0.830	0	3
35	1.555	1	3	1.064	0	3	3.324	2	6	1.592	1	3
36	1.910	1	4	4.731	2	8	0.309	0	2	3.851	2	6
37	1.343	1	3	5.796	3	9	0.925	0	3	0.683	0	3
38	1.340	1	3	5.758	3	9	0.925	0	3	0.683	0	3
39	0.772	0	3	2.304	1	5	1.462	1	3	0.579	0	2
40	0.268	0	2	0.714	0	3	0.815	0	3	3.638	2	6
41	2.324	1	5	2.753	1	5	0.303	0	2	0.414	0	2
42	2.575	1	5	5.549	3	9	0.303	0	2	1.904	1	4
43	0.239	0	1	5.559	3	9	1.377	0	4	3.143	1	6
44	0.704	0	3	5.101	2	9	1.578	1	3	2.208	1	4
45	0.584	0	2	4.110	2	7	0.552	0	2	0.567	0	2
46	0.973	0	3	2.670	1	5	0.307	0	2	2.404	1	5
47	1.439	1	3	1.832	1	4	0.240	0	1	1.650	1	3
48	1.305	1	3	1.079	0	3	1.175	0	4	4.258	2	7
49	0.670	0	3	2.074	1	4	0.440	0	2	1.542	1	3
50	2.838	1	6	2.635	1	5	0.353	0	2	2.071	1	4
51	1.319	1	3	9.410	5	15	1.374	0	4	0.640	0	3
52	1.937	1	4	3.992	2	7	0.380	0	2	2.004	1	4
53	2.099	1	4	6.785	4	11	1.043	0	3	3.000	1	6
54	3.788	2	7	3.372	1	6	0.303	0	2	1.929	1	4
55	1.421	1	3	1.207	1	2	0.105	0	1	1.072	1	2
56	0.867	0	3	1.366	1	3	0.159	0	1	0.196	0	1
57	0.033	0	1	4.012	2	6	0.692	0	3	1.568	1	3
58	1.574	1	3	1.105	1	2	1.337	1	3	6.201	4	9
59	1.904	1	4	1.619	1	3	0.118	0	1	1.604	1	3
60	6.469	4	9	2.270	1	4	1.064	1	2	1.031	1	2
61	2.024	1	4	2.006	1	3	0.083	0	1	3.418	2	5
62	1.098	1	2	3.796	2	6	0.937	0	3	1.089	1	2
63	3.537	2	6	5.019	3	7	0.083	0	1	1.068	1	2
64	1.699	1	3	2.343	1	4	1.578	1	3	2.935	2	5
65	2.561	1	5	0.039	0	1	1.239	1	2	2.481	1	4
66	0.459	0	2	0.046	0	1	0.083	0	1	1.066	1	2
67	2.010	1	4	2.528	1	4	1.129	1	2	1.033	1	2
68	3.061	1	5	1.233	1	2	1.333	1	3	1.136	1	2
69	1.219	1	2	3.065	2	5	0.107	0	1	4.939	3	7
70	0.110	0	1	1.849	1	4	0.726	0	3	0.205	0	1
71	1.543	1	3	1.086	1	2	1.366	1	3	1.338	1	3
72	0.072	0	1	5.267	3	8	1.197	0	4	6.760	4	10
73	0.029	0	1	2.918	2	5	1.800	1	4	1.087	1	2
74	1.398	1	3	1.685	1	3	2.341	1	4	1.297	1	2

75	2.834	1	5	2.312	1	4	1.177	1	2	0.067	0	1
76	1.833	1	4	0.046	0	1	1.174	1	2	3.004	2	5
77	2.252	1	4	3.874	2	6	0.090	0	1	1.070	1	2
78	1.622	1	4	1.660	1	3	0.180	0	1	1.190	1	2
79	1.450	1	3	0.040	0	1	0.103	0	1	1.299	1	3
80	1.344	1	3	4.373	3	7	0.118	0	1	0.060	0	1
81	1.807	1	3	3.172	2	5	0.284	0	2	4.402	3	7
82	0.714	0	3	0.555	0	2	0.374	0	2	2.934	1	5
83	1.545	1	3	1.973	1	4	1.217	0	4	1.686	1	3
84	0.113	0	1	2.008	1	4	0.624	0	3	1.070	1	2
85	2.265	1	4	1.794	1	3	1.001	0	3	1.687	1	3
86	0.066	0	1	1.172	1	2	0.990	0	3	1.078	1	2
87	1.231	1	2	0.582	0	2	2.491	1	5	1.618	1	4
88	0.163	0	1	0.082	0	1	1.705	1	4	1.957	1	4
89	1.322	1	3	1.243	1	2	0.714	0	3	1.189	1	2
90	0.123	0	1	1.463	1	3	0.543	0	2	1.259	1	2
91	0.111	0	1	1.242	1	2	0.971	0	3	1.218	1	2
92	1.160	1	2	1.988	1	4	1.962	1	4	1.477	1	3
93	0.764	0	3	1.072	1	2	0.195	0	1	1.347	1	3
94	0.896	0	3	1.154	1	2	0.165	0	1	0.082	0	1
95	0.254	0	2	1.676	1	3	0.498	0	2	1.387	1	3
96	0.606	0	2	0.085	0	1	1.725	1	3	1.571	1	3
97	1.808	1	4	1.267	1	3	0.480	0	2	1.470	1	3
98	1.621	1	4	0.055	0	1	0.310	0	2	1.108	1	2
99	1.985	1	4	1.072	1	2	0.208	0	1	0.075	0	1
100	0.570	0	2	1.296	1	2	0.203	0	1	1.160	1	2
101	2.306	1	4	1.372	1	3	1.634	1	4	1.148	1	2
102	1.172	0	4	0.070	0	1	0.151	0	1	1.097	1	2
103	0.329	0	2	0.052	0	1	0.714	0	3	0.144	0	1
104	2.387	1	5	0.059	0	1	1.280	1	3	2.272	1	4
105	1.948	1	4	1.541	1	3	1.162	1	2	2.527	1	4
106	3.610	1	7	0.116	0	1	0.251	0	2	2.147	1	4
107	2.852	1	5	0.076	0	1	1.515	1	3	0.126	0	1
108	2.692	1	5	0.071	0	1	1.155	1	2	1.947	1	3
109	1.713	1	4	1.842	1	3	0.813	0	3	3.413	2	6
110	1.989	1	4	0.072	0	1	0.155	0	1	0.083	0	1
111	0.512	0	2	1.069	1	2	1.241	1	2	2.187	1	4
112	0.351	0	2	2.194	1	4	0.321	0	2	0.173	0	1
113	1.722	1	4	0.580	0	2	2.828	1	5	0.350	0	2
114	1.591	1	3	1.597	1	3	0.349	0	2	5.487	3	9
115	0.578	0	2	3.510	2	6	0.151	0	1	0.143	0	1

116	2.201	1	4	5.864	4	9	0.151	0	1	1.176	1	2
117	2.068	1	4	1.881	1	4	2.161	1	4	1.163	1	2
118	1.283	1	3	3.307	2	5	0.415	0	2	1.682	1	3
119	0.755	0	3	1.484	1	3	1.158	1	2	3.050	2	5
120	0.713	0	3	3.357	2	6	1.160	1	2	1.626	1	3
121	0.754	0	3	3.797	2	6	0.151	0	1	3.423	2	6
122	0.700	0	3	3.014	1	5	0.151	0	1	3.740	2	6
123	1.685	1	4	2.181	1	4	0.161	0	1	5.332	3	8
124	0.396	0	2	1.434	1	3	0.307	0	2	1.694	1	3
125	0.680	0	3	2.647	1	5	0.151	0	1	2.320	1	4
126	0.427	0	2	2.398	1	4	1.282	1	3	0.183	0	1
127	3.546	2	6	4.614	3	7	1.300	1	3	1.615	1	3
128	0.398	0	2	4.057	2	6	1.443	1	3	3.797	2	6
129	0.796	0	3	0.239	0	1	0.151	0	1	0.172	0	1
130	0.734	0	3	3.282	2	5	0.207	0	1	1.210	1	2
131	0.765	0	3	2.237	1	4	0.151	0	1	5.389	3	8
132	1.619	1	4	1.542	1	3	0.151	0	1	1.915	1	4
133	1.038	0	3	5.098	3	8	0.250	0	2	0.491	0	2
134	0.778	0	3	1.821	1	4	0.201	0	1	5.941	4	9
135	1.165	1	2	3.615	2	6	2.352	1	5	8.164	5	12
136	0.466	0	2	3.633	2	6	0.250	0	2	1.186	1	2
137	1.185	1	2	1.192	1	2	0.675	0	3	5.899	4	9
138	0.125	0	1	1.421	1	3	2.934	1	5	2.723	1	5
139	1.372	1	3	4.421	3	7	1.327	1	3	3.138	2	5
140	2.134	1	4	3.426	2	6	0.268	0	2	2.353	1	4
141	1.700	1	3	4.651	3	7	1.300	1	3	1.377	1	3

Chapter 4: Area Requirements and Habitat Selection by the Tasmanian Spotted-Tailed Quoll in a Fragmented Agricultural Landscape



4.1 Abstract

Anthropogenic habitat loss, modification and fragmentation continue to drive mammal declines world-wide. Due to their wide-ranging behaviour, low population density, and specialised niche requirements, many forest-dwelling terrestrial mammalian predators are predicted to be particularly susceptible to decline with habitat change. However, some mesopredators thrive in agricultural landscapes, benefitting from the supplemental food resources provided by altered land use. Understanding scale and species-specific responses to habitat loss is essential to conservation planning.

In Tasmania, Australia, the spotted-tailed quoll is a threatened marsupial mesopredator that is assumed to be forest-dependent, but is nonetheless known to reach high densities in agricultural landscapes. Understanding how individual quolls use these heterogeneous landscapes is key to developing effective habitat conservation strategies for the species in this state. Here, we used GPS telemetry data to investigate space use and second-, third- and fourth-order habitat selection by adult female spotted-tailed quolls in an agricultural landscape at Woolnorth, north-western Tasmania.

Spotted-tailed quoll home range size was positively correlated with habitat loss and fragmentation. At all spatial scales, quolls showed preference for forested areas and avoided cleared land. Foliage or grass tussocks were most frequently used as dens, with burrows, tree hollows, and hollow logs also used. Dens were preferentially sited within forested patches and within the 50% core home range. We conclude that at the distribution scale, Tasmanian spotted-tailed quolls can tolerate agricultural habitat loss and fragmentation, but within these landscapes are largely restricted to patches of forest and scrub.

Given their large area requirements, effective conservation management of quoll populations will require cooperation among multiple stakeholders to achieve scale-specific

habitat management and retention strategies.

4.2 Introduction

Habitat loss and fragmentation are implicated in mammal declines globally (IUCN 2013; Visconti *et al.* 2011). Mammalian predators are considered particularly susceptible to population decline resulting from habitat change because they often possess intrinsic biological traits, including high trophic level, large home range, low population density, low lifetime fecundity, and specialised niche requirements that can make them sensitive to habitat loss and fragmentation (Cardillo *et al.* 2004; Purvis *et al.* 2000; Woodroffe and Ginsberg 1998). However, some generalist predators may benefit from habitat loss and fragmentation if the altered land-use increases or supplements availability of resources in the former habitat (Crooks 2002; Ryall and Fahrig 2006; Swihart *et al.* 2003). Because changes in the abundance or spatial distribution of predators can have detrimental effects on lower trophic levels (Estes *et al.* 2011; Johnson *et al.* 2007; Terborgh *et al.* 2001), especially in anthropogenically fragmented landscapes (Crooks 2002; Schneider 2001), understanding species-specific responses to habitat loss and fragmentation is key to developing conservation strategies and for predicting the effects of future habitat change on both carnivores and broader ecosystem health.

Animals select habitats containing resources at hierarchical spatial scales, referred to as selection orders (Johnson 1980). In decreasing spatial scales, these correspond to (i) the geographic extent of a species' distribution (first-order selection), (ii) the selection of a home range in the landscape (second-order), (iii) the selection of habitat units within the home range (third-order), and (iv) the selection of microhabitats associated with rest sites and feeding within habitat units (fourth-order). Resource selection at higher orders can influence patterns of space use and habitat preferences at lower orders (Johnson 1980). However, because selection

depends on availability of the resource, habitat preferences cannot necessarily be “scaled up” from high to low selection orders (Hobbs 2003), or transferred between geographical regions (Schaub *et al.* 2011). For example, mammalian predators that are forest-dependent at fine (third- and fourth-order) spatial scales can reach high abundance in heterogeneous landscape at broad (first- and second- order) spatial scales by utilising habitat edges (Andrén 1995; Dijk and Thompson 2000)

The spotted-tailed quoll (*Dasyurus maculatus*) is a medium-sized marsupial carnivore endemic to south-eastern mainland Australia and the large island of Tasmania. A number of studies have been conducted on the ecology of the south-eastern mainland spotted-tailed quoll. These have revealed the spotted-tailed quoll to be a solitary and wide-ranging species, with female home ranges usually discrete and 88 – 151 ha in area (Andrew 2005; Belcher and Darrant 2004; Claridge *et al.* 2005; Glen and Dickman 2006b; Nelson 2007) and larger male home ranges 359–5512 ha in area, encompassing other males and multiple females (Andrew 2005; Belcher and Darrant 2004; Claridge *et al.* 2005; Glen and Dickman 2006b). The south-eastern mainland spotted-tailed quoll has also been shown to be a dietary and habitat specialist, primarily inhabiting large tracts of continuous forest (Catling *et al.* 2002; Mansergh 1984), within which preferred habitat comprises structurally complex eucalypt forest that provides a high density of vertebrate prey and an abundance of potential den sites, such as rocky outcrops, hollow logs, tree hollows, or burrows (Belcher and Darrant 2006a; Belcher and Darrant 2006b; Glen and Dickman 2011). Quolls have a relatively short lifespan (maximum five years) and a low overall reproductive output, with some females breeding only once or twice during their lives (Andrew 2005; Belcher 2003; Körtner *et al.* 2004). This low rate of recruitment combined with natal female philopatry (Firestone *et al.* 1999; Glen *et al.* 2009) may limit the ability of the species to recolonise disturbed habitat. Thus, the spotted-tailed quoll possesses a number of

ecological traits common to species with a demonstrated sensitivity to habitat loss. Indeed, clearance of forest habitat is strongly implicated in the species' 50% range contraction since European settlement in south-eastern mainland Australia (Mansergh 1984) that have led the species to be listed nationally as endangered under the Australian Environment Protection and Biodiversity Conservation Act (1999). Habitat loss and fragmentation is considered the greatest threat to the species future persistence (Long and Nelson 2008). Therefore, conservation management strategies for the species focus on retention of critical forested habitat.

Despite the high number of recent studies of the south-eastern mainland population, there remains a lack of quantitative information about the space and habitat requirements of the Tasmanian spotted-tailed quoll. By necessity, this has resulted in information on the ecology of south-eastern mainland populations being used to develop guidelines for habitat management in Tasmania. Unfortunately, this approach could be problematic. The south-eastern mainland and Tasmanian spotted-tailed populations have been separated for at least 13,000 years (Lambeck and Chappell 2001) and now exist with different predator guilds and prey species, and experience different environmental conditions. Most notably, on south-eastern mainland Australia the spotted-tailed quoll co-occurs with the larger introduced European red fox (*Vulpes vulpes*) which is implicated in the decline and extinction of numerous small- and medium-sized mammals, including the spotted-tailed quoll and its prey (Johnson, 2006). In Tasmania the red fox is historically and probably functionally absent (Sarre *et al.* 2013) and the Tasmanian devil is the largest mammalian predator (Jones and Barmuta 2000), and declines of the spotted-tailed quoll and their prey have been less severe (Johnson 2006). The severe reduction in the distribution and abundance of the south-eastern mainland spotted-tailed quoll since European settlement means that current habitat associations may constitute refuge habitats, where exposure to threats such as competition or predation pressure from foxes is reduced, rather than

preferred habitat (Bilney *et al.* 2010; Kinnear *et al.* 1998; Kinnear *et al.* 2002) (Chapter 2).

Thus retention strategies developed from information on south-eastern mainland quolls may fail to protect important habitats in Tasmania.

The aim of this study was to quantify the area and habitat requirements of the Tasmanian spotted-tailed quoll in a fragmented agricultural landscape. As with many carnivores, spotted-tailed quoll population density is limited by female space use and fitness, which is in turn driven by resource abundance and distribution (Belcher and Darrant 2004; Glen and Dickman 2006b; Macdonald 1983; Trivers 1972). Accordingly, we focussed our investigations on the space and habitat requirements of adult female quolls.

First we used radio-telemetry data to define the size, relative use and overlap of adult female spotted-tailed quoll home ranges within our fragmented agricultural landscape, and used this information to compare space use and spatial organisation of the Tasmanian and south-eastern mainland spotted-tailed quoll. Then, based on current knowledge of the species' ecology, we tested the following hypotheses of expected Tasmanian spotted-tailed quoll habitat selection:

(i) At the second-order scale of habitat selection for placement of home range within the landscape, we expected the spotted-tailed quoll to show preference for eucalypt forest and to avoid open pasture. Furthermore, we expected a positive correlation between home range and core area size, and forest loss and fragmentation.

(ii) At the third-order scale of habitat selection within the home range, we expected quolls to show preference for eucalypt forest and to avoid pasture.

(iii) At the fourth-order scale of selection of den habitat, we expected quolls to show preference for using log and burrow dens within eucalypt forest and to avoid pasture. We also expected that den sites would primarily be located within core home ranges.

4.3 Methods

4.3.1 Study area

The study site encompassed approximately 4,400 ha of “Woolnorth”, a private pastoral property at Cape Grim in far northwest Tasmania, Australia. Woolnorth has a low, flat topography, with elevation varying from sea level to 100 m and slope 0 to 15 %. The climate is Mediterranean, with annual mean rainfall 762 mm and monthly mean temperature range 8.2-19.5°C. Remnant native vegetation consists of eucalypt forest and woodland, coastal scrub and heath, and melaleuca swamp forest embedded within a matrix of intensively grazed improved pasture (Figure 4.1). Areas of intact native vegetation are fenced to exclude stock, however fences do not restrict the movement of native wildlife. The study site was selected on the basis of long-term predator trapping data (Department of Primary Industries, Parks, Water and Environment (DPIPWE) Save the Tasmanian Devil Program unpublished data) that indicated the presence of a high-density quoll population in this fragmented agricultural landscape.

(a)



(b)



(c)



(d)



(e)



(f)



(g)



(h)



Figure 4.1: (a) Dry eucalypt forest (b) coastal scrub with emergent (*Melaleuca ericofolia*), European gorse *Urex europaeus* understorey and pasture edge (c) Wet eucalypt forest and pasture edge (d) coastal scrub and heath and pasture (e) European gorse (*Urex europaeus*) in foreground overlooking non-eucalypt forest and pasture mosaic (f) *Macrocarpa* (*Cupressus macrocarpa*) windbreak and pasture (g) island of remnant non-eucalypt forest embedded in pasture (h) overview of the agricultural landscape.

4.3.2 Vegetation communities

Vegetation communities were mapped in ArcGIS 9.2 (ESRI, Redlands, California, USA) using the Tasmanian vegetation mapping spatial database TasVeg 2.0 (TASVEG 2009) and verified through on-ground surveys and high resolution (1:5,000) digital orthophotographs (DPIPWE). We combined structurally- and floristically-similar vegetation communities to create four vegetation categories: (i) eucalypt forest (EF), including Smithton peppermint *Eucalyptus nitida* and Brooker's gum *Eucalyptus brookeriana* forest and woodland; (ii) non-eucalypt forest (NEF), including swamp paperbark *Melaleuca ericifolia* forest, and windbreaks and islands of introduced macrocarpa *Cupressus macrocarpa* and pine *Pinus radiata*; (iii) scrub (SC) including *Melaleuca squarrosa* scrub, coastal scrub, and coastal heath, and weed infestation of African boxthorn *Lycium ferocissimum* and European gorse *Urex europaeus*; and (iv) pasture vegetation (AG) comprised of improved pasture. For further analyses, we combined these to create two additional broad vegetation categories: cover (COV), consisting of eucalypt forest, non-eucalypt forest, and scrub; and forest (FOR) consisting of eucalypt forest and non-eucalypt forest). These six vegetation categories formed the basis of the metrics used in our analyses.

4.3.3 Trapping and radio-tracking

Trapping, collaring, and tracking were conducted between March and May 2011, in the period after juvenile dispersal and prior to the breeding season, when the adult female population is most likely to be stable and reproductive success is least likely to be adversely affected by collaring. To trap quolls, we used PVC pipe traps baited with pieces of wallaby meat placed along roadsides or the vegetation-pasture edge. Following capture, quolls were transferred without sedation to a hessian sack and weighed, sexed, and microchipped for future

identification.

Seven adult female quolls (defined by body-weight and teat development) were fitted with 70 g Telemetry Solutions Quantum 4000 Enhanced radio-collars equipped with a GPS logger, a single-stage VHF transmitter, and a UHF transmitter (collar weight 2.6% - 3.5% of body weight). The collar material of suede fabric was designed to stretch and degrade over time, and fall off should the animal not be recaptured. The GPS logger was programmed to record a location 'fix' every two hours, and the VHF was used to locate quolls to collect information on den use. As per our animal ethics conditions, in the first week after being collared, all animals were located once a day to ensure the collar was not preventing movement.

All collared quolls were re-trapped after one week to ensure that body weight and condition were maintained, and to check collar fit and ensure no chafing had occurred. GPS data was downloaded remotely approximately once a week. All quolls were successfully recaptured to enable retrieval of collars.

Although our sample size of collared quolls was small, collaring large numbers of adult female spotted-tailed quolls is not feasible due to territorial constraints on the number of adult females present within a landscape. Indeed, in previous quoll telemetry studies, sample sizes of adult females range from three to seven in any one year (Andrew 2005; Belcher and Darrant 2004; Claridge *et al.* 2005; Glen and Dickman 2006b; Körtner and Watson 2005; Nelson 2007). In our study area, 70% of known adult females were collared. This high proportional sample of the population, in combination with GPS technology and frequent VHF tracking to dens, provided a representative insight into quoll ecology.

4.3.4 GPS data preparation

Data obtained from collars for each fix included date, time, GPS coordinates, elevation,

number of satellites used to calculate the position, and horizontal dilution of precision (HDOP). GPS data require evaluation and screening for measurement error and bias prior to use in analysis (Frair *et al.* 2010). The horizontal dilution of precision (HDOP) provides an index of GPS coordinate precision, with lower HDOP values considered more precise (D'eon and Delporte 2005). To minimise the risk of including imprecise and erroneous fixes in data analysis, locations with HDOP greater than some arbitrary threshold are commonly removed (D'eon and Delporte 2005), however, HDOP provides only a relative measure of precision. Due to the small size of some vegetation patches in our landscape and our need to correctly classify fixes according to the vegetation community they fell within, our first step was to quantify the precision of GPS locations that were associated with different values of HDOP to ensure that positional accuracy was similar to that of our spatial vegetation data (± 5 m). We did this by examining variation in clusters of coordinates collected from quolls that were known (from VHF tracking) to be stationary (e.g. denning or resting). We calculated the mean linear error associated with each value of HDOP by measuring the linear distance between the mean coordinates of a cluster of points and each point in the cluster. We retained all fixes with a maximum linear error of 7.3 ± 0.53 m (Appendix 4.1).

We used the linear error analysis of GPS location and observations from VHF tracking of quolls to den sites to assign each GPS location an activity status: “Inactive”, and “Active”. Inactive GPS locations were defined as those recorded in periods of ≥ 6 hours where all step lengths and the total net displacement were ≤ 20 metres, when the animal was presumed to be resting. For all other locations quolls were considered Active (e.g. in transit or foraging). To avoid bias created by multiple fixes of an animal resting in the same location for many hours, we did not use Inactive fixes in our analysis. Our approach allowed for inclusion of prey handling or short periods of rest as part of activity, while excluding long periods of rest.

4.3.5 Home range estimation

We used the Active subset of GPS data to determine home range area. We expected that the short time interval between successive GPS fixes may lead to temporal autocorrelation in our data, which violates the assumption of independence required by kernel density home range estimation methods (Legendre 1993 (Harris *et al.* 1990; White and Garrott 1990)). On the other hand, studies using simulated and empirical data have concluded that autocorrelated data does not bias home range estimates and that removal of data to achieve statistical independence reduces the biological relevance of space use estimates (De Solla *et al.* 1999; Fieberg 2007).

In the first instance, we tested for temporal autocorrelation using the Schoener Index (Schoener 1981), which indicated high positive autocorrelation in GPS locations. We investigated time to statistical independence by sub-sampling GPS locations to increase the interval between point fixes. Points remained correlated (Schoener Index <1.6) until just one point per three days was used. This left 8-16 data points per individual, which was no longer a representative sample of locations (Otis and White 1999), was insufficient for kernel density estimation (Seaman *et al.* 1999) and resulted in gross underestimation of minimum convex polygon (MCP) home range sizes. We therefore used the entire Active dataset for each individual for home range estimation.

We used two methods to estimate home-range size (Burt 1943): MCP (Mohr 1947) and fixed kernel (Worton 1989). The 100% MCP home range is the area bounded by the smallest convex polygon that contains all locations. This method is often used to compare home-range estimates among studies (Harris *et al.* 1990; White and Garrott 1990) and we used this estimate to compare home range size between Tasmanian and mainland quoll populations. Despite its utility, the MCP method has a number of limitations, including sensitivity to outlier locations and inability to distinguish areas of intensive use (White and Garrott 1990). We therefore also

used 95% and 50% fixed kernel home range estimation for a more refined examination of home range size and use. This method distinguishes areas that are frequently used (“50% core area”, or the area where an animal spends 50% of its time) and those that are used less frequently (“95% home range”, or the area where an animal spends 95% of its time). Kernel home-ranges were estimated using an *ad hoc* smoothing parameter (Berger and Gese 2007; Kie *et al.* 2010), which limits over- or under-smoothing by choosing the smallest reference bandwidth that results in a contiguous 95% isopleth. All home ranges were calculated using the Home Range Tools Extension v 1.1 for ArcGIS 9. 2 (Rodgers *et al.* 2007). To investigate whether the 100% MCPs and 95% Kernel Density Estimates (KDE) were fully described, we created incremental area plots with home range area plotted against sequentially increasing sample size. We considered that a home range asymptote was reached when there was less than 5% variation in home range size for the last 10% of GPS locations used.

4.3.6 Home range overlap

To determine the extent of home range overlap among adult female spotted-tailed quolls, we calculated the proportion of each individual’s 95% KDE home range and 50% core area that encompassed that of a neighbouring individual.

4.3.7 Home range size and habitat loss and fragmentation

To investigate the relationship between quoll space use and the type, proportion, and degree of fragmentation of vegetation communities within the home range, we conducted linear regressions in R version 3.0 (R Core Team 2013) using the 95% KDE home range area and 50% KDE core area as the response variables, and the proportion and number of patches of the six previously described vegetation categories as the predictor variables.

4.3.8 Second-order selection of home range habitat within the landscape

We used selection ratio analysis (Manly *et al.* 2002) to investigate whether quolls preferentially selected or avoided any vegetation communities for placement of home ranges. Selection ratios are a simplified form of the resource selection function (Manly *et al.* 2002). We used a design 1 study (Thomas and Taylor 1990) and measured use and availability at the scale of the population. We calculated selection ratios to test individual and overall (all quolls in the study) preference for or avoidance of eucalypt forest, non-eucalypt forest, scrub, and pasture. A selection ratio of >1 (i.e. use of a vegetation community is greater than its proportional availability) indicates preference, and a selection ratio of <1 (i.e. a vegetation community is used less than its proportional availability) indicates avoidance. We calculated selection ratios and upper and lower 95% confidence intervals for each vegetation community using the R package `adehabitatHS` (Calenge 2006)

4.3.9 Third-order selection of habitat within home ranges

To investigate preference of vegetation communities within home ranges, we again calculated selection ratios as described for second-order selection above. Here, we used a design 3 study (Thomas and Taylor 1990) which allowed the use and availability of resources to differ among individuals. We defined use as the proportion of Active GPS locations that fell within each vegetation community in each 95% KDE, and availability as the proportion of each vegetation community within each 95% KDE. We used goodness-of-fit tests (χ^2_L) to determine whether use of vegetation communities was consistent among individuals, and whether individual quolls showed significant selection of vegetation community as outlined for second-order selection above. Selection ratios were calculated to test individual and overall

(population) selection.

4.3.10 Fourth-order selection of den habitat within home ranges

Whenever possible, quolls were tracked to their dens by “homing in” on the VHF signal (White and Garrott 1990), and den site locations mapped in ArcGIS 9.2 (ESRI, Redlands, California, USA). Due to the low numbers of den observations for some individuals, we pooled use and availability data across all quolls and conducted a design 1 selection ratio analysis (Thomas and Taylor 1990) to investigate whether quolls preferentially select or avoid any vegetation communities for denning. We defined use as the proportion of den locations that fell within each vegetation community in each 95% KDE, and availability as the proportion of each vegetation community within each 95% KDE.

At each den site, we recorded the structure and substrate of the used den. We planned to compare used dens to randomly selected points within the home range representing “available” dens and logistic regression or discrete choice analysis to investigate selection. However, the high density of un-collared male spotted-tailed quolls and Tasmanian devils (a potential competitor for dens, Smith 2012) in the study area meant that potentially available dens could actually be in use and thus unavailable to collared quolls. Therefore, we instead described adult female spotted-tailed quoll den substrate use rather than preference.

To investigate the spatial distribution of den sites within the home range, we tested quoll preference for denning within 50% KDE core areas using a chi-squared goodness of fit test. Due to the low number of den observations for some individuals, data for all quolls were pooled for statistical testing. Observed frequency was the sum of den sites that occurred within 50% core areas, and expected frequency was the total number of dens multiplied by the proportion of the home range that consisted of the 50% core home range.

4.4 Results

4.4.1 Trapping and GPS data

Trapping yielded 97 captures of 44 individual quolls over 1,367 trap nights. Ten of the captured quolls were adult females (i.e. ≥ 1.6 kg), of which seven weighing ≥ 2 kg were collared for 28 - 36 days. The GPS collars collected a total of 5,158 relocations from 7,110 attempts. We removed 121 fixes with an HDOP > 6 , which represented 2.35% of all successful relocations. The remaining 5,037 locations with HDOP ≤ 6 had a maximum linear error of less than 7.3 ± 0.53 m (Appendix 4.1). A total of 1,464 fixes were obtained at two hourly intervals, of which 808 were classified as Active.

4.4.2 Home range estimation

Home range size varied widely among the females tracked in this study, with 100% MCP estimates ranging from 191 to 470 ha, 95% KDE estimates from 152 to 485 ha, and 50% KDE estimates from 38 to 103 ha (Table 4.1, Figure 4.2). Home ranges reached an asymptote for all individuals for MCP estimates, and all but one individual (Female 3) for 95% KDE estimates (Table 4.1, Appendix 4.2). Home range sizes were similar to those recorded from south-eastern mainland Australia (Table 4.2).

ID	n	MCP		KDE	
		100%	95%	95%	50%
Female 1	251	229	152	38	
Female 2	158	386	349	76	
Female 3	211	470	382*	85	
Female 4	144	439	485	103	
Female 5	239	191	163	42	
Female 6	233	427	380	85	
Female 7	186	464	343	78	

Table 4.1: Home range size estimates for seven adult female Tasmanian spotted-tailed quoll Woolnorth, north-western Tasmania, tracked between March and May 2011 . ID = individual animal identity; n = the number of GPS locations used in home range estimation; MCP = Minimum Convex Polygon; KDE = Kernel Density Estimate. *Did not reach asymptote.

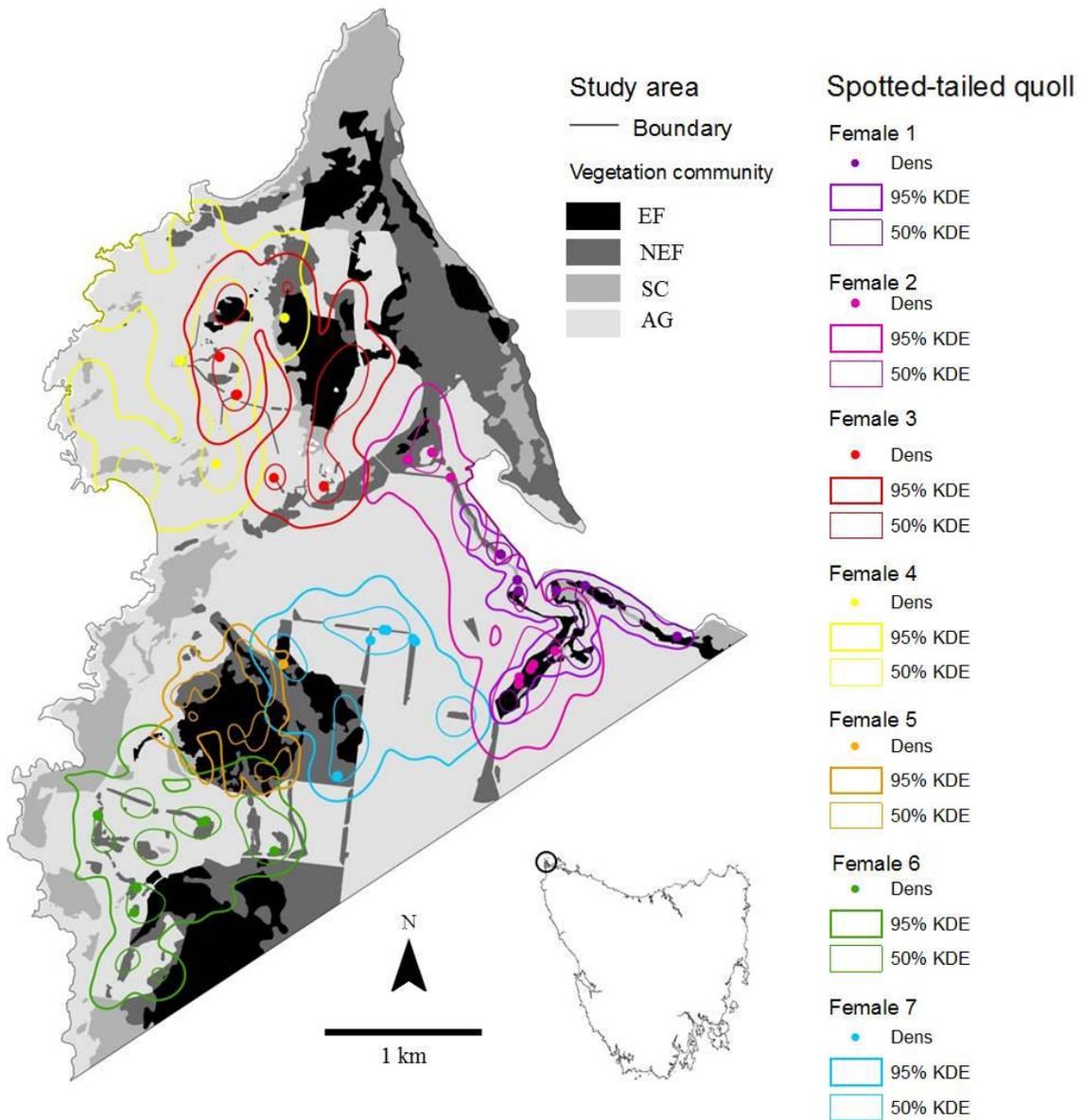


Figure 4.2: Location of kernel density estimate (KDE) home ranges and core areas, and den sites used by adult female spotted-tailed quolls ($n = 7$) at Woolnorth, north-western Tasmania. EF = eucalypt forest, NEF = non-eucalypt forest, SC = scrub, AG = pasture.

LOCATION	BROAD VEGETATION COMMUNITY	# F	MCP	Reference
SE mainland				
Marengo, NSW	Open dry sclerophyll forest	4	133 ± 23	Glen and Dickman 2006
Badja, NSW	Moist sclerophyll forest to subalpine woodland	3	596 ± 281	Belcher and Darrant 2006
Tallaganda, NSW	Moist sclerophyll forest to subalpine woodland	4	277 ± 52	Belcher and Darrant 2006
Suggan Buggan, VIC	Wet forest to open forest-woodland	2	613 ± 287	Belcher and Darrant 2006
Suggan Buggan, VIC	Wet forest to open forest-woodland	8	310 ± 324	Nelson 2007
Limeburners Creek, NSW	Eucalypt forest and woodland, non-eucalypt forest, shrub, heath, sedge, rush, wetland	3	862 ± 324	Andrew 2005
Byadbo, NSW	Dry sclerophyll forest.	6	244 ± 72	Claridge et al 2005
Tasmania				
Woolnorth, TAS	Dry sclerophyll forest, non-eucalypt forest, scrub, heath, grass, pasture.	7	372 ± 42	This study

Table 4.2: Comparison of spotted-tailed quoll MCP home range sizes among populations. SE mainland indicates south-eastern mainland spotted-tailed quoll. # F indicates sample size of adult female spotted-tailed quoll used in home range estimate. MCP estimates are mean ± standard error.

4.4.3 Home range overlap

Home range polygons showed that there was extensive spatial overlap between some females (Table 4.3). Most notable was the high degree of overlap in both the 95% KDE home ranges and 50% KDE core areas between Females 1 and 2, and between Females 3 and 4.

KDE	ID	F1	F2	F3	F4	F5	F 6	F7	% EXCLUSIVE
50%	F1	-	18.4	0	0	0	0	0	81.6
	F2	6.8	-	0	0	0	0	0.6	92.6
	F3	0	0	-	26.4	0	0	0	73.6
	F4	0	0	21.7	-	0	0	0	78.3
	F5	0	0	0	0	-	7.7	13.3	79
	F6	0	0	0	0	0	-	0	100
	F7	0	0.6	0	0	2.5	0	-	96.9
95%	F1	-	67.7	0	0	0	0	0	32.3
	F2	29.5	-	0	0	0	0	1.98	68.52
	F3	0	0	-	43.2	0	0	0	56.8
	F4	0	0	34.4	-	0	0	0	65.6
	F5	0	0	0	0	-	12.9	11.2	75.9
	F6	0	0	0	0	5.5	-	0	94.5
	F7	0	2.01	0	0	5.4	0	-	92.59

Table 4.3: Home range overlap between pairs of adult female spotted-tailed quoll at Woolnorth, north-western Tasmania. ID = individual animal identity; F1 – F7 = Females 1 - 7. KDE = Kernel Density Estimate. Values are percent overlap of individual listed in row by individual listed in column, e.g. Female 2 overlaps 18.4% of Female 1's 50% KDE core area.

4.4.4 Home range size and habitat loss and fragmentation

Home-range size increased with the number of discrete patches of vegetation cover ($R^2 = 0.586$, $P = 0.045$), and with the proportion of pasture ($R^2 = 0.571$, $P = 0.040$) in the 95% range.

There was a negative relationship between 95% home range area and the proportion of eucalypt forest in the home range ($R^2 = 0.652$, $P = 0.028$), but no relationship between 95% KDE home range size and eucalypt forest fragmentation (number of patches, $R^2 = 0.281$, $P = 0.220$). There were no other significant linear relationships between KDE 95% home range size and the proportion or number of patches of forest, non-eucalypt forest, or scrub.

4.4.5 Second-order selection of home range habitat within the landscape

At the second order scale, home ranges were preferentially located in areas that encompassed eucalypt and non-eucalypt forest but not scrub or pasture (Figure 4.3). Despite this, all home ranges included some pasture, and all but one included scrub. GPS locations revealed that each quoll used all vegetation communities present within their home range.

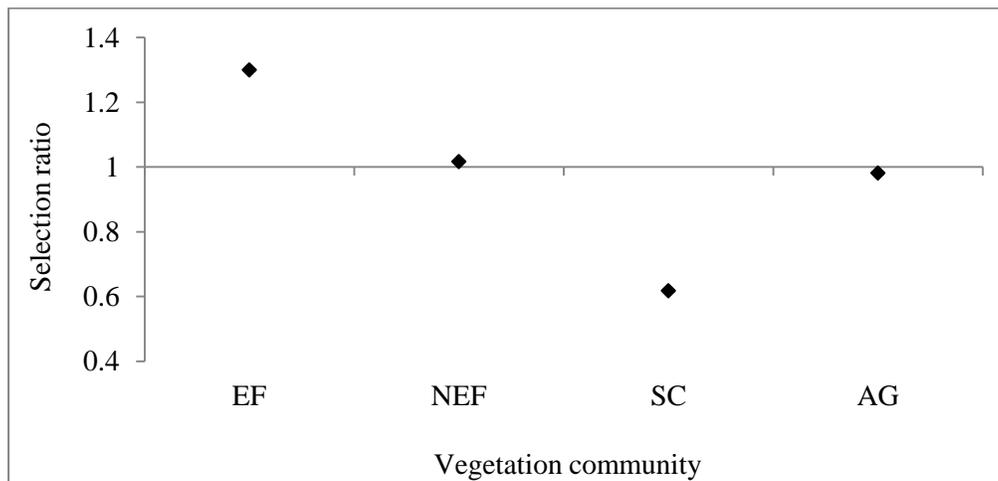


Figure 4.3: Second-order selection of home range habitat within landscapes by female Tasmanian spotted-tailed quolls ($n=7$) at Woolnorth, north-western Tasmania. EF = eucalypt forest; NEF = non-eucalypt forest; SC = scrub, AG = pasture.

4.4.6 Third-order selection of habitat within home ranges

At the third order scale, the overall (population) test of habitat selectivity was highly significant ($\chi^2_L = 480.545$, $df = 20$, $P < 0.001$), as were the tests for each animal ($\chi^2_{LI} = 16.430$ - 158.420 , $df = 2$ - 3 , $P < 0.001$). Individual-level selection ratios revealed that selection of vegetation communities differed among quolls. While all quolls preferentially used cover, the type of cover preferred and the magnitude of preference varied substantially among individuals (Figure 4.4a). Population-level selection ratios demonstrated significant preference by quolls for eucalypt forest, non-eucalypt forest, and scrub (Figure 4.4b), and significant avoidance of pasture.

4.4.7 Fourth-order selection of den habitat within home ranges

The fourth order test of overall habitat selection was significant ($\chi^2_L = 65.793$, $df = 3$, $P < 0.01$) indicating that use of habitats for denning was not proportional to availability of habitat within home ranges. Quolls showed preference for eucalypt and non-eucalypt forest, and avoidance of pasture communities, but scrub in proportion to its availability (Figure 4.5a). Dens were most frequently recorded in non-eucalypt forest, followed by eucalypt forest, scrub, and pasture (Figure 4.5b).

Clumps of vegetation and grass were the most commonly used structures for siting of dens (57.5%), followed by underground burrows (25%), hollows in live (7.5%) or dead (2.5%) trees, and hollow logs (7.5%) (Figure 4.5b, Figure 4.6). The high proportion of dens in vegetation and grass foliage differs from south-eastern mainland spotted-tailed quoll den use (Table 4.4). Dens found in vegetation were located within clumps of native Bower Spinach (*Tetragonia implexicoma*) (semi-succulent herbaceous ground cover plant growing as a mat over coarse or fine woody debris or stumps) or introduced African boxthorn, and European

gorse. Grass dens in open coastal dunes were sited within clumps or dense stands of native velvet tussock grass (*Poa rodwayi*), coastal tussock grass (*Poa poiformis*), coast sword sedge (*Lepidosperma gladiatum*), and introduced marram grass (*Ammophila arenaria*), and grass dens in forests were in and under dense clumps of cutting grass (*Gahnia grandis*) or sword sedge (*Lepidosperma spp*).

Of the 22 den sites recorded in non-eucalypt vegetation, five dens were located within small (0.07 – 4.2 ha) vegetation patches of remnant swamp paperbark and in either grass or sedge (n = 2), prickly introduced shrubs such as gorse (n = 2), or boxthorn (n = 1). Nine dens occurred within narrow (10 - 52 m wide) windbreaks of introduced *C. macrocarpa* or *P. radiata* and in either *T. implexicoma* (n = 5), grass (n = 2) or burrows (n = 2). For dens located in vegetation, grass, or burrows, den entrances and structures were cryptic. Den entrances in tree hollows were comparatively large and clearly visible (> 20 cm diameter).

Quolls showed significant preference for den sites located within their estimated 50% core home range (n = 30, $\chi^2 = 11.177$, df = 1, $P < 0.001$) (Figure 4.1). Six quoll dens were located within the 50% core area of another collared individual, and a further eight dens were located within another individual's 95% home range (Figure 4.1).

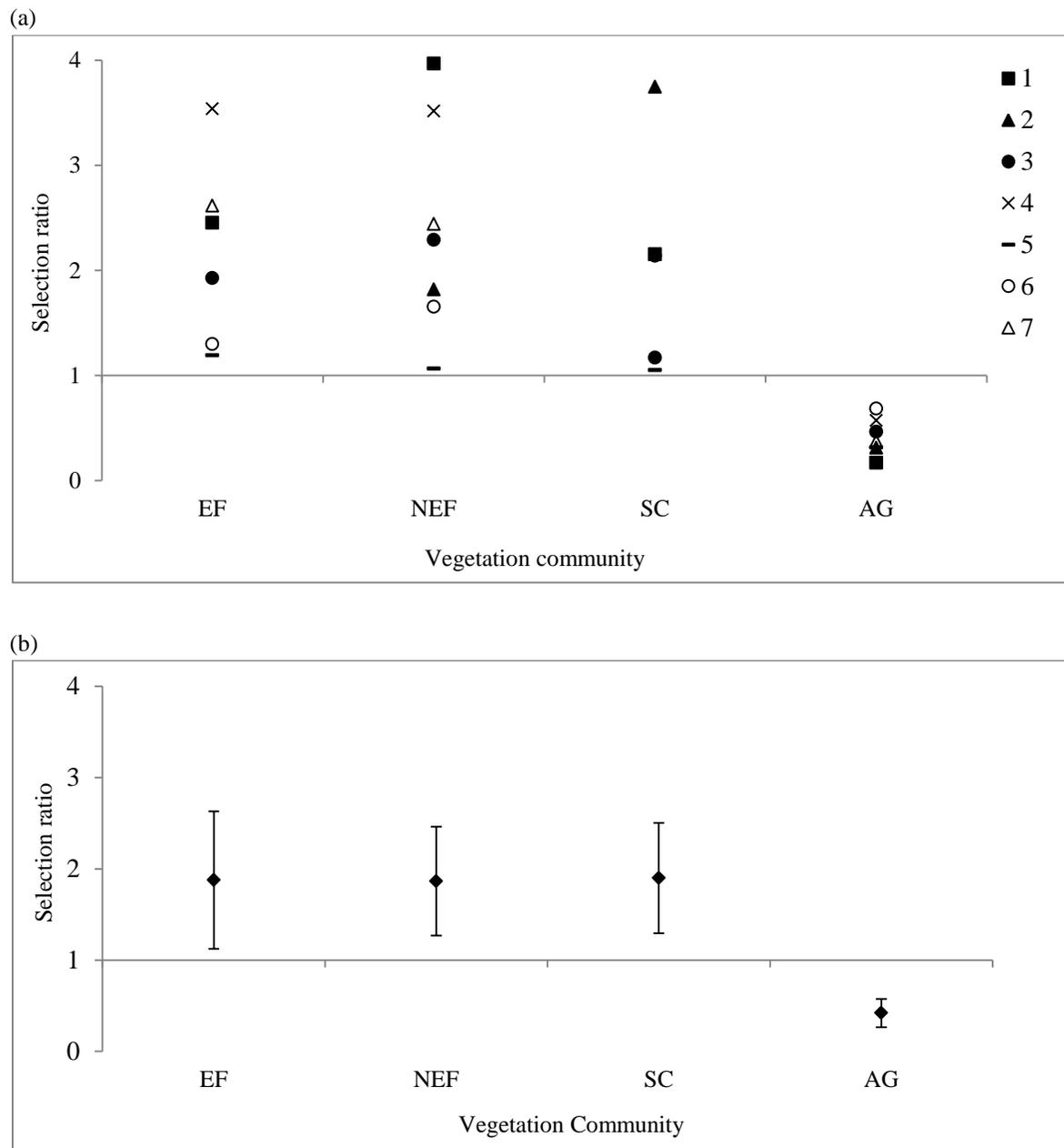
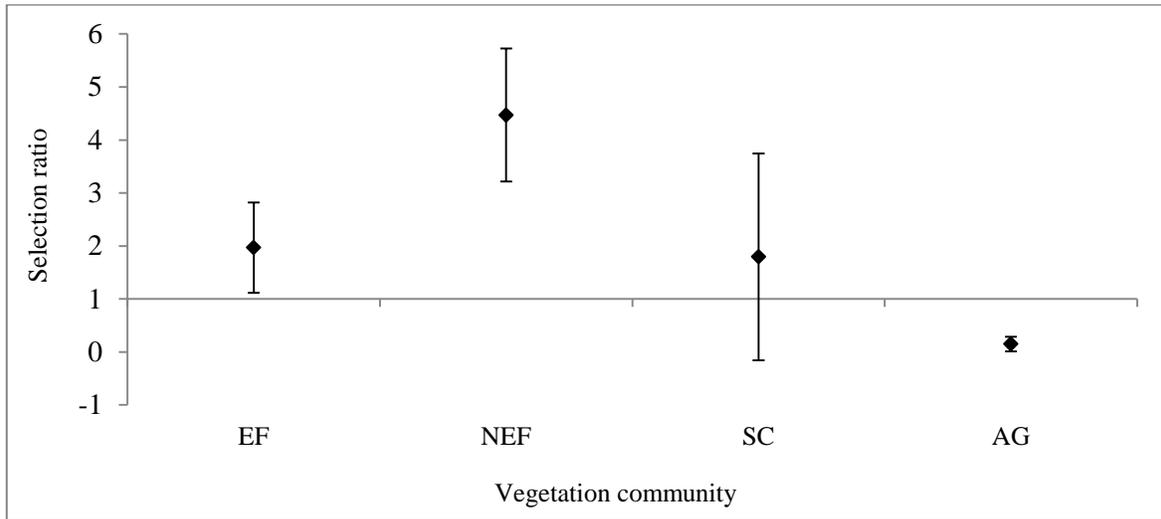


Figure 4.4: (a) individual-level and (b) population-level third-order selection of habitats within home ranges by female Tasmanian spotted-tailed quolls ($n=7$) at Woolnorth, north-western Tasmania. EF = eucalypt forest; NEF = non-eucalypt forest; SC = scrub, AG = pasture.

(a)



(b)

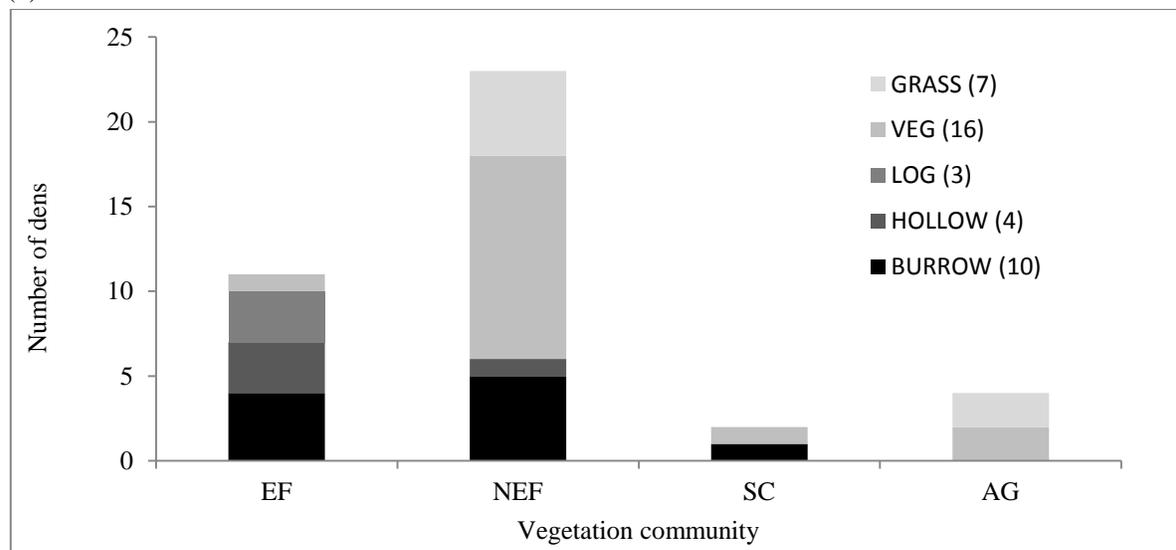


Figure 4.5: (a) den habitat selection and (b) den structure and den habitat use by adult female spotted-tailed quoll (n=7) at Woolnorth, north-western Tasmania.

LOCATION	SAMPLE SIZE		NUMBER OF DENS							REFERENCE
	#F	#M	TOTAL	LOG	BURROW	ROCK	FOLIAGE	HOLLOW	OTHER	
SE mainland										
Marengo, NSW	4	4	38	19	7	5	0	4	3	Glen and Dickman 2006
Badja, NSW	3	9	65	46	4	8	0	2	5	Belcher and Darrant 2006
Tallaganda, NSW	4	2	5	3	0	0	0	2	0	Belcher and Darrant 2006
Suggan Buggan, VIC	2	5	6	0	1	5	0	0	0	Belcher and Darrant 2006
Suggan Buggan, VIC	8	0	44	10	1	29	0	4	0	Nelson 2007
Limeburners Ck, NSW	3	3	53	31	7	1	0	10	4	Andrew 2005
Byadbo, NSW	6	9	30	0	29 ^a	0	0	0	0	Ruibal et al 2010
Girraween, QLD	0	3	6 ^b	0	5	1	0	0	0	Watt 1993
Tasmania										
Woolnorth, TAS	7	0	42	3	10	0	23	4	0	This study

Table 4.4: Comparison of den use among spotted-tailed quoll populations. SE mainland indicates south-eastern mainland spotted-tailed quoll. # F and # M shows number of female and male spotted-tailed quoll respectively. Values indicate frequency of den use.

^a Only four not associated with rocks ^b All located in caves, crevices or between granite boulders, five of 6 were subterranean.

(a)



(b)



(c)



(d)



(e)



Figure 4.6: (a) Log den in *Eucalyptus nitida* forest (b) Den under *Tetragonia implexicoma* within a pine windbreak (c) Den under *Tetragonia implexicoma* in an island of remnant non-eucalypt forest (d) Presumed entrance to a den in African boxthorn *Lycium ferocissimum* (e) Tree hollow den in dry eucalypt forest.

4.5 Discussion

Our study is the first to provide quantitative information on the area requirements, spatial organisation and habitat preferences of the spotted-tailed quoll in Tasmania. We also provide the first information on the ecology of the spotted-tailed quoll in an agricultural landscape, which can be used to predict the effects of habitat loss and fragmentation on this threatened species. Here, we discuss potential mechanisms driving our results, compare our findings to previous research on the south-eastern mainland spotted-tailed quoll, and conclude with implications for the conservation management of the spotted-tailed quoll and its habitat.

4.5.1 Home range size and spatial organisation

Home range size and population density are typically negatively correlated (Sanderson 1966). As such, comparison of home range size can be used to infer differences in density between populations. The home range sizes of female spotted-tailed quolls observed in the study site were within the range of those previously reported from south-eastern mainland populations (Table 4.3). As our study was undertaken in the highest density Tasmanian population known (Chapter 2 Figure 2.2), it appears that population density of Tasmanian quolls also falls within the range of those reported from forested landscapes on mainland Australia. Thus, although the spotted-tailed quoll is relatively widespread across Tasmania compared with the disjunct populations on mainland Australia, the density within populations appears to be similar in the two regions. A caveat on this interpretation is that the home ranges of most south-eastern mainland spotted-tailed quolls failed to reach an asymptote, meaning that home ranges could be larger than has been recorded. Furthermore, because home range estimates of the south-eastern mainland spotted-tailed quoll were derived using VHF-telemetry, it is possible that our use of GPS-telemetry resulted in larger and more accurate estimates of

home range. However, the short period of radio-tracking in this study (4-5 weeks) relative to those mainland studies means that home range size in Tasmania may also be underestimated and only represent a small or seasonal component of lifetime space use.

Unexpectedly, we found extensive overlap in the 95% home ranges and 50% core areas of some neighbouring adult female spotted-tailed quolls. Previous studies of spotted-tailed quoll space use inferred territoriality from a minimal spatial overlap in female home ranges (Andrew 2005; Belcher and Darrant 2004; Claridge *et al.* 2005; Nelson 2007), but territorial defence has not been directly observed. Furthermore, these studies did find that in some cases, pairs of individuals in fact had a high degree of spatial overlap between neighbouring individuals. In most cases, overlapping pairs comprised an older and younger female and assumed to be mother and daughter which is consistent with female natal philopatry (Firestone *et al.* 1999), but where estimated, core areas were exclusive (Nelson 2007). Similarly, pairs of individuals with overlapping home ranges in our study also comprised an older and younger female, and could therefore also be mother-daughter pairs. Territoriality is an endpoint along a continuum of spacing patterns, from non-overlapping to mutually exclusive home ranges (Maher and Lott 1995). Although some overlap is expected, in general, territorial species should have minimal overlap in total space use, and exclusive core areas (Powell 2000). The high degree of overlap in 50% core areas and the presence of adult female quoll dens within another female's 50% core area indicate that territorial defence of core areas may be limited in our study area. Thus, as well as natal female philopatry, there are at least four other potential explanations for the high degree of home range and core overlap found here relative to previous studies that call into question the degree to which quolls are territorial.

First, it is possible that habitat loss and fragmentation necessitated a degree of tolerance to space sharing, and that female quolls partition use of overlapping core ranges temporally to

acquire sufficient resources.

Second, given that most overlapping core areas encompassed forest fragments, the agricultural matrix may provide supplemental food resources (Dunning *et al.* 1992), and the cost of territorial defence outweighs the benefit of having an exclusive territory (Powell 2000). However, if that were the case, we would have expected to find smaller home ranges with increasing proportion of matrix or fragmentation (number of cover patches), but we found the opposite: home range size increased with the proportion of cleared land and fragmentation, and decreased with the proportion of eucalypt forest.

Third, it may be that although female spotted-tailed quoll area requirements and space use reflects the widespread patchy distribution of resources, quolls do not partake in defence of these resources. Indeed, their large home ranges would make territorial defence virtually impossible. Use of scent marking such as latrines has been suggested as a possible mechanism for territory maintenance in the spotted-tailed quoll (Andrew 2005; Belcher and Darrant 2004) and other quoll species (Oakwood 2002; Serena and Soderquist 1989), but given that non-territorial male spotted-tailed quolls also use latrines, it is more likely that scent marking facilitates intra-specific social communication rather than territorial defence (Ruibal *et al.* 2011).

Finally, it is possible that observed differences in home range overlap result from methodological differences among studies, rather than differences in social organisation. For example, the degree of smoothing around kernel locations or shape of an MCP home range relative to point locations may drive the extent of spatial overlap between individuals, even when some areas within the defined home range are rarely used (Hemson *et al.* 2005). Similarly, the lower temporal resolution of data from VHF radio-telemetry studies on south-eastern mainland Australia may have underestimated intraspecific interactions, as shown by

genetic results that revealed that breeding had taken place between two radio-collared quolls whose home ranges showed no overlap (Glen *et al.* 2009; Glen and Dickman 2006b). In the absence of data on female quoll relatedness, response to home range incursions, and resource availability, we are not able to conclusively determine the factors driving the high degree of overlap found among female quolls. Because space use dictates many aspects of reserve design and conservation management (Eads *et al.* 2014), determining the relationship between spatio-temporal overlap in spotted-tailed quoll space use, spatial organisation, relatedness and resource availability is an important area for future study.

Variation in resource availability is widely considered the most important factor affecting home range size in mammalian predators (Gittleman and Harvey 1982; Powell 2000). Predators often concentrate their space use into areas where resources are abundant (Harris *et al.* 1990; Powell 2000). Negative relationships between prey or den resources and home range size have been shown for many carnivores, including the American marten (*Martes martes*) (Powell 1994), fisher (*Gulo gulo*) (Zielinski *et al.* 2004), long-tailed weasel (*Mustela frenata*) (Gehring and Swihart 2004), and Pallas cat (*Otocolobus manul*) (Ross *et al.* 2012). The positive correlation between spotted-tailed quoll home range size and the proportion of pasture and number of patches of vegetation cover suggest that pasture contains few resources for quolls, and the inclusion of such areas within a female's home range increases the amount of space required to meet their resource demands. This idea is supported by the significant avoidance of pasture by quolls at the second-, third- and fourth-order scales.

The negative correlation between quoll home range size and the proportion of eucalypt forest cover supports findings from south-eastern mainland Australia that show mature eucalypt forest provides plentiful resources for spotted-tailed quolls (Belcher and Darrant 2006a; Belcher and Darrant 2006b; Glen and Dickman 2006b; Nelson 2007). Remnant mature dry

eucalypt forest such as that at Woolnorth is structurally complex, containing large-diameter hollow bearing trees, coarse woody debris, shrub cover, and patchy ground cover, which provide potential den sites and refugia for quolls and the small- and medium-sized mammals and birds upon which quolls prey (Belcher 2008; Belcher and Darrant 2006b; Catling *et al.* 2002; Glen and Dickman 2011).

Eucalypt forest at Woolnorth is fragmented and spatially limited, no single patch was large enough to contain an entire home range without use of additional vegetation communities, and all quolls were exposed to some pasture-forest edge. It is therefore possible that female home range size would be even smaller in contiguous eucalypt forest. However, trapping and remote camera surveys in a larger (> 1, 500 ha) tract of remnant mature forest adjacent to our study area indicated that female quoll density was actually higher in our fragmented landscape. Many medium-sized mammalian prey occurring at Woolnorth such as the common brushtail possum (*Trichosurus vulpecula*), Bennett's Wallaby (*Macropus rufogriseus*), and pademelon (*Thylogale billardierii*) are known to forage on the forest-pasture edges (Le Mar and McArthur 2005). The high availability of these prey resources in cleared areas adjacent to structurally complex eucalypt forest may have led to smaller space requirements and hence higher abundance of quolls in our fragmented study area. Accordingly, as has been seen in the pine marten (*Martes martes*) (Caryl *et al.* 2012) there may be a threshold effect of habitat loss and fragmentation on quolls, whereby some non-forest matrix adjacent to forest can be tolerated or is even beneficial in providing supplemental resources, but too much increases home range size and thus reduces the carrying capacity of landscapes for quolls.

4.5.2 Second-, third- and fourth-order habitat selection

As expected, spotted-tailed quolls showed significant preference for eucalypt forest and

avoidance of pasture and grassland at all selection orders. Our findings that Tasmanian spotted-tailed quolls preferentially select eucalypt forest for home range placement in the landscape, intra-home range movement and foraging, and for siting dens, further highlights the previously discussed importance of this vegetation community to the species, even when available forest is fragmented.

Our finding that quolls prefer non-eucalypt forest at all selection orders was surprising, given that this forest type is generally has little ground or shrub cover, and that spotted-tailed quolls are generally associated with areas of high structural complexity (Belcher and Darrant 2006b; Jones and Barmuta 1998). However, in our study area most patches of non-eucalypt forest included within quoll core areas consisted of narrow (<100 m) linear strips with a dense ground and shrub cover such as native bower spinach and introduced gorse and boxthorn. The dense understorey offer the spotted-tailed quoll denning opportunities and cover for movement, and may have also provided habitat to their prey. For example, we observed quolls foraging for larvae under the loose bark of tea-tree (*Melaleuca ericofolia*), and the ring-tailed possum upon which quolls prey (Green and Scarborough 1990) also commonly nests in use non-eucalypt forest (Munks 1999). Our results suggest that non-eucalypt as well as eucalypt forest can provide resources.

Selection for scrub was scale-dependent. Quolls avoided establishing a home range in landscapes with a high proportion of scrub, showed significant preference for using scrub within the home range, and used scrub in proportion with its availability as den habitat, with just two dens situated within this vegetation community. The most likely explanation for this pattern of scale-dependent habitat selection is that scrub offers few resources for the spotted-tailed quoll, and is used mostly as movement corridors or stepping stones between patches of forest. Thus, scrub can play an important role in maintaining functional connectivity for the

spotted-tailed quoll in agricultural landscapes, and may also offer limited den and probably prey resources. Similarly, recent studies have also shown that scrub habitats provide essential structural features for primarily forest-dwelling pine martens within the agricultural landscapes of Western Europe and the UK (Caryl *et al.* 2012; Pereboom *et al.* 2008; Santos and Santos-Reis). Given that the spotted-tailed quoll fills a similar ecological niche to the marten (Belcher 2008), it is not surprising that this habitat is also important for quolls within fragmented landscapes.

4.5.3 Fourth-order den use

Our finding that the Tasmanian spotted-tailed quoll makes frequent use of grass and dense vegetation as den structures is in striking contrast to den use by the south-eastern mainland spotted-tailed quoll, which have not been recorded from such foliage and use mostly hollow logs, tree hollows, rocky outcrops, and burrows as den structures (Table 4.4). It may be that a low availability of more traditionally-used den structures in this landscape may force quolls to seek alternative types of dens. However, while the almost total absence of rock substrate explains why rock dens were not recorded, this explanation does not hold for other den structures, such as the light sandy soil occurring over much of Woolnorth that appears ideal for burrow excavation. Even where quoll core ranges encompassed mature remnant eucalypt forest, tree hollow and log den use was rarely recorded, indicating that quolls didn't use these structures even when they were present.

The high frequency of use of foliage dens by the spotted-tailed quoll may also be related to inter-specific competition for and risk associated with some den structures. On south-eastern mainland Australia, the red fox is known to use similar den structures to the spotted-tailed quoll (Carter *et al.* 2012; Glen and Dickman 2006b; Glen and Dickman 2008; Marks and Bloomfield

2006). Dense fox populations may result in both competition for suitable den sites and predation risk to quolls, particularly dependent young, meaning that secure den structures with small entrances may be necessary to minimise competition and predation. Similarly, in much of south-eastern Australia, many small- and medium-sized mammals only persist where they have access to habitat that provides refuge from predation, such as rock piles and dense vegetation (Johnson 2006). We hypothesise that the historical absence of foxes results in Tasmanian spotted-tailed quolls having more flexibility in their denning ecology than their mainland counterparts. Interestingly, the Tasmanian devil also uses similar den structures to the spotted-tailed quoll, including burrows, rock dens and log piles (Pemberton 1990; Smith 2012). It is also possible that competition for den sites from the Tasmanian devil results in less frequent use of these den structures by the spotted-tailed quoll in Tasmania relative to the south-eastern mainland. Competition from the devil for more secure den sites such as burrows, rock and log piles may also explain the frequent use of foliage as rest sites by the spotted-tailed quoll in Tasmania.

Because we were not able to compare use with abundance or availability in the landscape, our data cannot be used to infer preference for den structures. Furthermore, because we only tracked quolls for a short period prior to the breeding season, no recorded structures were known to be maternal dens (used to raise young), and structures may be more accurately described as resting sites. Resting sites provide animals with protection from predators and unfavourable weather (Kilpatrick and Rego 1994; Weir *et al.* 2004). The degree to which temperature and competitor abundance influence den site selection have not yet been investigated for the spotted-tailed quoll. The use of insecure structures that are exposed to the elements, such as foliage, suggests that neither predation nor thermoregulatory constraints influenced the choice of resting site by the spotted-tailed quoll at Woolnorth during our study

period, however, within Tasmania these results may differ seasonally or regionally.

The characteristics of maternal dens versus resting sites have not yet been distinguished for the spotted-tailed quoll. It is possible that the structures used as resting differ from those used as maternal dens, as has been seen in other forest mesopredators such as the American marten and fisher that rest in a wide variety of structures but preferentially select secure structures such as tree cavities as maternal dens (Aubry *et al.* 2013; Bull and Heater 2000; Weir *et al.* 2004). Conversely, provided that foliage dens provide sufficient thermal regulation and protection from predators, foliage dens could potentially be used as maternal den sites. Although we would expect that tree hollows, logs and burrows would provide greater physical protection from predators than would foliage, vegetation dens were often located within prickly impenetrable weed infestations, and their entrances were more cryptic than other den structures, suggesting that they may provide similar levels of protection.

As expected, quoll dens were concentrated within the 50% core home range areas. In general, core areas represent parts of the home range that experience intense use due to high abundance of key resources, such as food and dens (Harris *et al.* 1990; Powell 2000; Wray *et al.* 1992). Because we estimated home ranges using the Active subset of data which excluded periods when quolls were resting or denning, the 50% core areas solely represent areas used frequently for foraging, and the concentration of dens in core areas shows that the Tasmanian spotted-tailed quoll dens in close proximity to key foraging areas. A similar strategy has been seen in the south-eastern mainland spotted-tailed quoll (Glen and Dickman 2006b; Nelson 2007) as well as other mesopredators (kit fox Arjo *et al.* 2003; e.g. swift fox Pruss 1999; arctic fox Szor *et al.* 2008), and may serve to minimise energetic costs and interspecific risks of travel from prey rich areas to specific den structures. For quolls, this strategy may be especially beneficial during the three month period that females have dependent young in the pouch or in

a maternal den (Oakwood 2002) and therefore need to meet the higher energy demands of lactation, carrying young, and increased hunting to feed themselves and their offspring (Andrew 2005; Fleay 1940; Settle 1978).

4.5.4 Implications for spotted-tailed quoll conservation

Although it is encouraging that quolls are able to inhabit fragmented landscapes, the larger home ranges that result may potentially result in increased energetic costs associated with territorial defence and travel (Jetz *et al.* 2004) as well as increased exposure to other threats including predators, competitors, road mortality and human persecution (Glen and Dickman 2013; Long and Nelson 2008). However many of these costs are low or absent at Woolnorth: the red fox appears to be absent or at very low density; feral cats occur at extremely low abundance; road density and traffic volume is low; and humans are tolerant of the native carnivore population. In other landscapes where this is not the case, animals with large home ranges in landscapes with fragmented vegetation cover may have lower survival and fitness than those with smaller home ranges inhabiting more contiguous habitat. Longer-term telemetry studies that include instrumentation deployment and track survival and reproductive success across multiple seasons, including reproductive and young-rearing periods, are required to confirm whether this is the case.

That quoll populations can utilise agricultural landscapes is in direct contrast to conventional wisdom on the broad habitat requirements of mainland quolls, which require large areas of continuous forest for their ongoing persistence (Long and Nelson 2008). We note that for two individuals, linear remnants and small patches of non-eucalypt forest and scrub provided the majority of vegetation cover within the home range, and thus must have been used almost exclusively for foraging and denning as well as transit. This suggests that, contrary to

the belief that the spotted-tailed quoll requires large areas of contiguous forest for their ongoing persistence (Long and Nelson 2008), quolls are able to persist in a network of linear remnants and stepping stones of forest and scrub. Thus, our results support evidence that corridors and stepping stones provide not only connectivity between larger patches of native vegetation, but are also important habitat in their own right (Bennett 1999).

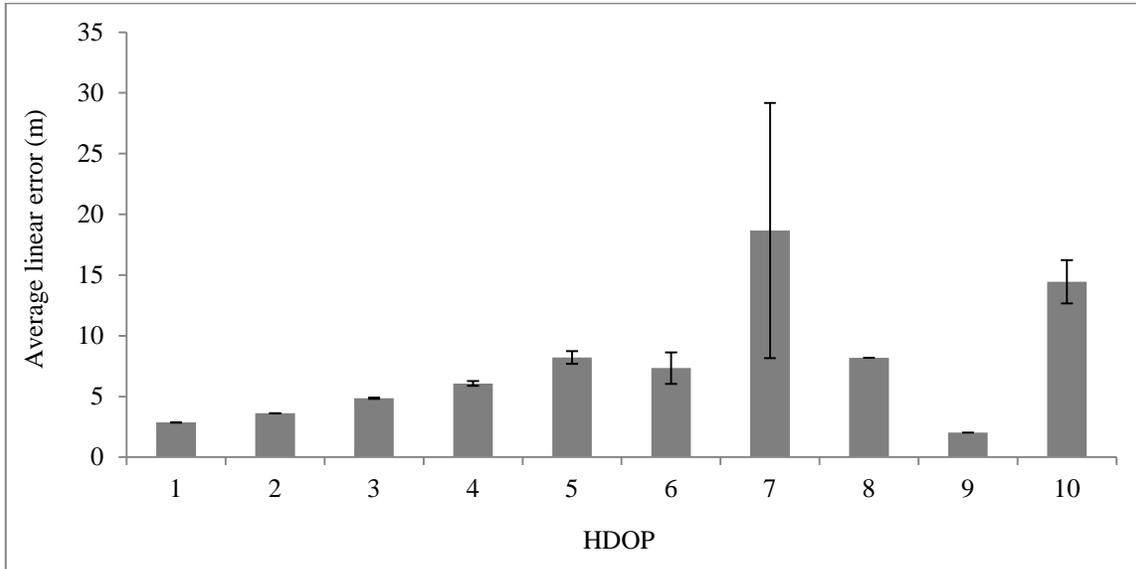
More broadly, the differences in habitat selection observed in this study highlight the importance of using population-specific ecological information to inform management strategies for threatened species. We make three specific recommendations to help ensure that Tasmanian quolls continue to persist in farming landscapes as the state develops its agricultural capabilities into the future. First, at the landscape scale (i.e. second- and third-order), large areas of continuous forest are important for the ecological and evolutionary persistence of the spotted-tailed quoll, and retention of such habitat should be the primary focus of quoll habitat management. However, features such as linear corridors and small islands, shelter belts of exotic vegetation, and woody weed infestations, can also be used by quolls, in some cases are preferred, and should be retained both in existing agricultural landscapes and in landscapes subject to conversion. Second, at the patch scale (i.e. fourth-order), habitat management prescriptions should focus on retention of potential den structures and structural complexity of vegetation (e.g. ground cover and logs for foliage and log dens, mid-storey cover for woody weeds, canopy cover for tree hollows) with forest vegetation. Third, as noted in previous studies, the large home range size of spotted-tailed quolls means they occur across a wide range of vegetation communities and land tenures (Belcher and Darrant 2006b; Lunney and Matthews 2001) and in Tasmania this includes agricultural land. Informing pastoralists about the important ecological role and current decline of the quoll, and engaging them in conservation management actions such as community surveys and avoiding clearance or disturbance of

remnant vegetation will be a vital component of management, recovery, and restoration of quoll populations.

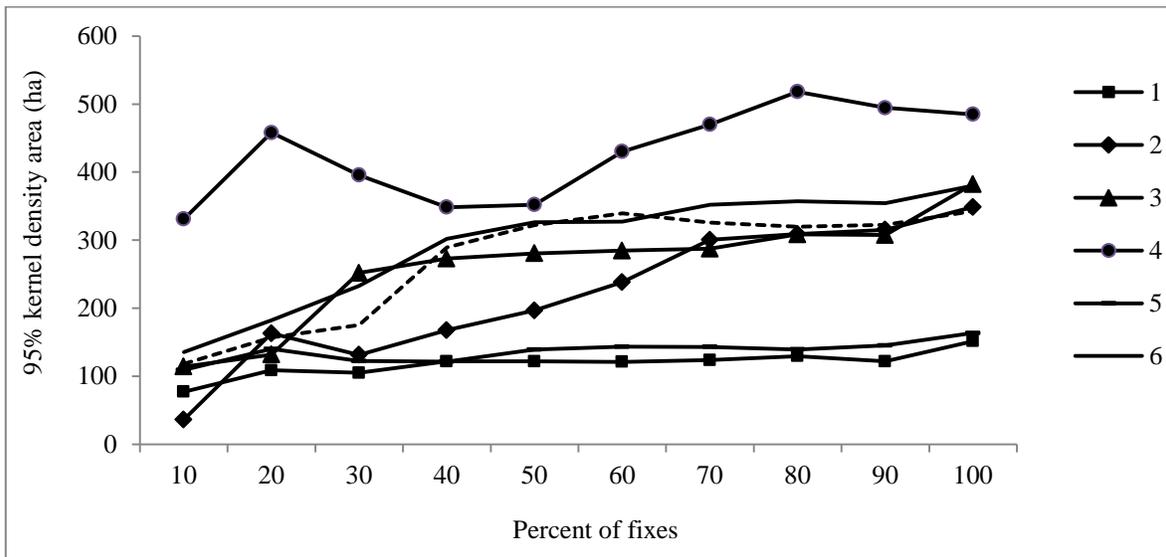
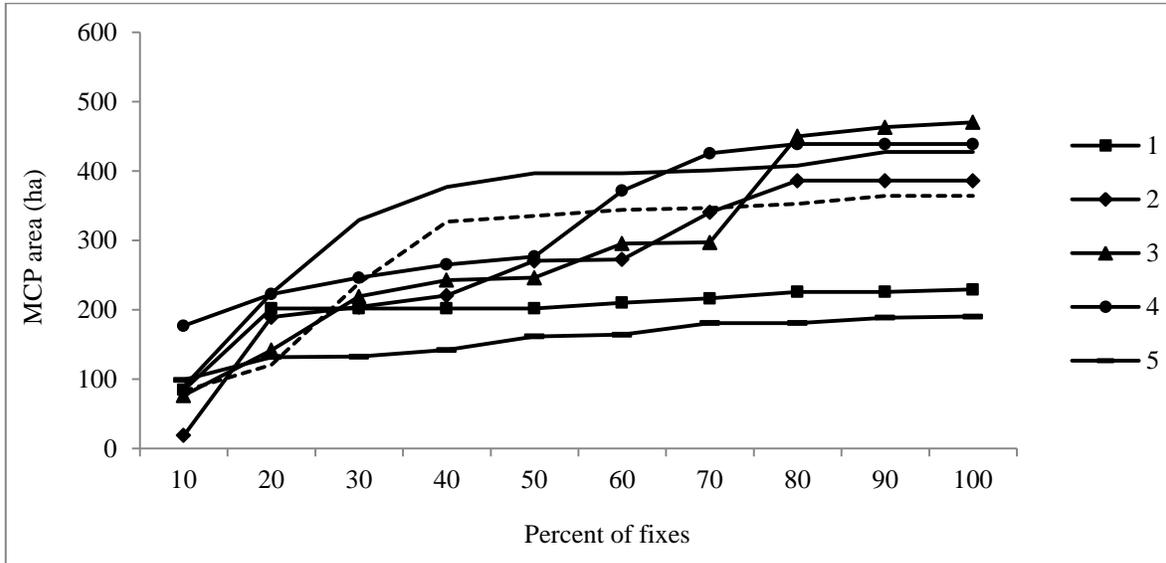
Three important limitations of this study are the short time period (4-5 weeks), restricted season, and constrained geographic extent of data collection. Although this has not yet been investigated, it is likely that quoll area requirements and habitat selection may have a seasonal component, and as such, should be investigated over longer time periods in future studies. Similarly, this study focussed solely on the adult female spotted-tailed quolls because their distribution and abundance is predicted to be closely linked to resource abundance and distribution (Belcher and Darrant 2004, Glen and Dickman 2006b). Future studies should also contrast adult female area requirements and habitat selection with that of male and juvenile spotted-tailed quolls to better understand the population ecology and critical habitat for the species as a whole. Finally, given that our results are from just one study area, extrapolation to other areas must be undertaken cautiously.

In conclusion, despite biological traits that render them inherently susceptible to habitat loss and fragmentation, spotted-tailed quoll populations are capable of inhabiting agricultural landscapes, but individuals are largely restricted to vegetation cover, in particular forest. As such, we caution that there is likely to be a landscape-level threshold in the amount of total habitat loss that quolls can endure, but that this is likely to be determined by resource availability rather than simple proportions of vegetation cover. Future research should aim to determine, at multiple spatial scales, how the use and availability of den and food resources varies with proportion of cover. Our study highlights the importance of investigating habitat use with reference to availability and spatial scale when quantifying the habitat preferences of wide ranging species. Understanding the habitat preferences of carnivores is essential to prevent further decline of these important species and the ecosystems that they serve.

Appendix 4.1: Average linear positional error (\pm se) for GPS fixes with varying values of horizontal dilution of precision (HDOP). Based on this figure, GPS positions with $\text{HDOP} \geq 7$ were excluded from home range estimation and habitat selection analysis.



Appendix 4.2: Asymptote plots for (1) MCP and (2) kernel density estimates of home range area for female spotted-tailed quoll at Woolnorth, Tasmania. Sample sizes and home range area estimates provided in Table 4.1.



Chapter 5: Movement Ecology of the Tasmanian Spotted-Tailed Quoll in a Fragmented Agricultural Landscape



5.1 Abstract

Loss and fragmentation of habitat from conversion of forest to agricultural land pose a great threat to fauna globally. Species persistence in agricultural landscapes depends on the ability of individuals to move among remaining patches of habitat. Therefore, studying the biotic and abiotic factors that facilitate or impede the movement of individuals through heterogeneous landscapes can in turn assist in guiding conservation management strategies to maintain connectivity.

We used movement data from GPS telemetry to investigate activity patterns, step selection and movement behaviour of a threatened marsupial mesopredator, the spotted-tailed quoll (*Dasyurus maculatus*), in an agricultural landscape at Woolnorth, north-western Tasmania, Australia.

Quolls were generally arrhythmic, and neither vegetation cover nor landscape context influenced activity times. Quoll movement rate was similar during the day and night, but higher during twilight, indicative of travel at that time. Step selection analyses showed that quolls preferred to move through forest, avoided the agricultural matrix, and did not differentiate between vegetation cover interior and edges. Analysis of movement behaviour suggested that pasture was primarily used at night, and for travel rather than foraging. Quoll movement was slow and tortuous along edges at night, indicating that quolls may utilise edges to forage for nocturnal prey.

Our results suggest that the spotted-tailed quoll times its activity and movement decisions to maximise exploitation of prey while minimising risks of competition and predation. The agricultural matrix was a filter but not a barrier to spotted-tailed quoll movement. Structural connectivity such as corridors or islands are used by the Tasmanian spotted-tailed quoll as both foraging habitat and features that facilitate the movement of

individuals through the matrix. Retention or restoration of structural connectivity should in turn lead to the maintenance of functional connectivity, and promote the persistence of the Tasmanian spotted-tailed quoll in agricultural landscapes.

5.2 Introduction

Habitat loss is considered the greatest threat to wildlife globally (Baillie *et al.* 2004), and deforestation for conversion to agricultural land use is the leading cause of habitat loss (Tilman *et al.* 2001). With human food production predicted to increase by 70% by 2050 to meet the demands of a growing population (FAO 2006), there is increasing pressure to expand agricultural land, potentially to the further detriment of wildlife populations.

Species-specific responses to habitat loss and fragmentation are well documented: while some species thrive, others decline or disappear (Andr n 1994; Crooks 2002). The species at greatest risk of decline in fragmented landscapes have large individual area requirements, low population abundance, low population growth rate; low mobility; and specialised dietary or habitat requirements (Henle *et al.* 2004;  ckinger *et al.* 2010; Swihart *et al.* 2003). Mammalian carnivore species often possess many of these traits and are therefore predicted to be particularly susceptible to habitat loss and fragmentation (Cardillo *et al.* 2004; Purvis *et al.* 2000; Woodroffe and Ginsberg 1998). However, while some carnivores are highly sensitive to habitat loss and fragmentation, others, particularly smaller generalist mesopredators, are able to exploit increased abundance of some prey resources and the hunting opportunities provided by habitat edges (Caryl *et al.* 2012; Gehring and Swihart 2003; Ryall and Fahrig 2006). Due to their strong effects on lower trophic levels (Estes *et al.* 2011; Prugh *et al.* 2009; Ritchie and Johnson 2009), understanding and predicting the effect of agricultural land use on carnivores is of global conservation concern.

Agricultural conversion not only reduces the amount of resources available to wildlife, but also alters the spatial pattern of remaining resources, creating landscape mosaics of disjunct remnant habitat patches (e.g. forest) surrounded by a matrix of cleared land (Saunders *et al.* 1991). The capacity of species to persist in such landscapes depends on the permeability of the non-forest matrix, the ability of individuals to move among habitat patches, and their ability to exploit supplementary or complementary resources provided by the matrix (Fahrig 2003; Prugh *et al.* 2008). Impeded movement of individuals through the landscape not only reduces individual fitness, but, at the population-level, may alter population dynamics, gene flow, interspecific interactions, and ultimately, population persistence (Bowler and Benton 2005; Holyoak *et al.* 2008; Morales and Ellner 2002; Nathan *et al.* 2008). Conversely, if animals are able move through the matrix, individuals can acquire resources from multiple patches; reproduction, gene flow and recolonisation can be maintained; and populations remain functionally connected, potentially forming stable meta-populations (Hanski 1999). Thus, studying the environmental factors that facilitate or impede the movement of individuals through heterogeneous landscapes provides a mechanistic basis for understanding species-level responses to habitat loss and fragmentation, and gives insight into how to prevent or mitigate any adverse effects.

The spotted-tailed quoll (*Dasyurus maculatus*) is a medium-sized marsupial predator that occurs throughout eastern Australia including the large island of Tasmania (Edgar and Belcher 2008). As a wide-ranging, solitary, low-density, habitat and dietary specialist largely restricted to forest (Belcher 2008; Belcher and Darrant 2006b; Jones and Rose 1996; Mansergh 1984), the spotted-tailed quoll is predicted to be at high risk of decline due to habitat loss and fragmentation (Long and Nelson 2008). Indeed, deforestation is implicated in the past decline of the species (Mansergh 1984), and is considered the greatest threat to its ongoing persistence

(Long and Nelson 2008). The south-eastern mainland spotted-tailed quoll is now restricted to large continuous areas of forest, particularly eucalypt forest, and only rarely occurs on the fringes of cleared areas (Mansergh 1984). However, in Tasmania, the species is also frequently observed in non-forest vegetation (Green and Scarborough 1990; Rounsevell *et al.* 1991). Further, recent research indicates that the Tasmanian spotted-tailed quoll reaches highest abundance in landscapes with some non-forest cover, including cleared agricultural land (Chapter 2, Chapter 4). To date, there has been no research into the movement of quolls in agricultural landscapes.

In this study, we use GPS telemetry data to investigate the movement ecology of the spotted-tailed quoll in a fragmented agricultural landscape. Specifically, we aimed to investigate the influence of vegetation cover (e.g. eucalypt forest, non-eucalypt forest, scrub, or agricultural land), landscape context (e.g. matrix, edge or interior), and time of day on the activity patterns, step selection, and movement rate of adult female spotted-tailed quolls to discern the habitat characteristics that influence movements of individual quolls and determine persistence and connectivity at the population-scale. We focussed our study on adult females because they have lower dispersal capability than males (Belcher 2004; Claridge *et al.* 2005; Firestone *et al.* 1999; Glen and Dickman 2006b), which may make them more sensitive to habitat loss and fragmentation (Henle *et al.* 2004).

Our first objective was to determine the influence of vegetation cover and landscape context on activity times. The Tasmanian spotted-tailed quoll has been described as nocturnal (Jones *et al.* 1997), but the south-eastern mainland spotted-tailed quoll has also been shown to be active during the day (Belcher and Darrant 2004; Claridge *et al.* 2005; Glen and Dickman 2006b) and described as crepuscular (Belcher 2003). We expected that spotted-tailed quolls would be most active at night, with some day-time activity. Due to the strong association with

forest seen in previous studies (Belcher and Darrant 2006b; Jones and Barmuta 1998), we expected quolls to be most active within closed vegetation, particularly eucalypt forest, and least active in the agricultural matrix and along edges, at all times of day and night.

Our second objective was to quantify how vegetation cover and landscape context influenced spotted-tailed quoll step selection in different diel periods. We expected that the quolls would avoid moving through agricultural land, or toward the agricultural matrix or edges, and show strong preference for moving within vegetation cover, especially eucalypt forest. We expected that preference for cover and avoidance of the agricultural matrix and edges would be strongest during the day.

Our third objective was to quantify how vegetation cover and landscape context influenced spotted-tailed quoll movement behaviour. Movement rate and tortuosity can be used to distinguish animal movement behaviours, with fast linear movement indicating travel through low suitability habitat (Crist *et al.* 1992), and slow tortuous movement corresponding to foraging in preferred habitats (Wiens *et al.* 1995). Analysis of diet and fine-scale movement data suggest that the Tasmanian spotted-tailed quoll spends considerable time foraging arboreally (Jones and Barmuta 2000). Our GPS loggers were not able to resolve whether quolls were moving in the arboreal or the terrestrial dimension, but regardless, short local movement as a result of arboreal activity would also result in a slow movement consistent with foraging. We expected that quolls would forage primarily in eucalypt forest (Belcher and Darrant 2006b; Glen and Dickman 2006a; Jones and Barmuta 1998) and to a lesser extent in non-eucalypt forest and scrub, and that movement would therefore be slow and tortuous in those vegetation cover types. Conversely, we expect the agricultural matrix and edges to be used only for travel between patches of forest and scrub, indicated by fast and linear movement.

We use our combined results to assess the relative risk that habitat loss and fragmentation

due to agricultural development poses to the spotted-tailed quoll, discuss potential mechanisms driving movement patterns, and offer suggestions to maintain or restore landscape connectivity for the spotted-tailed quoll in agricultural landscapes.

5.3 Methods

5.3.1 Study area

The study site encompassed approximately 4,400 ha of Woolnorth, a dairy, beef and sheep property at Cape Grim in far northwest Tasmania, Australia (Figure 5.1). Woolnorth has a low, flat topography, with elevation varying from 0 - 100 m and slope 0 – 15 %. The climate is Mediterranean, with annual mean rainfall 762 mm and monthly mean temperature range 8.2-19.5°C. Remnant native vegetation consists of eucalypt forest and woodland, melaleuca swamp forest, and coastal scrub and heath embedded within a matrix of intensively grazed improved pasture. The study site was selected on the basis of long-term predator trapping data (Department of Primary Industries, Parks, Water and Environment (DPIPWE) Save the Tasmanian Devil Program unpublished data) that indicated the presence of a high-density quoll population in this fragmented agricultural landscape.

5.3.2 Vegetation predictor variables

Vegetation communities were mapped in ArcGIS 9.2 (ESRI, Redlands, California, USA) using the Tasmanian vegetation mapping spatial database TasVeg 2.0 (TASVEG 2009) and verified through on-ground surveys and high resolution (1:5,000) digital orthophotographs (DPIPWE). We combined structurally- and floristically-similar vegetation communities to create four vegetation cover types: eucalypt forest (EF); non-eucalypt forest (NEF); scrub (SC); and pasture (AG). We then combined EF, NEF, and SC to create a fifth category, cover (COV).

To investigate spotted-tailed quoll response to landscape structure, we created a further four categories to describe landscape context: the cover-pasture interface (EDGE); cover interior (INTERIOR); agricultural matrix (MATRIX); and distance to edge from within cover (DISTEDGE). These nine variables that formed the basis of the predictor variables used in our analyses are described in more detail in Table 5.1.

5.3.3 Trapping and radio-tracking

Trapping, collaring, and tracking were conducted between March and May 2011, in the period after juvenile dispersal and prior to the breeding season, when the adult female population is most likely to be stable and reproductive success least likely to be adversely affected by collaring. To trap quolls, we used PVC pipe traps baited with pieces of wallaby meat placed along roadsides or the vegetation-pasture edge. Following capture, quolls were transferred without sedation to a hessian sack and weighed, sexed, and microchipped for future identification.

Seven adult female quolls (defined by body-weight and teat development) were fitted with 70 g Telemetry Solutions Quantum 4000 Enhanced radio-collars equipped with a GPS logger, a single-stage VHF transmitter, and a UHF transmitter (collar weight 2.6% - 3.5% of body weight).. The GPS logger was programmed to record a location ‘fix’ every two hours, and the VHF was used to locate quolls to collect information on den use. As per our animal ethics conditions, in the first week after being collared, all animals were located once a day to ensure the collar was not preventing movement. All collared quolls were re-trapped after one week to ensure that body weight and condition were maintained, and to check collar fit and ensure no chafing had occurred. GPS data were downloaded remotely approximately once a week. All quolls were successfully recaptured to enable retrieval of collars.

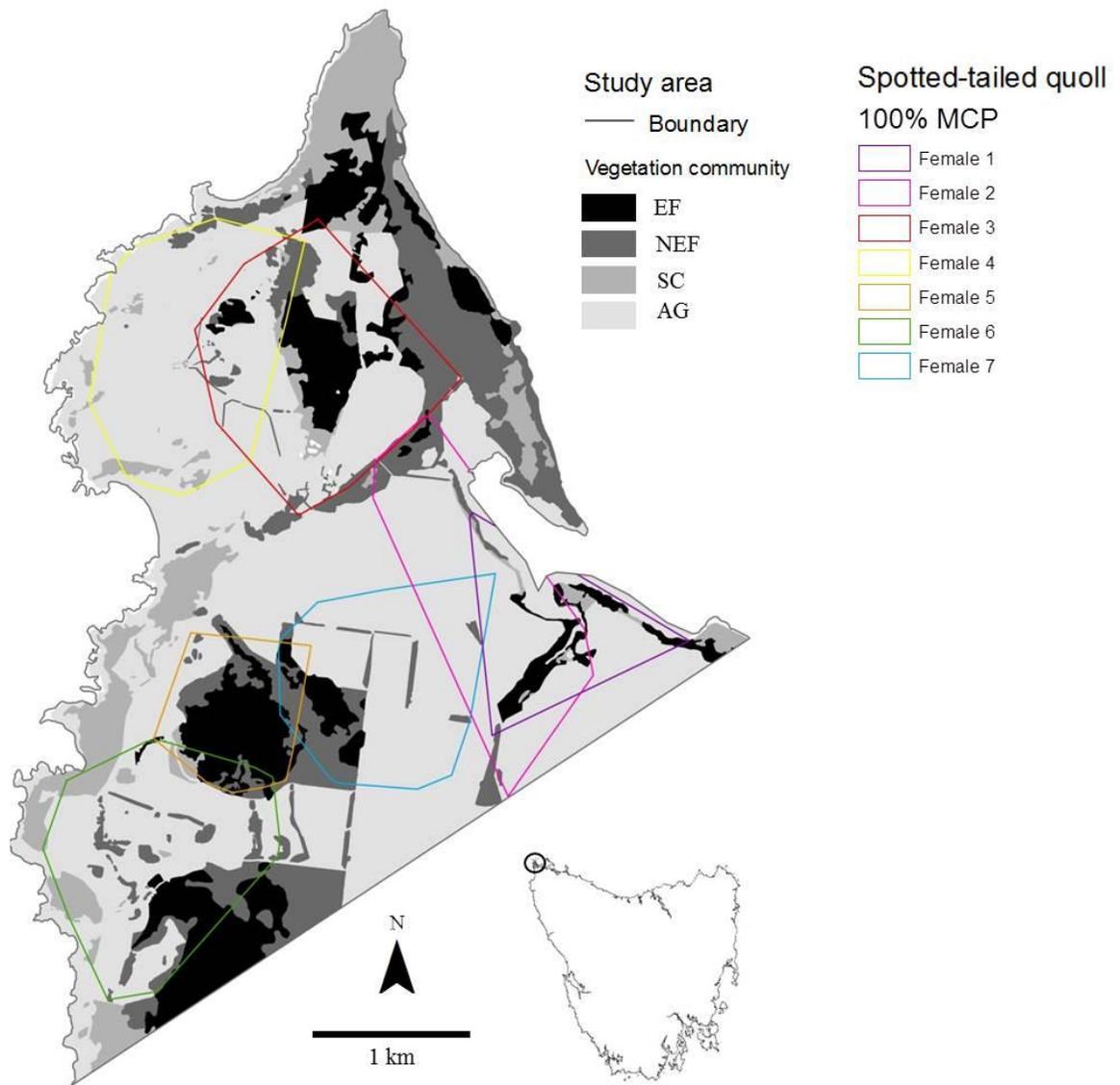


Figure 5.1: Distribution of vegetation communities and adult female 100% Minimum Convex Polygons (MCP) home ranges ($n=7$) within the study area at Woolnorth, north-western Tasmania.

VARIABLE	TasVeg 2.0 COMMUNITIES	VARIABLE DESCRIPTION
VEGETATION COVER		
EF	DNI <i>Eucalyptus nitida</i> dry forest WBR <i>Eucalyptus brookeriana</i> wet forest	Eucalypt Forest Mature age, large diameter and hollow bearing trees with a high proportion of canopy cover, and a well-developed shrub and ground cover layer.
NEF	NLE <i>Melaleuca ericofolia</i> NLM <i>Melaleuca squarrosa</i> FPU <i>Pinus radiata</i> FPU <i>Cupressus macrocarpa</i>	Non-Eucalypt Forest Dense stands of small to medium diameter non-hollow bearing trees with a high proportion of canopy cover, and sparse open shrub and ground cover. Non-native <i>Pinus radiata</i> and <i>Cupressus macrocarpa</i> occur in small stands or windbreaks
SC	SAC <i>Acacia longifolia</i> coastal scrub SMR <i>Melaleuca squarrosa</i> scrub FWU European gorse <i>Urex europaeus</i> FWU African boxthorn <i>Lycium ferocissimum</i>	Scrub Dense stands of multi-stemmed woody vegetation. Forest canopy cover < 20%
AG	FAG Improved pasture	Agriculture Agricultural field, pasture or low (< 30 cm) crop with <10% shrub or canopy cover
COV	N/A	Cover Combined Eucalypt Forest, Non-Eucalypt Forest and Scrub
LANDSCAPE CONTEXT		
EDGE	N/A	Edge 20 m wide buffer either side of the cover-agriculture interface.
INTERIOR	N/A	Interior COV minus cover EDGE
MATRIX	N/A	Matrix AG minus EDGE
DISTEDGE	N/A	Distance to Edge Distance (metres) from end of step to cover-agriculture interface

Table 5.1: Environmental covariates used in movement analyses.

Although our sample size of collared quolls was small, collaring large numbers of adult female spotted-tailed quolls was not feasible due to territorial constraints on the number of adult females present within a landscape. Indeed, in previous quoll telemetry studies, sample sizes of adult females range from three to seven in any one year. In our study area, 70% of known adult females were collared. This high proportional sample of the population, in combination with GPS technology and frequent VHF tracking to dens, provided a representative insight into quoll ecology.

5.3.4 GPS data preparation

Each GPS logger was programmed to record a location every two hours seven days a week (henceforth two hour interval data), and every fifteen or twenty minutes every second and sixth day (henceforth fifteen minute interval data). The VHF was used to locate quoll positions in real time. Data obtained from collars for each fix included date, time, GPS coordinates, elevation, number of satellites, and horizontal dilution of precision (HDOP). GPS data require evaluation and screening for measurement error and bias prior to use in analysis (Frair *et al.* 2010). The horizontal dilution of precision (HDOP) provides an index of GPS coordinate precision, with lower HDOP values considered more precise (D'eon and Delparte 2005). To minimise the risk of including imprecise and erroneous fixes in data analysis, locations with HDOP greater than some arbitrary threshold are commonly removed (D'eon and Delparte 2005), however, HDOP provides only a relative measure of precision. Due to the small size of some vegetation patches in our landscape and our need to correctly classify fixes according to the type of vegetation cover they fell within, our first step was to quantify the precision of GPS locations that were associated with different values of HDOP to ensure that positional accuracy was similar to that of our spatial vegetation data (± 5 m). We did this by examining variation in

clusters of coordinates collected from quolls that were known (from VHF tracking) to be stationary (e.g. denning or resting). We calculated the mean linear error associated with each HDOP value by measuring the distance between the mean coordinates of a cluster of points and each point in the cluster. We retained all fixes with a HDOP of ≤ 6 , which corresponded with a maximum linear error of 7.3 ± 0.53 m (Appendix 4.1).

We used the linear error analysis of GPS location and observations from VHF tracking of quolls to den sites to assign each GPS location an activity status: “Inactive”, and “Active”. Inactive GPS locations were defined as those recorded in periods of ≥ 6 hours where all step lengths and the total net displacement were ≤ 20 metres, when the animal was presumed to be resting. For all other locations quolls were considered Active (e.g. in transit or foraging). Our approach allowed for inclusion of prey handling or short periods of rest as part of activity, while excluding long periods of rest.

5.3.5 Influence of diel period, vegetation cover and landscape context on activity

To investigate activity times, we calculated the mean proportion of locations active (PLA) by dividing the number of times that quolls were classified as Active by the total number of relocation attempts for each two-hour fix interval. We plotted PLA against time of day to visualise temporal patterns in activity. Based on these plots, we assigned each location in the two-hour interval Active data into one of three diel periods according to the time that the step was initiated: day (D); night (N); and nautical twilight (T) (Lucherini *et al.* 2009). Each location was categorised into one of four vegetation cover types (EF, NEF, SC or AG) and one of three landscape contexts (EDGE, INTERIOR or MATRIX); . To investigate how diel period, vegetation cover, and landscape context influenced activity patterns, we analysed data with a generalised linear mixed model (GLMM) in the lme4 package version 1.0-5 (Bates *et al.* 2012)

in R version 3.0 (R Core Team 2013). We used a binary predictor indicating whether the animal was active or inactive as the response variable; diel period and either vegetation cover or landscape context as categorical predictor variables; and included a random effect of individual identity. Models were fit with an interaction effect between diel period and vegetation cover or landscape context. The interaction effect was retained in the model only if its inclusion reduced AIC by more than two relative to an additive model (Burnham and Anderson 2002). Significant differences in the proportions of location active among levels of diel period and vegetation cover were assessed using Tukey's pairwise comparison tests in the multcomp package (Hothorn *et al.* 2008) in R version 3.0 (R Core Team 2013).

5.3.6 Influence of vegetation cover and landscape context on step selection

A step refers to the straight line that connects two consecutive locations. Step length is the straight line distance (metres) between two consecutive locations. The turning angle is the angular difference in the bearing of two consecutive steps. We used a step selection function (SSF) to identify how vegetation cover and landscape context influenced adult female spotted-tailed quoll movement (Fortin *et al.* 2005). Statistically, SSF models are identical to discrete choice (or case-control) habitat selection studies (Boyce *et al.* 2003; Manly *et al.* 2002), except that steps rather than point locations are the dependent variable, which provides a more mechanistic model of animal movement (Roever *et al.* 2010). SSF models estimate the influence of environmental characteristics on the probability of step selection by comparing the environmental characteristics along or at the end of used steps to those along or at the end of possible but unused steps (Figure 5.2). The SSF does not assume that animals travel a straight-line path, only that movement decisions are influenced by habitat between the start and end points of steps (Fortin *et al.* 2005).

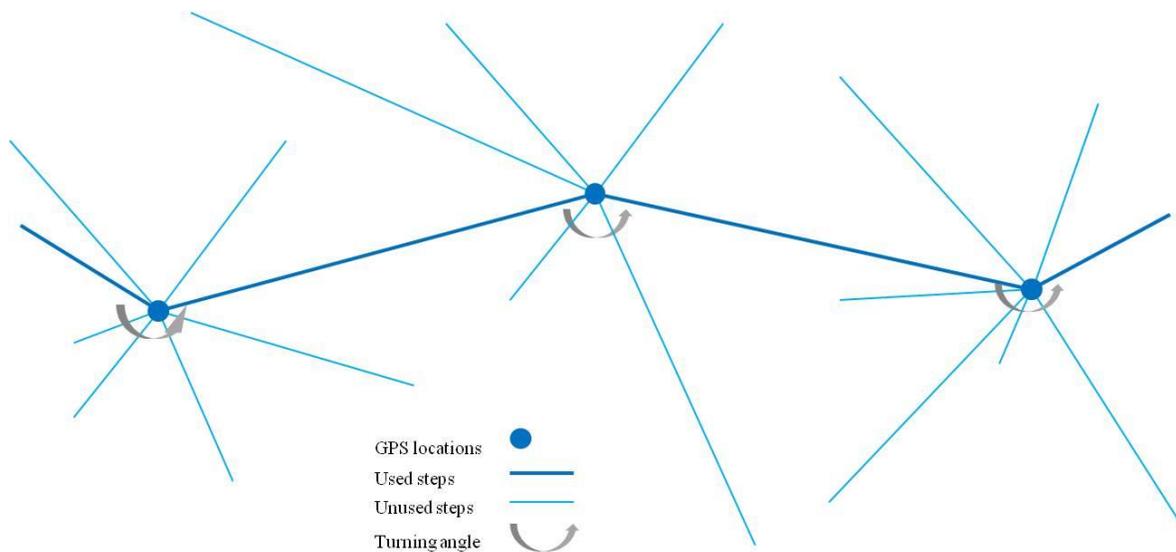


Figure 5.2 Theoretical depiction of data used in a Step Selection Function that compares each used step to five randomly generated possible but unused steps for each GPS location. Environmental characteristics are sampled along or at the end of steps to investigate the influence of habitat features on step selection. Step length is given by the distance between GPS locations; turning angles are shown as grey arrows. Adapted from Squires *et al.* (2013).

We used the two-hour fix interval Active data for analysis to maximise the chances of meeting the SSF assumption of temporal independence of response data. The data were again categorised into of three diel periods (D, N, T) according to the time that the step was initiated, for which step selection was modelled separately. Prior to analysis, we checked for temporal autocorrelation in the distribution of used step lengths for each diel period using a Wald-Wolfowitz test of random distribution, and by inspection of autocorrelation function plots (ACF) of step length for up to five consecutive fixes, both of which revealed no temporal autocorrelation for any animal in any diel period.

For each used step, 14 random unused steps were generated using the program Geospatial Modelling Environment version 0.7 (Beyer 2012). Random steps originated from the same starting point as the used step, and had lengths and turning angles drawn randomly

from the used step length and turning angle distributions of other animals in the same diel period (Fortin *et al.* 2005). For each animal, random steps were restricted to the area contained by a 100% minimum convex polygon (MCP) home range generated in ArcGIS using the Hawth's Tools Animal Movement Extension (Beyer 2004) in ArcGIS version 9.2 (Environmental Systems Research Institute Inc, Redlands, CA). To quantify how vegetation influenced the probability of step selection, we measured the proportion of vegetation cover types (EF, NEF, SC, and AG) along used and unused steps, and recorded each used and unused steps ended in the matrix (MATRIX), edge (EDGE) or interior (INTERIOR) using the intersect tool in ArcGIS version 9.2 (Environmental Systems Research Institute Inc, Redlands, CA).

The SSF models were estimated using the TwoStepCLogit package version 1.2.1 (Craiu *et al.* 2013) in R version 3.0 (R Core Team 2013). The response variables were the choice set of used and unused steps. Predictor variables for vegetation cover were EF and NEF only; AG and SC were excluded from the model because preliminary analysis indicated that EF and AG had a strong negative correlation ($r < -0.75$), and the absence of SC in the choice set of some individuals used or available steps resulted in problems during model fitting. The predictor variable for landscape context was categorical, with three levels corresponding to whether the step ended in MATRIX, EDGE or INTERIOR. The effect of vegetation along a step on quoll step selection was inferred by examination of the magnitude and direction of the beta coefficient. When 95% confidence intervals for beta coefficients did not span zero, the effect of the environmental covariate on step selection was considered statistically significant.

5.3.7 Influence of vegetation cover and landscape context on movement behaviour

These analyses investigated quoll movement behaviour once a step was selected and being used. We analysed movement rate and turning angle to compare movement behaviour by

spotted-tailed quolls in relation to diel period, vegetation cover and landscape context. We used the fifteen minute fix interval Active data for these analyses, as the frequent fix interval allows a more sensitive measurement of behavioural response to environment. For the first movement rate analysis, we investigated the effect of vegetation cover and diel period on movement rate. We first calculated movement rate (metres per minute) by dividing step length by the fix interval (15 or 20 minutes). For analysis of the effect of vegetation cover on movement rate, only steps that fell completely within EF, NEF, SC, and AG were used. Movement rate data were analysed using linear mixed effects models in the package nlme (Pinheiro *et al.* 2013) in R version 3.0 (R Core Team 2013). We used log-transformed movement rate as the response variable; vegetation cover type, diel period, and their interaction as predictor variables; and included a random effect of individual. The interaction effect was only retained in the model if its inclusion reduced AIC by more than 2 (Burnham and Anderson 2002). Significant differences in movement rates among levels of diel period and vegetation cover were assessed using Tukey's pairwise comparison tests in the multcomp package (Hothorn *et al.* 2008) in R version 3.0 (R Core Team 2013).

For the second movement rate analysis, we investigated the effect of landscape context and diel period on movement rate. Due to the low number of steps that fell completely within EDGE, it was not possible to model the relative effect of landscape context categories on movement rate. Instead, using only steps that fell completely within cover (COV), we analysed how quoll movement rate varied with distance to edge (DISTEDGE). Data were again analysed using linear mixed effects models in the package nlme (Pinheiro *et al.* 2013) in R version 3.0 (R Core Team 2013). We used log transformed movement rate as the response variable, square root transformed DISTEDGE as the predictor variable, and a random effect of individual. These data were analysed separately for each diel period.

The short time interval between successive relocations (15-20 minutes) meant there was high potential for temporal autocorrelation among successive observations, which would violate the assumption of statistical independence (Nielsen *et al.* 2002). To check for temporal autocorrelation in the movement rate model residuals, we examined semi-variograms of deviance residuals through time separately for each of the six models.

We used circular statistics (Batschelet and Batschelet 1981) to investigate the influence of diel period, vegetation cover and landscape context on the distribution of turn angles to infer the tortuosity of quoll movement paths. We analysed the distribution of turning angles from the 15 minute interval data using the program Oriana version 4 (Kovach Computing Services, Wales, UK). Summary statistics and directionality were computed separately for the vegetation cover categories EF, NEF, SC, and AG and the landscape context categories MATRIX, INTERIOR and EDGE for each diel period. Summary statistics included the sample size (n), mean (a) and standard error (s) of the turning angle. A mean centred around 0 with a small standard error provided evidence for linear movement, while a non-zero mean and / or a large standard error indicated a wide variety of turning angles were used *i.e.* non-linear movement. Directionality was estimated using the mean vector length (r) (Batschelet and Batschelet 1981), a measure of the magnitude and directionality of turn angles from 0 (uniform turning angle distribution) to 1 (concentration of data around the mean direction, a tendency to maintain a similar direction from one step to the next). Significant directionality of movement was investigated using a Rayleigh Z-test (Fisher 1995), where $Z = nr^2$, a significant result ($P < 0.05$) provides evidence for a preferred turning angle. We then used the Watson-Williams F test (Batschelet and Batschelet 1981), the circular equivalent of an ANOVA, to determine if the mean turning angle differed with vegetation cover and landscape context. The test assumes that samples are drawn from a population with a von Mises distribution, and that concentrations (k)

of the two samples are similar and sufficiently large (>2) to distinguish differences (Batschelet and Batschelet 1981).

5.4 Results

5.4.1 Trapping and GPS data

Trapping yielded 97 captures of 44 individual quolls over 1,367 trap nights. Ten of the captured quolls were adult females (e.g. ≥ 1.6 kg), of which seven weighing ≥ 2 kg were collared for 28 - 36 days. The GPS collars collected a total of 5,158 relocations from 7,110 attempts. To minimise the risk of including fixes with location errors in data analysis, we removed 121 fixes with a horizontal dilution of precision (HDOP) >6 , which represented 2.35% of all successful relocations. The remaining 5,037 locations with HDOP ≤ 6 had a maximum linear error of 7.3 ± 0.53 m. At two hourly intervals, a total of 1,464 fixes were obtained, of which 808 were classified as Active. At 15 or 20-minute intervals, 3,533 fixes were obtained, with 1,785 of these classified as Active.

5.4.2 Influence of diel period, vegetation cover and landscape context on activity

Visualisation of PLA indicated that, on average, quolls were most active at or just after sunset (Figure 5.3). Although activity was generally lower during the day than at night, there was no period of the day when quolls were consistently inactive. There was considerable variation in PLA among individuals: Females 1, 2, 3 and 4 had an increase in activity at dusk, extensive nocturnal activity, and a decrease at dawn; whereas Females 5, 6 and 7 were as active at dawn and during the day as they were overnight (Figure 5.3).

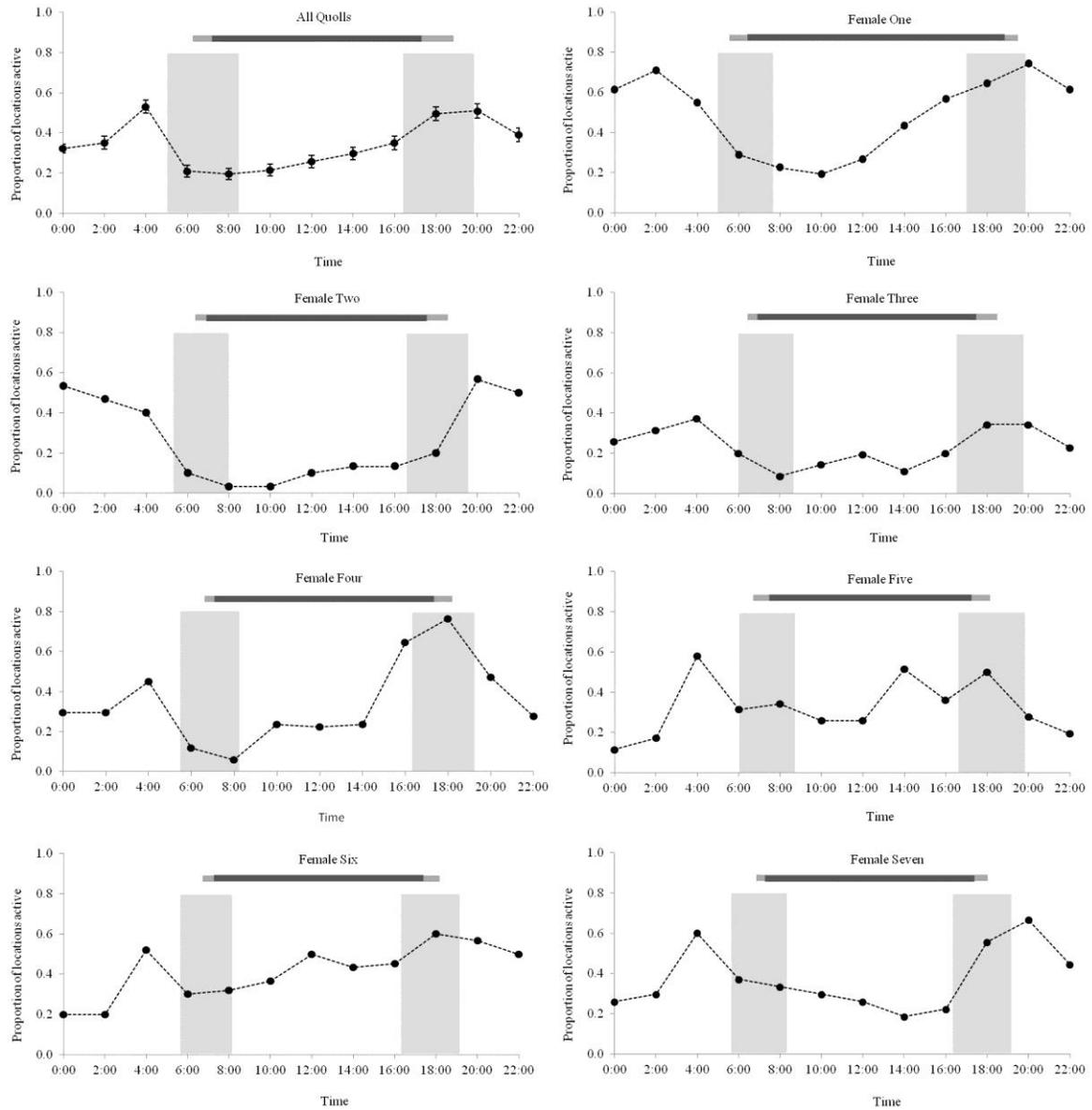


Figure 5.3: Proportion of locations active (PLA) for adult female spotted-tailed quolls (n=7) from 2,466 location records collected between 9 March and 9 May 2011 at Woolnorth, north-western Tasmania. Figure for ‘All Quolls’ shows mean (\pm standard error). Daylight is represented by the dark grey bar (shortest day) and extending light grey bar (longest day). Light grey boxes show twilight. Total sample size n = 808. Range per bi-hourly period = 40 – 105 locations.

Although the bi-modal peak in activity was suggestive of a crepuscular activity pattern, the morning peak always occurred during twilight, and quolls showed differing degrees of diurnal and nocturnal activity.

There was no support for an interactive effect of diel period and vegetation cover type on the proportion of locations active (additive model AIC = 1959.480 < interaction model AIC = 1964.326). There were no significant effects of vegetation cover ($P = 0.084 - 0.967$) or diel period ($P = 0.698 - 0.951$) on PLA. Similarly, there was no support for an interactive effect of diel period and landscape context on PLA (additive model AIC = 2057.658 < interactive model AIC = 2065.257), and there were no significant effects of either landscape context ($P = 0.135 - 0.967$) or diel period ($P > 0.738 - 0.951$) on PLA.

5.4.3 Influence of vegetation cover and landscape context on step selection

Adult female spotted-tailed quolls showed significant preference for steps that consisted of a high proportion of EF at all times of day (Table 5.2). The strong negative correlation ($r < -0.75$) between EF and AG means that preference for EF also indicates avoidance of steps containing a high proportion of AG. Quolls also showed preference for NEF during the day (Table 5.2).

Landscape context also had a consistent effect on step selection across diel periods (Table 5.2). At all times of day, quolls were significantly more likely to select steps that ended in INTERIOR or EDGE, and avoid taking steps that ended in MATRIX. There was no significant difference in the effect of EDGE and INTERIOR on the probability of step selection; quolls were equally likely to take steps that ended within EDGE or INTERIOR.

	Day	Night	Twilight
VEGETATION COVER			
EF	2.437 (0.605 - 4.268)	0.421 (0.059 - 0.783)	0.920 (0.097 - 1.743)
NEF	1.823 (0.271 - 3.375)	-0.269 (-1.521 - 0.983)	-0.476 (-1.576 - 0.625)
LANDSCAPE CONTEXT			
EDGE-MATRIX	1.264 (0.289 - 2.238)	2.273 (1.556 - 2.99)	1.205 (0.469 - 1.941)
INTERIOR-MATRIX	0.697 (0.16 - 1.233)	2.443 (1.256 - 3.63)	1.354 (0.44 - 2.269)
EDGE-INTERIOR	0.488 (-0.044 - 1.02)	-0.21 (-0.768 - 0.348)	-0.103 (-0.792 - 0.587)

Table 5.2: Estimated beta coefficients (with lower and upper 95% confidence interval in parentheses) for the step selection function (SSF) model of adult female spotted-tailed quoll ($n = 7$) movement at Woolnorth, north-western Tasmania. Step selection functions (SSF) were generated from used steps generated from relocations taken at two hour intervals ($n = 797$) and compared to 14 randomly generated steps ($n = 11,158$). SSF models were generated separately for each diel period. Values in bold indicate a statistically significant effect of vegetation community on step selection.

5.4.4 Influence of vegetation cover and landscape context on movement behaviour

The maximum distance moved between two consecutive GPS locations was 876 metres for the 15 minute fix interval data and 1,992 metres for the 2 hour fix interval data. Movement rates were significantly faster during twilight than during the day or night, but there was no difference between day and night (Table 5.3, Figure 5.4).

TEST	REFERENCE	Estimate	SE	<i>z</i>	<i>P</i>
Day	Twilight	-0.565	0.131	-4.315	<0.001
Night	Twilight	-0.333	0.116	-2.874	0.011
Night	Day	0.232	0.108	2.141	0.081

Table 5.3: Regression coefficient estimates, their standard error, and associated *z* and *P* values from a linear mixed effects models and subsequent post hoc Tukey's tests to investigate the effect of diel period on the movement rate of adult female Tasmanian spotted-tailed quolls ($n=7$) at Woolnorth, north-western Tasmania. Coefficients show difference between two variables (test and reference). A negative coefficient indicates that movement speed is slower in the test diel period than the reference. Rows in bold indicate a statistically significant ($P < 0.05$) difference in movement rate between the test and reference diel periods.

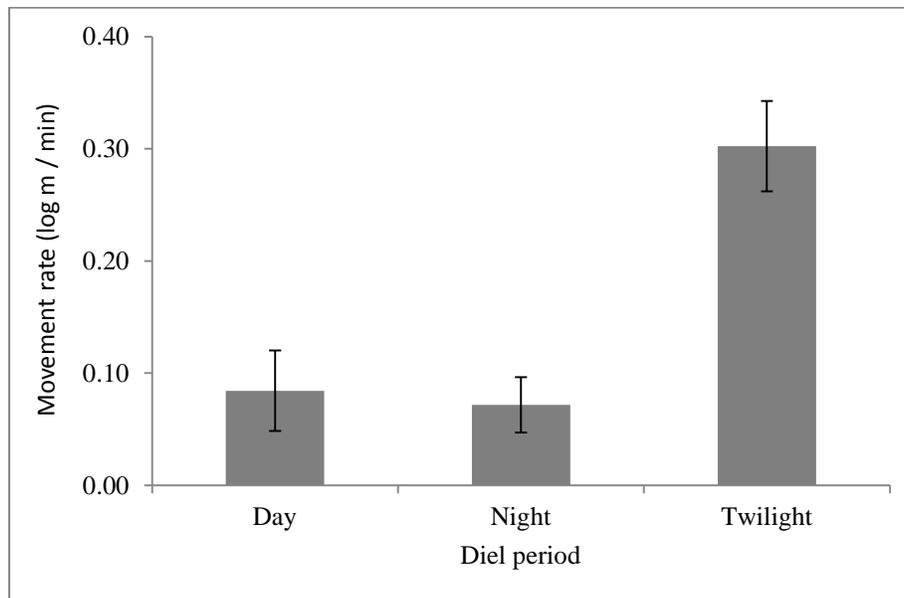


Figure 5.4: Mean (\pm standard error) movement rate (log metres per minute) of adult female spotted-tailed quolls ($n=7$) across diel periods at Woolnorth, north-western Tasmania.

There was strong support for an interaction effect of diel period and vegetation cover type on movement rate (interaction model AIC = 4270.577 < additive model AIC = 4294.439).

Movement rate was significantly higher in AG than in EF, NEF, and SC, but only at night

(Table 5.4, Figure 5.5). There were no significant differences in movement rate between any other vegetation cover types at night, or between any vegetation cover types during the day or at twilight (Table 5.4, Figure 5.5), perhaps because there were few steps taken completely within NEF during twilight, and in SC and AG during the day (Figure 5.6).

DIEL PERIOD	TEST	REFERENCE	Estimate	SE	<i>t</i>	<i>P</i>
Day						
	EUC	AG	-1.442	0.531	-2.316	0.25
	NEF	AG	1.867	0.795	2.348	0.165
	SC	AG	-2.279	0.834	-2.734	0.064
	NEF	EUC	0.425	0.587	0.725	0.987
	SC	EUC	0.837	0.638	1.313	0.78
	SC	NEF	0.412	0.343	1.199	0.844
Night						
	EUC	AG	-3.02	0.652	-4.633	<0.01
	NEF	AG	-2.621	0.707	-3.71	<0.01
	SC	AG	-2.881	0.506	-5.691	<0.01
	NEF	EUC	0.398	0.343	1.161	0.862
	SC	EUC	0.139	0.474	0.293	1
	SC	NEF	-0.259	0.547	-0.474	0.999
Twilight						
	EUC	AG	-0.482	0.469	-1.027	0.919
	NEF	AG	-1.111	0.522	-2.129	0.26
	SC	AG	-1.062	0.616	-1.724	0.504
	NEF	EUC	-0.629	0.288	-2.182	0.235
	SC	EUC	-0.58	0.436	-1.33	0.77
	SC	NEF	0.049	0.493	0.099	1

Table 5.4: Regression coefficient estimates, their standard error, and associated *t* and *P* values from a linear mixed effects models and subsequent post hoc Tukey's tests to investigate the interactive effects of vegetation cover and diel period on the movement rate of adult female Tasmanian spotted-tailed quolls ($n = 7$) at Woolnorth, north-western Tasmania. Coefficients show difference between two variables (test and reference). A negative coefficient indicates that movement speed is slower in the test vegetation than the reference. Rows in bold indicate a statistically significant ($P < 0.05$) difference in movement rate between the test and reference vegetation community.

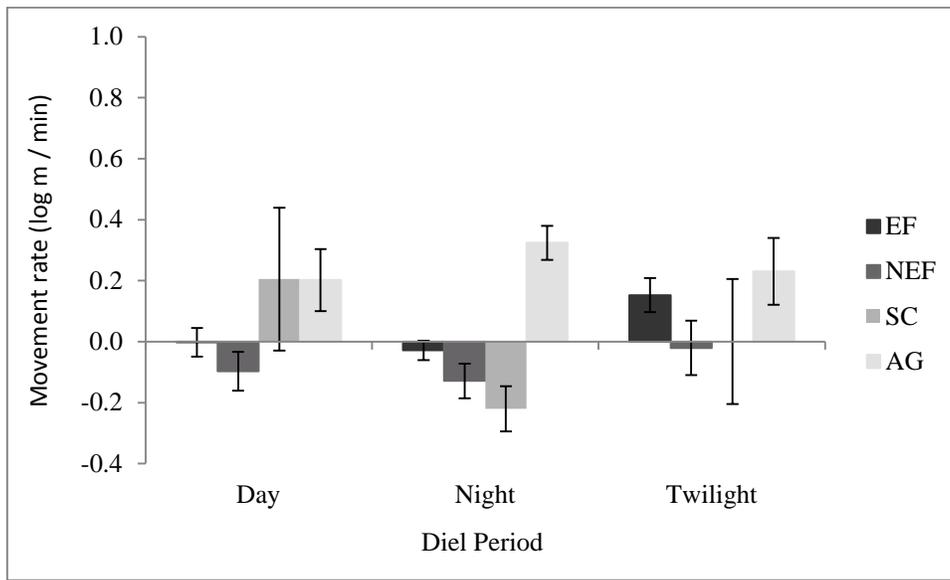


Figure 5.5: Mean (\pm standard error) movement rate (log metres per minute) of adult female spotted-tailed quolls ($n=7$) within vegetation cover types across three diel periods at Woolnorth, north-western Tasmania. EF = Eucalypt forest NEF = Non-Eucalypt forest; SC = Scrub; AG = Agriculture.

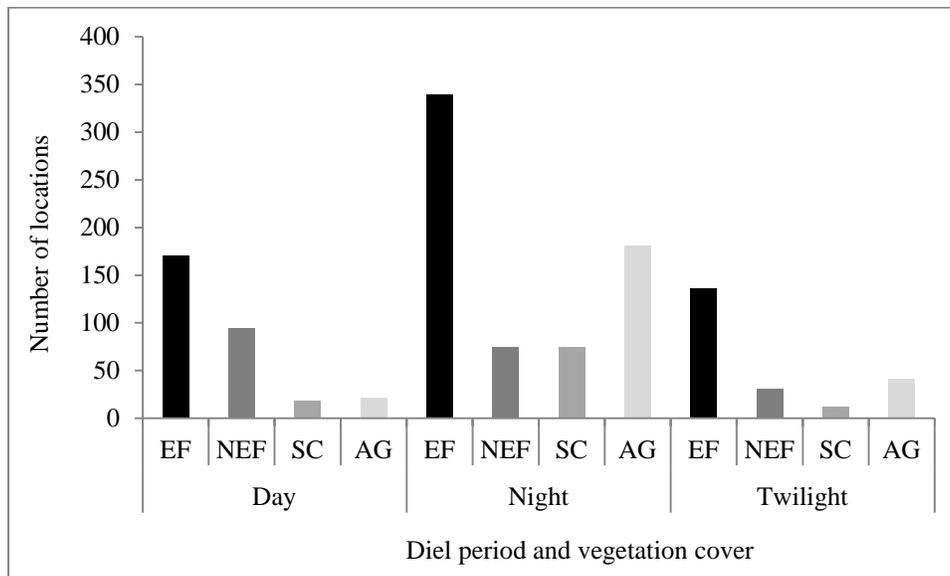


Figure 5.6: Number of adult female spotted-tailed quolls ($n=7$) within vegetation cover types at Woolnorth, north-western Tasmania. EF = Eucalypt forest NEF = Non-Eucalypt forest; SC = Scrub; AG = Agriculture.

Within COV, quolls movement rate decreased as proximity to edge (EDGEDIST) decreased at night (Estimate = 0.002, SE = 0.0002, df = 543, $t = 2.979$, $P < 0.01$) but not during the day (Estimate = 0.000016, SE = 0.0003, df = 319, $t = -0.248$, $P = 0.8044$) or twilight (Estimate = 0.0005, SE = 0.0004, df = 209, $t = 1.102$, $P = 0.272$). There was no evidence for temporal autocorrelation in any movement rate model residuals (Appendix 5.1).

The short mean vector lengths ($r < 0.6$) and low concentrations ($k < 1$) indicated a wide distribution of turning angles in all vegetation cover types (Table 5.5). The low concentrations meant that the assumptions of the Watson-Williams F -Test were violated and we therefore present only the results of the Rayleigh tests of directionality. At dawn and dusk, spotted-tailed quolls exhibited significant forward directional movement in all vegetation cover types and landscape contexts (Table 5.5). During the day, turn angles in EF tended to be tortuous, but all other test values for directionality was non-significant. At night, quolls exhibited significant directional movement only in AG and the MATRIX, where they were most likely to move in a straight forward direction (Table 5.5). The high standard error of the mean turning angle, lack of directional movement, and short vector length in EF, SC, EDGE, and INT indicates that quolls used a wide distribution of turn angles when moving through these cover types.

	VEGETATION COVER				LANDSCAPE CONTEXT		
	EF	NEF	SC	AG	MATRIX	EDGE	INTERIOR
DAY							
Sample size (<i>n</i>)	179	119	30	45	25	106	242
Mean turn angle (<i>a</i>)	256 °	40°	38°	16°	325°	359°	241 °
Standard error turn angle (<i>s</i>)	40°	92°	23°	63°	125°	23°	36 °
Mean vector length (<i>r</i>)	0.103	0.04	0.31	0.096	0.027	0.167	0.073
Concentration (<i>k</i>)	0.115	0.081	0.652	0.194	0.054	0.338	0.146
Rayleigh <i>Z</i>	1.353	0.194	2.881	0.418	0.018	2.944	1.283
Rayleigh <i>P</i>	0.117	0.824	0.055	0.661	0.982	0.053	0.277
NIGHT							
Sample size (<i>n</i>)	388	131	98	268	165	404	313
Mean turn angle (<i>a</i>)	12°	-93°	42°	-7 °	4°	336°	331°
Standard error turn angle (<i>s</i>)	43°	39°	110°	12°	11°	110°	29°
Mean vector length (<i>r</i>)	0.047	0.089	0.037	0.199	0.271	0.018	0.078
Concentration (<i>k</i>)	0.094	0.18	0.074	0.407	0.562	0.037	0.157
Rayleigh <i>Z</i>	0.864	1.05	0.136	10.639	12.09	0.135	1.928
Rayleigh <i>P</i>	0.421	0.35	0.873	<0.001	<0.001	0.873	0.145
TWILIGHT							
Sample size (<i>n</i>)	137	46	21	52	22	129	105
Mean turn angle (<i>a</i>)	344°	343 °	321°	350°	335°	351°	333 °
Standard error turn angle (<i>s</i>)	13 °	30 °	16°	26.99°	20°	16°	14°
Mean vector length (<i>r</i>)	0.259	0.195	0.514	0.206	0.406	0.219	0.273
Concentration (<i>k</i>)	0.537	0.398	1.193	0.421	0.887	0.449	0.567
Rayleigh <i>Z</i>	9.204	1.756	5.545	3.01	3.618	6.2	7.818
Rayleigh <i>P</i>	0	0.017	0.003	0.015	0.025	0.002	< 0.001

Table 5.5: Summary statistics for distribution of turning angles within vegetation cover types for adult female spotted-tailed quolls ($n = 7$) at Woolnorth, north-western Tasmania. Values in bold indicate a statistically significant effect ($P < 0.05$) of vegetation cover or landscape context variables on turning angle.

5.5 Discussion

This study provides the first detailed information on the activity patterns and movement ecology of the spotted-tailed quoll. We did not find a significant effect of diel period, vegetation cover or landscape context on activity times. As predicted, the step selection analysis revealed that quolls preferred to move through eucalypt forest and avoid agricultural land during all diel periods, and showed additional preference for non-eucalypt forest during the day. However, contrary to our expectations, quolls showed similar selection for the interiors and edges of patches of forest and scrub. Analysis of movement behaviour showed that quoll movement rate was highest at twilight, when movement was linear and directed in all vegetation types and landscape contexts, suggestive of travel. Movement rates were similar during the day and night. As expected, movement rate was higher in agricultural land than in forest and scrub, but only at night, probably in part due to the low use of agricultural land during the day and twilight. Movement in agricultural land at night was also linear and directed, suggesting quolls were in transit rather than foraging. Contrary to our expectations, quolls did not travel quickly along edges; in fact at night, movement speed slowed with distance to edge, indicating that quolls may forage along edges for nocturnal prey. Below, we discuss potential ecological mechanisms that may drive the observed relationships between diel period, vegetation cover, landscape context and spotted-tailed quoll activity patterns and movement. We then use our results to suggest ways to retain and restore habitat and functional connectivity for the spotted-tailed quoll in fragmented landscapes.

5.5.1 Activity times

Our results on activity time did not support classification of quolls as nocturnal, diurnal or crepuscular, or detect any influence of vegetation cover or landscape context on activity

patterns. Given that the spotted-tailed quoll has been described as nocturnal (Jones *et al.* 1997) or crepuscular (Belcher 2003), the high degree of diurnal activity found in this study was unexpected. However, previous radio-tracking studies have noted some diurnal quoll activity (Belcher and Darrant 2006b; Glen and Dickman 2006b; Nelson 2007). For example, quolls have been observed entering rabbit burrows and hunting arboreal prey in nest hollows during the day (Belcher and Darrant 2006b; Glen and Dickman 2006b; Nelson 2007). Likewise, we observed quolls entering rabbit burrows in scrub, and foraging for larvae under loose bark of tea-trees (*Melaleuca ericifolia*) during the day.

Animal activity patterns can be driven by innate biology (e.g. circadian rhythm), abiotic factors (e.g. photoperiod, temperature, moonlight), and biotic factors (e.g. sex, reproductive status, season, age, predation risk, prey availability) (Zielinski 2000). We found no evidence for a defined circadian rhythm; photoperiod and temperature did not differ throughout the study area; and our activity data were collected from quolls of the same sex, age class, and reproductive status, in the same season. Therefore, we consider it most likely that differences in observed activity patterns among animals in our study area were primarily driven by temporal patterns in prey availability and predation risk, and that the lack of effect of vegetation cover and time of day on activity pattern may reflect a wide distribution of predators and prey throughout the landscape.

The spotted-tailed quoll is a generalist predator that feeds predominantly on small- to medium-sized mammals (Belcher and Darrant 2006a; Dawson *et al.* 2007; Glen and Dickman 2006a; Jarman *et al.* 2007; Jones and Barmuta 1998). At Woolnorth, the most abundant mammals in this size range, including the Bennett's wallaby (*Macropus rufogriseus*), Tasmanian pademelon (*Thylogale billardieri*), common brushtail possum (*Trichosurus vulpecular*), common ringtail possum (*Pseudocheirus peregrinus*) and European rabbit

(*Oryctolagus cuniculus*), are crepuscular or nocturnal. Diurnal hunting of inactive arboreal mammals such as the greater glider (*Petauroides volans*) by the south-eastern mainland spotted-tailed quoll has been hypothesised as energetically efficient foraging strategy to exploit food resources that would otherwise be costly to capture (Belcher *et al.* 2007). We contend that diurnal activity by quolls in our study may also be explained by diurnal predation of inactive nocturnal or crepuscular prey species during the day (i.e. rabbits in burrows). The observed peak in quoll activity at or just after dusk followed by a drop in activity may reflect hunting and consumption of active prey as they emerge from rest to forage, and then resting when satiated. Similarly, Settle (1978) noted that in captivity, spotted-tailed quoll activity was governed by food availability, and that animals rested if satiated but otherwise continued to forage. Therefore, use of arrhythmic activity patterns by quolls may optimise exploitation of a diverse prey base of nocturnal and diurnal species, or reflect both times that species are active and easy to find, or inactive and easy to catch.

It is possible that the very different activity patterns of individual adult female quolls in this study may be a result of individual-level specialisation on prey that vary in abundance throughout the landscape. A broad range of vertebrate and invertebrate taxa exhibit individual-level dietary specialisation, whereby individuals have a substantially narrower dietary niche than the population as a whole for reasons not attributed to sex, age or other discrete morphological group (Bolnick *et al.* 2003). In particular, territoriality in a patchy environment results in individual specialisation in several mammalian carnivores (Bolnick *et al.* 2003). For example, both the arctic fox (*Alopex lagopus*) and the American pine marten (*Martes americana*) exhibit dietary differences associated with habitat heterogeneity within territories (Angerbjörn *et al.* 1994; Ben-David *et al.* 1997). Similarly, high inter-individual variation in the diet of the European mink (*Mustela lutreola*) and American mink (*Mustela vison*) reflect

spatial differences in prey abundance at the home-range scale (Sidorovich *et al.* 2001). In this study, all of the quolls were adult females of similar body weight, and did not exhibit any obvious morphological variation. I hypothesise that spatial variation in the abundance of different prey with varying activity times across individual quoll home ranges may have resulted in individual-level specialisation on different prey types, and subsequent individual-level differences in quoll activity times as they seek to maximise their foraging efficiency by hunting at times that prey are most vulnerable. Depending on the prey type, this may include times that prey are active and easier to detect, or inactive and easier to capture (Halle and Stenseth 2000).

Predator activity is affected both by the need to maximise foraging efficiency and the risks of encountering other predator species (Lima and Dill 1990; Linnell and Strand 2000). High abundance of a larger predator may affect the activity patterns of a smaller predator via direct effects, indirect effects, or a combination of the two (Brown *et al.* 1990). First, risk of conflict may force the smaller predator to forage when the larger predator is less active. For example, avoidance of competition from the nocturnal lion (*Panthera leo*) leopard (*Panthera pardus*) and spotted hyaena (*Crocuta crocuta*) is the primary cause of crepuscular and diurnal activity patterns in the wild dog (*Lycaon pictus*) and cheetah (*Acinonyx jubatus*) (Hayward and Slotow 2009). Second, high predator abundance results in increased vigilance of prey, meaning that prey become more wary and difficult to capture (Brown *et al.* 1990), which in turn feeds back to changes in the activity times of the smaller predator, which is still aiming to maximise foraging efficiency by hunting on vulnerable prey. At Woolnorth, the spotted-tailed quoll co-occurs with a high-density population of its main intra-guild competitor, the Tasmanian devil (*Sarcophilus harrisi*). The devil and spotted-tailed quoll have high dietary overlap (Jones and Barmuta 1998), but the devil is exclusively nocturnal (Jones *et al.* 1997). It is possible that

crepuscular and diurnal activity may occur because quolls trade-off the peak activity of prey at night with the heightened risk of conflict with devils and higher difficulty of capturing vigilant prey. This hypothesis is supported by the finding that quolls have higher nocturnal activity in parts of the state that devil abundance is reduced as a result of Devil Facial Tumour Disease (DFTD) (Hollings 2013). Likewise, in south-eastern mainland Australia, crepuscular and diurnal activity by the spotted-tailed quoll may minimise potential competition (Glen and Dickman 2005) with the larger and usually nocturnal red fox (*Vulpes vulpes*). To evaluate how quoll activity patterns are influenced by competitors and prey species, the temporal activity of all species should be considered in synchrony with one another and with other biotic and abiotic factors at varying levels of top predator abundance. The inclusion of dietary analyses to investigate the occurrence of individual-level dietary specialisation within populations may also shed light on the mechanisms driving quoll activity patterns, and the role and extent of intraspecific vs interspecific niche competition among the spotted-tailed quoll and other mammalian carnivores.

5.5.2 Step selection and movement behaviour

Movement rate of quolls was faster and more linear around twilight than during the day or night, indicating that quolls travel at dawn and dusk. This result is consistent with our earlier finding that quoll activity peaks just prior to dawn and at or after dusk, which we attributed to interception of prey leaving or returning to their diurnal resting habitat. In heterogeneous landscapes such as our study area, where high-quality patches are widely dispersed, straight movements are a highly efficient search pattern (Zollner and Lima 1999). When searching for mobile prey, the behaviour of ambush predators such as the spotted-tailed quoll (Jones and Stoddart 1998) can take two discrete modes: active (cruising) search, to maximise the area

searched in a given time period, or sit-and-wait (ambush) search, remaining still to maximise the probability of detecting prey (Alpern *et al.* 2011). Theory suggests that when ambush predators begin a search, cruising mode predominates, and once prey are located to a small area, ambush behaviour is used (Alpern *et al.* 2011). Thus, the increase in movement rate of quolls at dawn and dusk could be indicative of a cruising search for selection of a profitable patch to ambush nocturnal prey that are either leaving or returning to shelter in dense vegetation. Moving in the crepuscular period would provide quolls with some refuge from diurnal avian predators, and avoids the nocturnal peak in activity and therefore potentially competition from their larger marsupial competitor, the Tasmanian devil. Alternatively, Glen and Dickman (2006b) suggested that quolls return to a core area to den after each night's activity, which would also generate the travel pattern seen here. However, because we previously found that quoll dens are located within their core areas (Chapter 4), this explanation is unlikely to explain our results.

At all times of day, the spotted-tailed quoll showed strong selection for steps that contained a high proportion of eucalypt forest, which probably reflects selection for both cover and foraging resources. Previous studies in south-eastern Australia have found that mature eucalypt forest, such as that occurring at Woolnorth, contains a high abundance of microhabitats associated with high prey abundance, including structurally complex vegetation, tree hollows, logs, and dense canopy cover (Andrew 2005; Belcher 2008; Belcher and Darrant 2006b; Nelson 2007). In particular, medium-sized arboreal mammals that rely on tree hollows and foliage for den, refugia and foraging resources are a major dietary component of the spotted-tailed quoll (Belcher *et al.* 2007; Jones and Barmuta 1998). Furthermore, in Tasmania, macropod prey shelter in eucalypt forest during the day (Le Mar and McArthur 2005), where they are susceptible to quoll predation. Therefore, search for and predation on resting

macropods or arboreal marsupials may explain selection for eucalypt forest by quolls. As predicted, selection for eucalypt forest was greatest during the day, at which time quolls also showed preference for steps containing a high proportion of non-eucalypt forest cover. This additional preference for moving through forest during the day may indicate a greater need for crypsis, or alternatively, selection of diel-specific prey resources that occur in non-eucalypt forest.

Movement rate did not differ among scrub, eucalypt and non-eucalypt forest at any time, and turning angles varied and had large means, indicating that quolls probably both travelled and foraged in all cover vegetation communities. This suggests that although quolls prefer to move through eucalypt forest, they also utilise nearby patches of non-eucalypt cover and scrub to meet their resource needs and to travel between foraging patches.

As expected, quoll showed significant avoidance of agricultural land. When agricultural land was used, movement rates were higher than when moving through vegetation cover, but this difference was significant only at night. This lack of effect is probably due to the low number of used steps within agricultural land during the day and at twilight (Figure 5.6). The fast movement rate combined with linear movement suggests that quolls use the agricultural matrix for travel between patches of forest and scrub, but not foraging. There are two potential reasons that the spotted-tailed quoll does not forage in the agricultural matrix. First, prey may be insufficiently available in the matrix. At our study area, the only prey species that use the agricultural matrix intensively are the Bennett's wallaby (*Macropus rufogriseus*) and pademelon (*Thylogale billardierii*); both species shelter in dense vegetation during the day (Le Mar and McArthur 2005) and are thus not present in the matrix to be exploited at that time. At night, these macropods forage a minimum of 90 m from edges at night in other sites, presumably as an anti-predator strategy to reduce the risk of successful attacks by ambush and

pounce-pursuit predators such as the quoll and devil (Nielsen 2009). Second, the risk of competition from the larger Tasmanian devil may be heightened in the matrix. The Bennett's wallaby and pademelon are also predated by the Tasmanian devil (Jones and Barmuta 1998), from which the quoll experiences exploitation and potentially interference competition (Jones 1995). Devils use more open habitats than quolls, and higher arboreal activity by quolls relative to devils has been proposed as a mechanism of niche partitioning between these two species. Foraging away from forest cover would deny quolls an escape route from the larger and behaviourally dominant devil, and increase the frequency of competitive interactions, which on the basis of body size, quolls are predicted to lose (Jones and Barmuta 2000). Thus, despite the high abundance of prey in the agricultural matrix, the likelihood of quolls being able to exploit it is low, and the cost of attempting to do so may outweigh any benefits.

Contrary to our expectations, quolls did not avoid moving through edges, and in fact showed similar selection for forest and scrub edges and interiors. Quoll movement rate did not vary with proximity to edge during crepuscular or daytime periods, but quolls moved more slowly close to edges at night. Similarly, turning angles were straight and directed during crepuscular and daytime periods, but varied widely at night. Combined, these results strongly suggest that quolls used edges, including the narrow corridors (20 meters) and small islands (< 20 m²) in our study site, for movement during crepuscular and diurnal periods, and for both movement and foraging at night. Previous studies have found that edge habitats provide multiple benefits to mesopredators, including enhanced concealment due to higher vegetation, and a higher abundance and diversity of prey (Chalfoun *et al.* 2002; Šálek *et al.* 2010). However, increased predation pressure by mesopredators in heterogeneous landscapes has been associated with declines in prey, especially in the absence of top predators (Crooks 2002; Schneider 2001; Terborgh *et al.* 2001). In our study, lack of preference for edge over interior

and use of multiple vegetation communities suggests that predation pressure by quolls is currently spatially dispersed among patches of vegetation cover.

5.5.3 *Conserving connectivity*

Landscape connectivity refers to the degree to which landscape elements facilitate or impede movement, and incorporates a species' ability to movement through, its behavioural response to, and risk involved in moving through different landscape elements (Fahrig 2003). The spotted-tailed quoll did sometimes used the agricultural matrix, so it was clearly not an impermeable barrier, yet they tended to avoid it, and when they did use it they generally adopted rapid directed movements consistent with travelling rather than foraging behaviour. Comparable results have been found in other carnivores that are considered to be sensitive to habitat loss and fragmentation, including the Iberian lynx (*Lynx pardinus*), the fisher (*Martes pennantii*), and the long-tailed weasel (*Mustela frenata*) (Buskirk and Powell 1994; Ferreras 2001; Gehring and Swihart 2004). Combined, our results indicate that although quolls are largely restricted to forest and scrub cover, the agricultural matrix presents a filter but not a complete barrier to movement.

Female spotted-tailed quolls are able to travel through the agricultural matrix between patches of vegetation cover to gain access to food and den resources, and linear corridors and small patches of vegetation facilitate this movement. Because male quolls are larger and more vagile than females (Belcher and Darrant 2004; Glen and Dickman 2006b) we therefore also expect that male quolls can move through agricultural land to acquire resources, search for mates, reproduce, and recolonise new habitats, ultimately maintaining gene flow and metapopulation persistence. Thus, functional connectivity of quoll populations appears possible even in fragmented agricultural landscapes. However, we caution that there is likely to be an

upper limit to the amount of fragmentation that quolls can tolerate, beyond which there will be insufficient resource to support adult breeding females.

Our study provides information that point to the considerable conservation potential of agricultural landscapes for the spotted-tailed quoll. Habitat management for the spotted-tailed quoll in agricultural landscapes should focus on providing or maintaining structural connectivity through the agricultural matrix. The strong selection for eucalypt forest found here suggests that, ideally, linear corridors and stepping stones should encompass this forest type, especially areas of high structural complexity. However, in areas that have previously been cleared and where quolls are known to persist, retention of any forest or scrub, including small islands and windbreaks, should assist in maintaining functional connectivity for quolls.

Three important limitations of this study are the short period (4-5 weeks), restricted season, and constrained geographic extent of data collection. Although this has not yet been investigated, it is probable that many aspects of quoll movement ecology, such as activity times, may have a seasonal component, and should therefore be investigated over longer time periods in future studies. Similarly, this study focussed solely on the adult female spotted-tailed quolls because their distribution and abundance is predicted to be closely linked to the abundance and distribution of resources linked with mature forest (Belcher and Darrant 2004, Glen and Dickman 2006b), which could theoretically render female quolls more susceptible to the effects of habitat loss and fragmentation than are wide ranging male quolls. Future studies should contrast adult female movement ecology with that of male and juvenile spotted-tailed quolls to better understand the population dynamics of the species as a whole. Finally, given that our results are from just one study area, extrapolation to other areas must be undertaken cautiously.

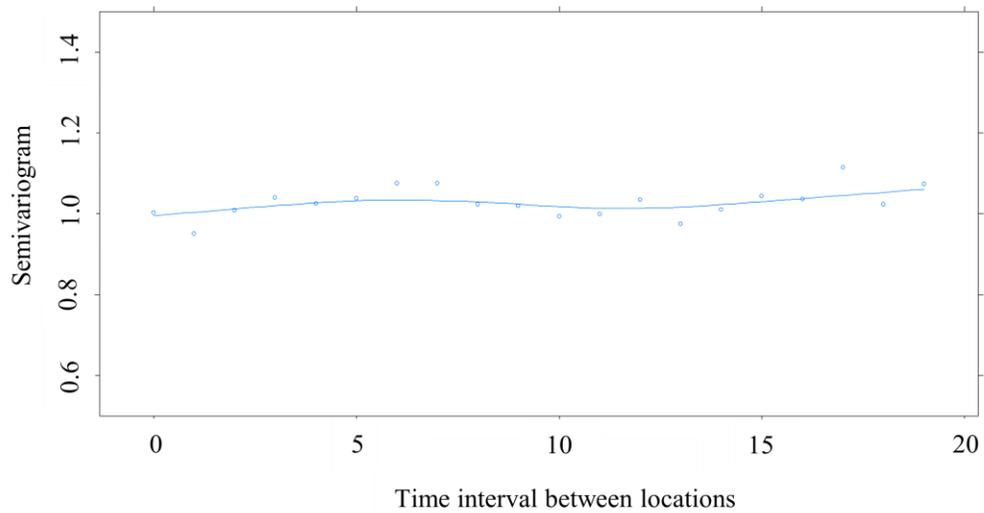
5.5.4 Conclusions

More broadly, our results highlight that different measures of activity and movement may measure different biological processes and motivations. Quolls can simply be classified active in a habitat without moving a detectable distance between consecutive locations, and their activity times probably reflect those of their competitors and prey. Step selection quantified preference or avoidance of habitat for movement, which likely reflects habitats with the highest availability of prey and lowest potential for interactions with intraguild competitors. Analysis of movement behaviour (e.g. movement rate or tortuosity) then allowed inference on the underlying behavioural state of the animal once it has selected a movement step, revealing the habitats in which quolls forage versus travel. Our results demonstrate that integration of different measures of activity and movement allow a more complete understanding of movement ecology than would one method alone.

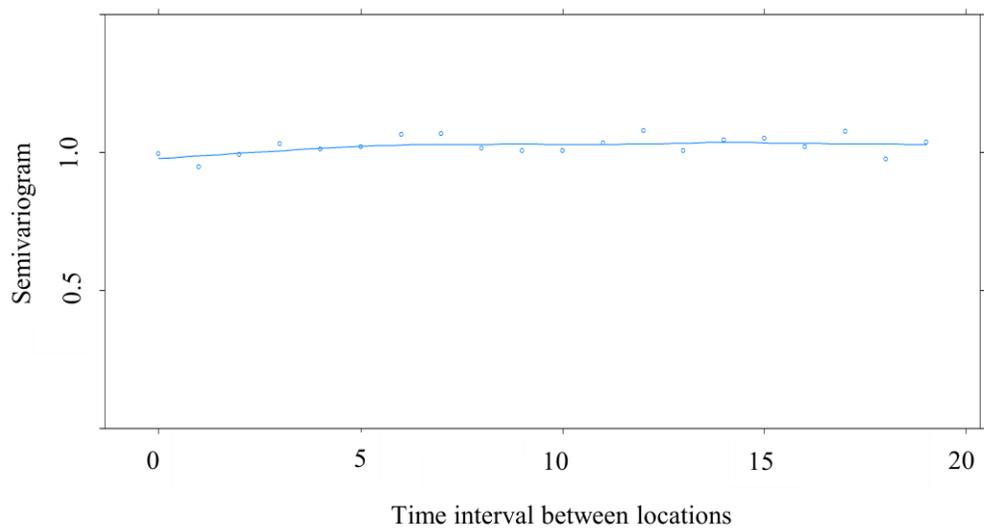
Conversion of forest to agriculture is often considered a zero-sum game, but this may not be the case for wildlife that inhabit these landscapes. Despite possessing traits that render them susceptible to habitat loss and fragmentation, the spotted-tailed quoll, like many mesopredators, are able to persist in agricultural landscapes by timing their movement to exploit increased prey resources associated with fragmentation and to avoid competition and predation. Our study adds to a growing body of evidence indicating that anthropogenic landscapes can provide resource rich environments for habitat generalists that are capable of utilising edges. Further investigation of mesopredator movement ecology in anthropogenic landscapes should pair information on mesopredator activity times, movement and diet with the activity, spatial distribution and movement of their prey to better understand and predict the ecological mechanisms driving species-specific responses to habitat loss and fragmentation.

Appendix 5.1: Semi-variograms of deviance residuals from linear mixed effects models of quoll movement rate. A positive slope would indicate presence of temporal autocorrelation.

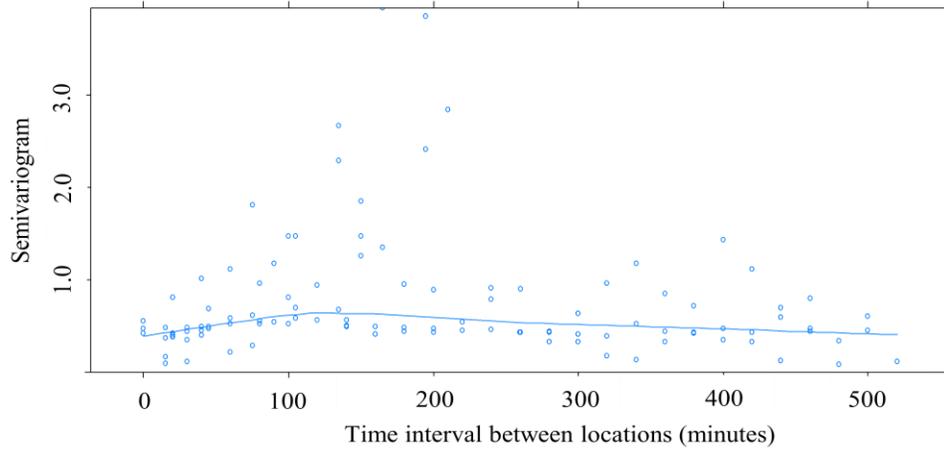
(a) Interactive effect of vegetation community and diel period on movement rate.



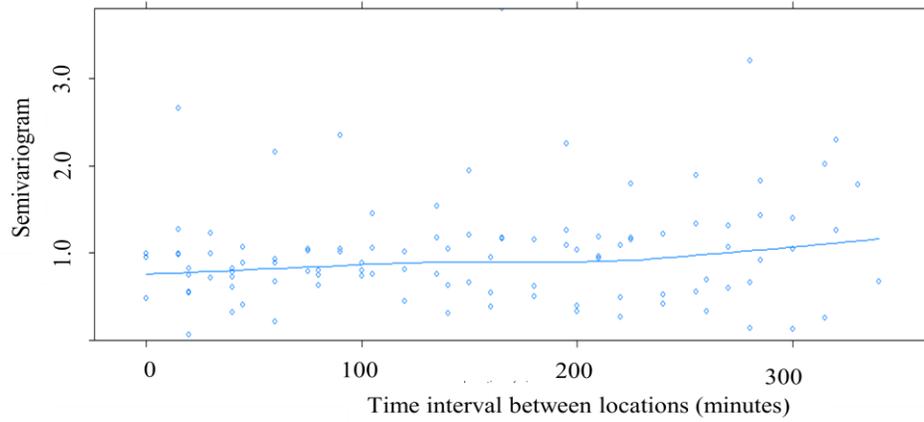
(b) Effect of diel period on movement rate.



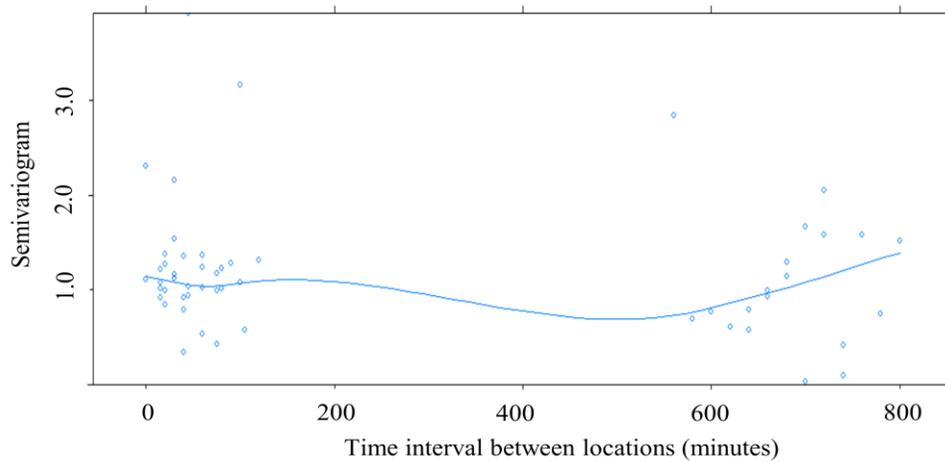
(c) Effect of proximity to edge on movement rate during the day.



(d) Effect of proximity to edge on movement rate at night.



(e) Effect of proximity to edge on movement rate at twilight.



Chapter 6: General Discussion

The purpose of this study was to investigate the distribution and habitat associations of the Tasmanian spotted-tailed quoll. My specific objectives were to: 1. Determine the biotic and abiotic correlates of Tasmanian spotted-tailed quoll distribution, abundance, space use, and movement; 2. Compare the environmental associations of the Tasmanian spotted-tailed quoll to their mainland conspecifics; 3. Contribute information to the development of conservation management recommendations for the spotted-tailed quoll. I structure my approach to studying the spatial ecology of the spotted-tailed quoll to address habitat associations at multiple spatial scales, from distribution (first-order selection) to home range placement in the landscape (second-order), within-home range habitat use (third-order) to den site selection (fourth-order habitat selection).

In this chapter, I summarise the key findings of the thesis on the abiotic and biotic correlates of quoll spatial ecology (Aim 1; Section 6.1). In Section 6.2, I synthesise these findings to address Aim 2. I begin by discussing my results in the context of predator guild composition, and how predator dynamics influence habitat preferences, with particular reference to the differences in quoll habitat preferences between Tasmania and the mainland but considering predator dynamics in a global context (Aim 2; Section 6.2.1). This is followed with a broad discussion of why habitat selection may vary across spatial scales (Section 6.2.2). I then translate the key findings of this study to quoll conservation (Aim 3; Section 6.3). I begin with providing updated information on the current status of the Tasmanian spotted-tailed quoll (6.3.1) and the difficulties of obtaining robust data on population size and trends (6.3.2). I then outline four actions that can be undertaken now to assist in the conservation of the Tasmanian spotted-tailed quoll (6.3.3 – 6.3.6). Finally, I outline priorities for future research (Section 6.4).

6.1 Biotic and abiotic correlations of Tasmanian spotted-tailed quoll occurrence

6.1.1 First-order selection

At the distribution (first-order) scale, I found that in Tasmania the spotted-tailed quoll reaches highest abundance in productive landscapes, as measured by either a combination of high annual mean temperature and regular seasonal rainfall (Chapter 2) or by mean annual net primary production (Chapter 3). At this scale, I did not find a significant relationship between spotted-tailed quoll abundance and the amount of native forest cover or forest fragmentation. In Chapter 2 I suggested that the observed lack of a relationship between the spotted-tailed quoll and forest cover could be confounded by a detection bias: if a species is restricted to forest, the probability of detecting them may increase in cleared landscapes because they are more likely to encounter a survey device set in a smaller amount of forest. However, in Chapter 3, I was able to separately model the effect of forest cover on both detection probability and abundance, and found this was not the case. Quoll abundance was also not well explained by rainfall, terrain ruggedness, or avoidance of agricultural land.

I found no evidence for an effect of the Tasmanian devil on the relative abundance of the spotted-tailed quoll: there was no change in spotted-tailed quoll relative abundance following devil decline, and no apparent relationship between pre-disease devil habitat suitability and spotted-tailed quoll abundance (Chapter 2). Furthermore, I did not find an effect of predicted devil abundance on spotted-tailed quoll abundance, nor on quoll detection probability (Chapter 3). Indeed, there was no effect of the predicted abundance of any predator or combination of predators on one another, suggesting that any competitive interactions among the Tasmanian predators are likely to be fine-scaled and to promote co-existence, rather than broad-scaled leading to competitive exclusion.

I found that the spotted-tailed quoll reaches highest abundance in the north and northwest of Tasmania and on private land, where there is a high overlap between the most suitable habitat for the spotted-tailed quoll and the introduced red fox (Chapter 2). The lack of an effect of region on quoll abundance in Chapter 3 may be because the majority of camera surveys were conducted on public land, which I showed in Chapter 2 generally has lower quoll abundance.

6.1.2 Second-order selection

At the landscape scale, I found that home range size is similar to reports from mainland Australia. Home range size increased linearly with the number of patches of native vegetation cover and the proportion of open vegetation, suggesting that fragmentation increases the area required for quolls to meet their resource needs. Similarly, home ranges preferentially occupied areas with a higher proportion of eucalypt and non-eucalypt forest than was generally available in the study area, and avoided areas with a high proportion of scrub and open vegetation.

6.1.3 Third-order selection

At the third-order scale of selection of habitat within the home range, quolls showed significant preference for closed vegetation cover (e.g. forest and scrub) and avoidance of open vegetation (Chapter 4). Patterns of temporal activity varied among individuals, and were not influenced by selection of vegetation community. Quolls showed similar selection for steps in the interior and edge of vegetation cover, suggesting that they are not inherently susceptible to adverse edge effects (Harris 1988). Comparison of movement speed and turning angles suggested that quolls selected steps along edges for movement at dawn, dusk, and night, and

selected the cover interior for foraging during the day and night. Quolls avoided moving through the agricultural matrix at all times of day; they made more use of the matrix at night than during the day, but even so their movements through the matrix were faster and more directed than within vegetation cover, indicating they may perceive open pasture as risky and/or lacking resources.

6.1.4 Fourth-order selection

At the fourth-order scale of habitat for den sites, quolls showed preference for forest and avoided open vegetation. In order of prevalence, I observed quoll dens were in clumps of vegetation or grass, underground burrows, tree hollows, and hollow logs. Quolls showed significant preference for den sites within their core home range area, suggesting that food and den resources were situated in close proximity to one another. A small proportion of den sites were located within shared portions of female home ranges or core areas, providing further evidence that female quoll territoriality may be more flexible than previously believed.

6.2 Synthesis

6.2.1 Habitat preferences and predator interactions

(i) Differences between mainland and Tasmanian spotted-tailed quolls

This study has revealed striking differences in the habitat preferences of south-eastern mainland and Tasmanian spotted-tailed quolls. At the distribution scale, the Tasmanian spotted-tailed quoll reaches highest abundance in warm, low elevation landscapes (Chapter 2, Jones and Rose 1996), and I did not find a strong effect of rainfall, topography, forest cover or

fragmentation, or cleared land on their distribution (Chapter 2 and 3). In contrast, the south-eastern mainland spotted-tailed quoll is generally considered forest-dependent with a preference for extensively forested areas in landscapes with fertile soils at high elevation, with high annual mean rainfall and low temperatures (Catling *et al.* 2002; Mansergh 1984; Wintle *et al.* 2005). Within these forested landscapes, the south-eastern mainland spotted-tailed quoll prefers components (e.g. gullies) that provide structurally complex habitats furnishing high availability of potential den sites and a high abundance of vertebrate prey (Belcher and Darrant 2004; Glen and Dickman 2006b; Nelson 2007). Although I did not quantify vegetation complexity, meaning direct comparisons must be made with caution, there was no apparent selection by Tasmanian quolls for structurally complex forest. Quolls showed preference for both structurally complex eucalypt forest and structurally simple non-eucalypt forest in a topographically homogenous landscape. Finally, while the south-eastern mainland spotted-tailed quoll most frequently uses log, rock, or burrows as dens, adult female Tasmanian spotted-tailed quolls most frequently used apparently less secure grass or vegetation dens. I propose that these differences in south-eastern mainland and Tasmanian spotted-tailed quoll habitat preferences are driven by differences in their predator communities, specifically, the presence of the introduced red fox on mainland Australia but not in Tasmania.

Various lines of evidence indicate that, on the mainland, foxes have brought about not only declines and range contractions in many of the spotted-tailed quoll's prey species, but also niche contractions (Bilney *et al.* 2010; Johnson 2006; Kinnear *et al.* 1998). Small- and medium-sized terrestrial mammals form the majority of the spotted-tailed quoll's diet (Andrew 2005; Belcher 1995; Belcher *et al.* 2007; Dawson *et al.* 2007; Glen and Dickman 2006a; Glen *et al.* 2011; Jarman *et al.* 2007; Jones and Barmuta 1998). The severe decline of these mammals in southern Australia since European settlement is well documented, and has been primarily

attributed to foxes (Johnson 2006). Along with consequent range contractions, it is becoming apparent that many critical weight range mammals have also suffered niche contractions, and formerly occurred in a greater diversity of habitats than they do currently (Bilney *et al.* 2010; Kinnear *et al.* 1998). Species that occur in dry, lightly forested or productive cleared areas preferred by foxes have experienced the greatest declines, and in many cases their distributions have now largely contracted to the tall, wet, dense continuous forests at high elevation where foxes are least abundant (Bilney *et al.* 2010; Catling *et al.* 2002; Johnson 2006). At a finer scale, critical weight range mammals are most likely to persist where there is refugial habitat that limits access by foxes, such as rocky outcrops, gorges, burrows, or if they have refuge-seeking behaviour such as climbing (Johnson 2006).

My findings indicate that the habitat currently occupied by the spotted-tailed quoll on the mainland, while critical to the species' persistence there, does not necessarily represent its optimal habitat under natural conditions, nor the full range of habitats in which it could potentially occur. The habitat choices of surviving critical weight range mammals in southern Australia are likely to reflect refuge habitat where their probability of survival is increased, rather than preferred habitat. This process has been termed niche denial (Bilney *et al.* 2010; Kinnear *et al.* 1998), whereby external biotic threats limit a species' ability to use parts of its niche, even when abiotic environmental conditions are suitable. Accordingly, it is likely that competition with foxes for critical weight range prey resulted in the formerly widespread distribution of the south-eastern mainland spotted-tailed quoll contracting to wet, tall, high elevation areas where foxes are least abundant, and their terrestrial critical weight range mammal prey still persist. Within these forests, it is likely the spotted-tailed quoll selects structurally complex habitat because it provides refuge for terrestrial mammalian prey and secure dens, as well as a high abundance of arboreal prey, all of which provide a means of

niche partitioning to reduce competition with foxes. Indeed, low fox density and extensive areas of forest containing a high abundance of arboreal prey are proposed as the most likely reasons for the high abundance of the spotted-tailed quoll in north-eastern New South Wales relative to other parts of their range. While this habitat is clearly critical to the persistence of the south-eastern mainland spotted-tailed quoll, it is important to realise that habitat currently occupied by the mainland spotted-tailed quoll does not necessarily reflect optimal habitat under natural conditions, or the full range of habitats in which the species could potentially occur. Thus, this study highlights the influences of competition and predation on habitat preferences, and the importance of considering interspecific interactions within predator guilds as well as bottom-up resource availability before transferring information on habitat preferences between geographic regions for conservation purposes.

(ii) Tasmanian predators

The potential for competitive pressure from the devil has led to the prediction that the spotted-tailed quoll will increase in abundance following devil decline (Jones *et al.* 2007; McQuillan *et al.* 2009; Meyer-Gleaves 2008), a view that while unsubstantiated has gained widespread acceptance in Tasmania. In contrast to the top-down forces shaping mainland quoll distribution, I found no evidence that the distribution or abundance of the Tasmanian spotted-tailed quoll is regulated by either the larger devil or the ecologically similar feral cat. I also found no support for an increase in the relative abundance of the spotted-tailed quoll following devil decline (Figure 2.2). Thus, to date, there is still no evidence for numerical release of the spotted-tailed quoll following devil decline, or for a numerical relationship between spotted-tailed quoll and cat abundance.

Although there is evidence of dietary overlap among the spotted-tailed quoll and the Tasmanian devil (Jones and Barmuta 1998), and the Tasmanian devil and the feral cat (Lazenby 2012), and on mainland Australia, between the spotted-tailed quoll and the cat (Glen *et al.* 2011; Molsher 1999), competition is only likely to occur if resources are scarce (Schoener 1983). It is possible that the high abundance of prey resources in the Tasmanian ecosystem may minimize actual competition among these species. If intraguild exploitation competition is weak, apex predator decline will have only minor effects on mesopredators (Brashares *et al.* 2010). However interference competition can occur irrespective of resource abundance (Creel *et al.* 2001). Both direct and indirect interference competition have been demonstrated between the spotted-tailed quoll and the devil. At carcasses, adult devils are dominant and can displace spotted-tailed quolls (Jones and Barmuta 1998). Indirectly, spotted-tailed quolls and devils have been demonstrated to partition on different habitat types and microhabitat structures and on the extent of arboreal use of habitat (Jones and Barmuta 2000). The lack of evidence for competition found in this study may be a result of resource overlap being mitigated by processes not investigated here, such as selection of different microhabitats or activity times. Furthermore, the lack of evidence for limitation of abundance by other predators found here does not preclude the possibility of behavioural suppression (Ritchie *et al.* 2012). Changes in mesopredator behaviour following top predator decline can affect the behaviour, health, reproductive success, survival, and ultimately community structure of mesopredators and prey (Berger and Conner 2008; Brown *et al.* 1990; Lima 1998). Quantification of such sub-lethal effects were outside the scope of this study.

Despite being widespread and prevalent (Ritchie and Johnson 2009), mesopredator release following top predator decline is not ubiquitous (Prugh *et al.* 2009; Sergio *et al.* 2008; Steinmetz *et al.* 2013). Even ecologically similar species can respond differently to apex

predator decline and this can be influenced by factors other than changes in predator numbers. For example, in the absence of the black-backed jackal (*Canis mesomelas*), the abundance of the cape fox (*Vulpes charma*) increased as expected, but the abundance of the bat-eared fox (*Otocyon megalotis*) decreased, a result was attributed to lower food availability of their preferred prey in the jackal free site (Kamler *et al.* 2013).

Given the apparently conflicting conclusions drawn from the studies on the relationship between Tasmanian predators to date (Chapter 3; Hollings *et al.* 2014; Lazenby and Dickman 2013; Saunders 2011), I suggest that my results and inference on the relationships among Tasmanian predators should be considered preliminary. To better understand the potential for mesopredator release and trophic cascades in the Tasmanian system, further fundamental information on the nature of the relationships among Tasmanian mammalian predators is required. This should include quantifying resource preferences in relationship to availability and the abundance of competitors.

(iii) Mesopredator release

There has been a recent explosion of literature on the importance of apex predators in maintaining ecosystem structure, function and resilience (e.g. reviews in Johnson 2010; Prugh *et al.* 2009; Ripple *et al.* 2014; Ritchie and Johnson 2009). Within this framework, the ecology of mesopredators has mostly been considered in the context of their increased abundance, expanded distribution or altered behaviour and potential threat to lower trophic levels following apex predator decline. In many of these cases, the mesopredator is considered a pest species, either because it is introduced (Crooks and Soule 1999) or is a native species that has become overabundant and threatens their prey (Garrott *et al.* 1993). In contrast, the situation where a mesopredator is also of conservation concern has received less attention.

Are there ecological characteristics that could be used to better predict whether mesopredators are likely to irrupt in response to decline of apex predators? I hypothesize that the same factors that are correlated with a species response to habitat loss and fragmentation, such as social organisation, degree of specialization, population density, and recruitment rates (Swihart *et al.* 2003; Wolff 1999), may also predict likelihood that mesopredator density will increase following apex predator decline. Typically, mesopredators that are released from competition are dietary and habitat generalists characterised by high potential density, high rates of recruitment, and high dispersal rates (Prugh *et al.* 2009), and are relatively resistant to habitat loss and fragmentation. Interestingly, these are the same ecological traits that are used to predict whether mammals are likely to be successful invaders (Forsyth *et al.* 2004; Lockwood *et al.* 2013). In some cases, the overabundant mesopredator is in fact an invasive species (e.g. red fox in Australia (Jarman 1986), cats on islands (Rayner *et al.* 2007), American mink in Europe (Bonesi and Palazon 2007), but in others cases species become overabundant in parts of their native range (e.g. raccoon and opossum in North America, Garrott *et al.* 1993).

As a species that exists at very low population density due to hypercarnivory, low recruitment rates, and female intrasexual territoriality and natal philopatry (Belcher 2003; Glen 2008), the spotted-tailed quoll shares ecological traits with other mesopredators that also do not respond positively to apex predator declines, and are themselves threatened (Brodie and Giordano 2013). It may be that mesopredator species with these traits are constrained by their life history to be incapable of rapidly converting increased resource abundance into increased population density or expansion in distribution (Kamler *et al.* 2013). Furthermore, the low density and smaller body size of rare mesopredators may mean that behavioural changes enforced by top predators may not have strong influences on the rate at which rare mesopredators kill or threaten prey. Consequently, these conditions may result in low potential

for behaviourally-mediated trophic cascades following removal of larger predators. Beyond body size, the predicted response of a mesopredator population to the decline of an apex predator population should be quantified with reference to the ecology, and evolutionary and life history of intraguild predators, so that conservation managers can choose an appropriate management plan for their community of interest. In many communities of large carnivores, intermediate-sized as well as large species are threatened or endangered but are often less studied. In these cases, more attention to mesopredator ecology will assist in developing conservation strategies.

6.2.2 The nature of Tasmanian spotted-tailed quoll forest dependence

(i) Scale- and sex-dependent habitat associations

My findings support the outcome that animal habitat selection can differ with spatial scale (Johnson 1980; Wiens 1989). I found that Tasmanian spotted-tailed quolls showed strong preference for forest cover and avoidance of cleared land at fine spatial scales, but this did not translate to selection for contiguously forested landscapes at the scale of the entire geographic distribution. An explanation for these relationships is that different habitat is required for different ecological processes. At fine scales, female quolls strongly prefer forest for denning and foraging, but their ability to move short distances through the matrix, utilizing corridors, stepping stones and edges for movement, denning and foraging, and perhaps supplement their food resources by exploiting increased prey abundance resulting from edge effects (Dunning *et al.* 1992), means that quolls can reach high abundance in heterogeneous landscapes.

Differences in the habitat requirements of male and female spotted-tailed quolls may also explain the variation in habitat preferences among selection orders. The distribution-scale

models were built using occurrence data from both sexes, but the fine-scale radio-telemetry data were collected from adult females only. Habitat selection by female spotted-tailed quolls is likely to be governed by resource availability: because females provide all parental care, their large area requirements secure the resources they need to provide parental care (food and secure shelter) and successfully rear young (Belcher and Darrant 2004; Burnett 2001; Glen and Dickman 2006b). Strong preferences for forest at second-, third- and fourth-order scales suggest that in Tasmania, forest provides these resources. In contrast, male spotted-tailed quolls range widely (359 ha – 5,512 ha) to secure access to multiple mates rather than resources, and do not contribute to parental care (Andrew 2005; Belcher and Darrant 2004; Claridge *et al.* 2005; Glen and Dickman 2006b). Male quolls are therefore likely to have more flexible habitat requirements than female quolls. Similarly, female giant pandas (*Ailuropoda melanoleuca*) are more strongly dependent upon forest than are males, because forests provide critical natal den sites and dense bamboo cover to obscure young (Qi *et al.* 2011). Thus, the inclusion of male quolls in the distribution models (Chapter 2 and 3) may underestimate the importance of forest cover to the spotted-tailed quoll at this scale.

(ii) Thresholds for clearing

For the Tasmanian spotted-tailed quoll, attempts to answer the question “how much forest is enough” may not be helpful, because quoll occurrence is related not to the amount of forest per se, but rather to the abundance and availability of resources in forest relative to those in the matrix. Quantifying how much habitat is required to ensure population persistence is a key question to be answered if conservation efforts are to be successful (Fahrig 2001; Fahrig 2002). For some species, threshold effects of landscape change have been identified, beyond which the likelihood of species persistence declines (Hanski *et al.* 1996; Radford *et al.* 2005).

For the Tasmanian spotted-tailed quoll, female preference for forest, avoidance of cleared land, and increase in home range size with forest fragmentation and pasture all indicate that there is likely to be an upper limit of tolerance to habitat loss and fragmentation. In south-eastern Australia, prey and den resources for quolls are linked to mature or structurally complex forests (Belcher 2008; Belcher and Darrant 2006b), so it is reasonable to assume that forest extent is representative of resource availability. However, in Tasmania, hollow-dependent and forest-dependent fauna are supplemented by other mammalian fauna that are capable of using the non-forest matrix such as rabbits (*Oryctolagus cuniculus*) and pademelons (*Thylogale billardierii*) (Sorenson 2013) and den use includes non-forest elements (Chapter 5). Furthermore, just as the abundance of den and prey resources within remnant forest in agricultural landscapes is likely to depend on the age and configuration of remnant forest as well as its extent, the abundance of prey resources in the non-forest matrix may depend on the extent, type and configuration of the non-forest matrix.

(iii) Corridors for movement

The avoidance of pasture by quolls and increase in home range size with increasing amounts of agricultural land and forest patches provides evidence that the spotted-tailed quoll is somewhat sensitive to habitat loss. Connectivity among habitat patches is critical for the viability of populations in fragmented landscapes (Bennett 2003; Crooks and Sanjayan 2006) and must be considered at multiple spatial scales, including movement within home ranges, and dispersal among home ranges and populations (Fahrig 2003). The long-term persistence of quoll populations in fragmented landscapes is likely to be dependent on the ability of unrelated males to move among fragments to breed with resident females, females within fragmented landscapes to access sufficient resources to successfully rear young, and subadult males to

disperse away from their natal range and contribute to gene flow and metapopulation persistence, and female quolls to recolonise previously extirpated areas. I showed that within their home ranges, adult female spotted-tailed quolls make some use of but largely avoid the agricultural matrix, concentrating their foraging, denning and movement on patches and linear strips of woody vegetation cover. The larger body size and vagility of male spotted-tailed quolls suggests that they should be more tolerant of habitat fragmentation than are female quolls, and therefore at least as able as females to utilise heterogeneous landscapes.

My results apply to movement within home ranges, and therefore caution must be applied when directly predicting factors influencing connectivity among populations. Nonetheless, the finding that quolls are able to use linear strips of woody vegetation within their home range suggests that such vegetation corridors could be used by adult males travelling widely to access multiple mates during the breeding season, subadult males travelling through the landscape during natal dispersal away from the parental home range, or gradual female recolonisation of previously occupied areas. Thus, corridors between isolated habitat patches may not only assist females in accessing resources within their home range, but also promote dispersal and gene flow (Hanski and Ovaskainen 2000; Mech and Hallett 2001), aid demographic factors and metapopulation dynamics (Hanski 1998; Hanski and Gilpin 1991), and reduce extinction risk (Frankham 2005). Although planned corridors (e.g. habitat retention or restoration) should target forest vegetation as preferred by quolls, other woody vegetation communities, including native shrub and introduced woody weeds, may also provide connectivity, and should not be discounted, especially in landscapes that have already been heavily cleared. Similarly, other carnivore species including fisher (*Martes pennanti*) (LaPoint *et al.* 2013) and cougar (*Puma concolor*) (Sweaner *et al.* 2000), are able to use less preferred

cover types to connect optimal habitat. Future work should aim to identify putative corridors in the Tasmanian landscape, and test their use with spatial and genetic methods.

6.3 Conserving the spotted-tailed quoll

6.3.1 Conservation status

The adult female spotted-tailed quoll home range sizes that I recorded at Woolnorth in northwest Tasmania, which is the highest density population known in Tasmania, are comparable to home ranges recorded on the south-eastern mainland of Australia. Trap success at Woolnorth (7.1%) was lower than that recorded in the highest density population known on the south-eastern mainland, in the tablelands of north-eastern New South Wales (13%) (Glen 2008). Assuming that home range size is inversely related to density, and trap success is positively related to density, it appears that the better conservation status of the Tasmanian spotted-tailed quoll results from a more extensive continuous distribution than a higher density of quolls within populations.

The Tasmania spotted-tailed quoll is listed as vulnerable under federal legislation (EPBC 1999), Rare under Tasmanian legislation (TSPA 1995), and the species as a whole is considered Near Threatened under international criteria (IUCN 2013). Listing, delisting, or updating the status of threatened species requires estimates and trends in area of occurrence or population size, yet the lack of surveys and monitoring for the spotted-tailed quoll means that there are no robust data from which to base this information. Although local declines have been recorded (e.g. Narawntapu, Figure 2.2), the extent of the reduction in numbers at the population level is unknown.

The only estimates of spotted-tailed quoll population size place the total number of mature adults throughout Australia at less than 10,000 mature individuals (Jones *et al.* 2003), and the Tasmanian population at a median of 3,646 mature individuals (minimum = 3,125 – maximum = 4,167) (Jones and Rose 1996). Using the predictive habitat suitability model (Chapter 2) as an index of habitat quality, and information on female home range size, sex ratio, and a relative abundance, I estimate that the current size of Tasmanian spotted-tailed quoll population at between 1,612 and 14,632 mature individuals, with a mean estimate of 5,691 mature individuals (Appendix 6.1). The large confidence intervals around this estimate reflect the uncertainty around predicted values of habitat suitability and variation in the minimum number of animals known to be alive among surveys. Due to this uncertainty, this population estimate cannot be used as a baseline from which to measure population trends. However, the mean population size estimate and relatively high proportion of core habitat occurring on private land indicates that the Tasmanian spotted-tailed quoll should remain listed as Rare under the *Threatened Species Protection Act 1995* Criterion 4B (“The total population consists of fewer than 10,000 mature individuals, and no more than 2,500 mature individuals occur on land that is in an area free from sudden processes capable of causing largely irreversible loss of individuals or habitat”) and Vulnerable under the *Environment Protection and Biodiversity Conservation Act 1999* Criterion 3b (“The estimated total number of mature individuals is limited and the number is likely to continue to decline and its geographic distribution is precarious for its survival”). Thus, even considered as subspecies distinct from the south-eastern mainland spotted-tailed quoll, the Tasmanian subspecies meets the criteria for listing under state and federal legislation. Separate consideration of the Tasmanian and the south-eastern mainland spotted-tailed quoll at a federal level, including updating nomenclature

to reflect subspecies rather than populations would assist in developing management recommendations to mitigate the different factors threatening the species in different areas.

6.3.2 Systematic surveys and monitoring

The spotted-tailed quoll is one of just three terrestrial mammals listed as threatened in Tasmania. Despite its threatened status, there is currently no robust systematic monitoring of the Tasmanian spotted-tailed quoll that would allow measurement of future population trends. In reality, the low density and cryptic nature of quolls means that, although theoretically possible, broad scale surveys designed to measure population trends are likely to be logistically and financially challenging. Remote cameras offer a reliable and effective survey method, but also have limitations. Because it is not possible to reliably identify individuals or determine sex and reproductive status, camera surveys do not provide well resolved information on abundance and population composition. A combination of live trapping at monitoring sites and camera surveys at broader scales will probably be most useful for monitoring population trends.

The challenges of conserving low density, cryptic threatened carnivores such as the spotted-tailed quoll are demonstrated by the results of an exercise to prioritise recovery actions for Tasmania's threatened species (Threatened Species Section 2010). This listed the spotted-tailed quoll as the lowest priority species to secure, out of the 171 endangered and vulnerable species considered, in order to cost efficiently minimise extinction risk in Tasmania over the next 50 years. This low ranking partly reflects the relatively low extinction risk for this species, but also the high cost and low feasibility of addressing its key threat, and the high cost of monitoring the species. However, the prioritisation exercise incorporates a five-yearly review, which is now due, in recognition of the changing nature of conservation status, threats and available information. Notwithstanding this output, from my results I identified four

conservation actions that can be undertaken now to assist the conservation and recovery of spotted-tailed quoll populations.

6.3.3 Fox eradication in Tasmania

Eradication of the introduced red fox should be considered as the highest priority action to conserve the Tasmanian spotted-tailed quoll and its mammalian prey. Results from this study indicate that the Tasmanian spotted-tailed quoll has a broader ecological niche than the mainland quoll due to the historical and functional absence of foxes. If foxes become established in Tasmania, the same decline of critical weight range mammals seen on mainland Australia can be expected. Furthermore, in the presence of foxes, the magnitude of the effect of habitat loss and fragmentation is also likely to increase, resulting in the decline and disappearance of the Tasmanian spotted-tailed quoll and its prey from their currently preferred habitats. A program to eradicate the fox from Tasmania was implemented in 2002 and is ongoing.

6.3.4 Community engagement

Increasing engagement with private landholders is essential for ongoing persistence of the Tasmanian spotted-tailed quoll. Increasing community awareness of the spotted-tailed quoll and involving the community in its recovery is a key objective identified in the spotted-tailed quoll draft recovery plan (Long and Nelson 2008). While direct protection of habitat through reservation of government land is an important conservation tool, its scope is limited for widely ranging mammalian predators such as the spotted-tailed quoll. Furthermore, the high proportion of Tasmanian spotted-tailed quoll core habitat occurring on private land means that reservation alone will not secure the species' most important habitat, and conservation practitioners must

deploy additional strategies to achieve compatible land use. On private land, the Tasmanian spotted-tailed quoll still faces human persecution due to its penchant for killing domestic poultry. Furthermore, the continual dilution of legislation around land clearing (DIER 2011) means that the conservation of critical habitat on private land is becoming increasingly dependent on the goodwill of landholders. Unfortunately, members of the Tasmanian community seemed generally unaware of the plight of the spotted-tailed quoll, and in a surprisingly high number of cases, unaware that the species even existed (pers obs). Well planned citizen science (Cohn 2008) whereby private landholders participate as field assistants in remote camera surveys could provide multiple benefits, including robust and effective ongoing monitoring of native and introduced predators, and increased land holder interest in the natural values of their property. A simple scheme for free provision of materials to construct quoll-proof poultry enclosures could defuse human persecution. Finally, creating networks of informal reserves on private land through conservation covenants may increase the level of protection of high quality habitat for both occupation and landscape connectivity.

6.3.5 Habitat retention and restoration

The Tasmanian spotted-tailed quoll prefers forest at fine spatial scales (e.g. second- to fourth-order selection of habitat for home ranges and den sites). Therefore, disturbance of forest habitat has the potential to disrupt fine scale ecological processes. Although this study showed that quolls are tolerant to some disturbance, the amount of habitat loss that they can tolerate is unknown and is likely to be context specific. Even so, general recommendations on habitat management strategies can still be drawn from my results. For areas that are scheduled to be converted from native forest to other land uses, habitat retention strategies should aim to preserve a mixture of islands and interconnected networks of linear strips of preferably eucalypt

forest, but potentially also including non-eucalypt forest and other woody vegetation. For quolls occupying already cleared agricultural land, especially in predicted core habitat, retention of existing vegetation, including large and small patches, linear strips, and windrows of both native and introduced vegetation appear important for the ongoing persistence of the species, especially but not necessarily where they connect to larger patches of vegetation. Similarly, as my results show that quolls are capable of using corridors, habitat restoration such as plantings to create new forested corridors is likely to benefit quolls, both for dispersal in the short term and as primary habitat in the longer term. Where little native vegetation occurs, introduced woody weeds may provide habitat, and thus its control or eradication and replacement should be gradual to ensure that quolls can continue to use the area.

Despite not being conducted in forestry areas, some results from this study can be used to inform management recommendations for the spotted-tailed quoll in production forest landscapes. At the stand scale, habitat retention should focus on retaining eucalypt forest, with other native forest of secondary importance. Other research on the south-eastern mainland and Tasmanian spotted-tailed quoll have both demonstrated quoll preference for structural complexity (Belcher and Darrant 2006b; Jones and Barmuta 2000). Therefore, areas with high canopy cover, well developed shrub layer, and ground cover, along with a high density of potential den sites should be targeted for retention. Results of this study have contributed to development of coupe-scale habitat retention guidelines for the Tasmanian spotted-tailed quoll in forested landscapes (Forest Practices Authority 2014). At the landscape scale, corridors of undisturbed native forest vegetation should be retained to maintain connectivity may otherwise be lost, at least temporarily, following timber harvesting (Belcher 2008). An important caveat on these recommendations is that they were developed in an agricultural landscape. The spotted-tailed quoll may respond in a different way to differences in the type, structure and

spatial arrangement of the matrix, and in the structure and age of forest farming and timber harvesting landscapes.

6.3.6 Reintroductions and restoration

Reintroducing species to parts of their former range where they have become extirpated is a tool that is increasingly used by conservation biologists as a result of increasing awareness of the need to conserve biological diversity and reduce extinctions (Seddon *et al.* 2007). Currently, the spotted-tailed quoll recovery plan states that there is currently insufficient information to identify potential habitat that the species may recolonise or to which it could be reintroduced (Long and Nelson 2008). The habitat model developed in this study (Chapter 2) provides information on potential habitat that the species may recolonise or to which it could be reintroduced, conditional on effective suppression of foxes. In Tasmania, large parts of both Flinders and King Islands where the spotted-tailed quoll is now extinct have high habitat suitability. The cause of the decline of quolls on these islands is unclear, but native vegetation clearance, human persecution and attacks by domestic dogs are all implicated (Green and McGarvie 1971). My models suggest that abiotic components of the habitat are suitable despite extensive vegetation clearance, and thus success of reintroduction would hinge on community support. If foxes do establish on mainland Tasmania, these large islands have the potential to provide refuge for the spotted-tailed quoll.

My results also provide information that could assist with recovery of the mainland spotted-tailed quoll. Historical records indicate that the distribution of the mainland spotted-tailed quoll formerly encompassed coastal areas that are now fertile farmland (Lunney and Matthews 2001) and extended west of the Great Dividing Range to the edge of the semi-arid zone (Atlas of Living Australia). The persistence of Tasmanian spotted-tailed quoll

populations in heterogeneous landscapes suggests that, if fox baiting is effective and results in increases in the abundance and distribution of small- to medium-sized mammalian prey, it may be possible to supplement or reintroduce south-eastern mainland quolls to parts of their former range, or to areas where quolls have undergone substantial declines. In support of this, following over a decade of fox baiting that aimed to increase survival of critical weight range mammals, the spotted-tailed quoll was recorded in the semi-arid Grampians National Park for the first time in 141 years, and in coastal heath in the south coast of New South Wales (Australian Broadcasting Commission 2011), both in areas not perceived as “good” spotted-tailed quoll habitat according to current information on south-eastern mainland spotted-tailed quoll habitat preferences.

Important considerations for planned reintroductions include not only which habitat conditions are required, but also the required density of prey and den resources, genetic makeup of introduced (and perhaps resident) animals, how post release survival and dispersal can be improved by ongoing management, as well as logistic constraints such as high costs and difficulty in measuring the factors that determine whether the reintroduction was successful (IUCN/SSC 2013). Additionally, for areas also occupied by humans, the support of the community will be critical to reintroduction success.

6. 4 Future research

6.4.1 Effects of forest management

To determine how production forestry, particularly clearfell burn and sow, affects the ecology of the Tasmanian spotted-tailed quoll, future studies need to link habitat use by quolls to proportion of age classes and their connectivity in surrounding landscape, age of forest stand.

This can be achieved through a combination of population monitoring and radio-telemetry to investigate habitat preference and movement through the landscape. The first challenge of such a project is to find a high density quoll population occurring in a production forest landscape that would allow robust inference to be made. To date, two research projects that aimed to investigate quoll ecology in production forest landscapes have been initiated; both met substantial challenges in obtaining adequate sample sizes to address their key questions (trap success <1%, S. Troy unpublished, C. Hawkins unpublished).

6.4.2 Interspecific interactions

Further fine-scale information on interspecific interactions among predators (e.g. prey and den preferences, spatial overlap, activity times) and between predators and prey are required from multiple locations and landscape contexts across Tasmania. Importantly, it should not be assumed that observed fine-scale behavioural relationships such as spatial or temporal niche separation between apex and mesopredators “scale up” to demographic and population level changes; to definitively demonstrate that a mesopredator is adversely affected by an apex predator, patterns in resource and space use or activity time use should be linked to measures of fitness.

6.4.3 Population and landscape genetics

An understanding of the environmental factors that enhance or inhibit connectivity among populations would be valuable in guiding habitat restoration and conservation planning. Knowledge of genetic variation within and among Tasmanian spotted-tailed quoll populations is scant. Population genetic data would assist in determining whether the Tasmanian spotted-tailed quoll consists of one or more management units or subpopulations, and identifying

genetically isolated populations. Combined with spatial data on predicted habitat suitability, vegetation, climate, and topography, landscape genetic approaches will allow investigation of the environmental factors that enhance or inhibit connectivity among populations, and in turn inform habitat restoration and conservation planning (Rabinowitz and Zeller 2010).

6.4.4 Concluding remarks

This study demonstrates the important interactive roles of spatial scale and extent and bottom-up and top-down processes in shaping wildlife distribution and abundance. As exemplified herein, the challenges in determining the factors influencing the spatial ecology of wide-ranging, cryptic, and rare carnivores are many, including the logistical and analytical constraints associated with difficulties in species detection and small sample sizes. Regardless of these challenges, extrapolating species space or habitat requirements across spatial scales or geographic regions may underestimate the habitat, niche or distribution of species, and could ultimately lead to ineffective or misdirected conservation action. Within the selection-order structure of Johnson (1980), this thesis provides a framework for investigating the biotic and abiotic influences of wildlife spatial ecology at multiple spatial scales to inform their conservation management.

Appendix 6.1: Estimation of Tasmanian spotted-tailed quoll population size.

1. Classify trap sites as low, medium, high, or very high density.

Number of trapped individuals is considered to be minimum known to be present at the site.

Trap site*	# Trapped individuals 2004-2010			Density
	Mean minimum	Minimum minimum	Maximum minimum	
Woolnorth	16	9	24	Very High
Arthur River, Temma, Mt Housetop, Detention River	6	3	6	High
Cradle, Freycinet, Buckland, Cann Creek, Dunalley, Kempton, Hastings, Ida, Lake Rowallan, Milkshake Hills, Mt Hicks, Mt William, Narawntapu, Reedy Marsh, Surrey Hills	2.7	1	6	Medium
Granville Harbour, Roger River, Savage River, Takone, Bronte Park	0.2	0	1	Low

* Department of Primary Industries, Parks Water and Environment Save the Tasmanian Devil Program trap sites

2. Calculate density at trap sites.

Qualitative density	Quantitative density (# trapped individuals / survey area)		
	Mean minimum	Minimum minimum	Maximum minimum
Very High	0.64	0.36	0.96
High	0.24	0.12	0.24
Medium	0.108	0.04	0.24
Low	0.008	0	0.04

3. Extrapolate density across Tasmania.

The % of Tasmania estimated to have the same density as trap sites was approximated by dividing the habitat model (Chapter 2) predictions into four classes: Very High, High, Medium, Low; and calculating the % area encompassed by the predicted values. The area of Tasmania estimated to have the same density of trap sites was estimated using the total area of mainland Tasmania (62, 000 km²).

Qualitative density	% of Tasmania estimated to have the same density as trap sites	Area of Tasmania estimated to have same density as trap site (km²)
Very High	0 - 2.5	1550
High	2.5 - 10	4650
Medium	10 - 30	12400
Low	30 - 100	43400

4. Estimate population size by multiplying area of Tasmania estimated to have same density as trap site with quantitative density.

Minimum population estimate is quantitative density * area.

Maximum population estimate is quantitative density * 2 (assuming that half of the animals present are not trapped during surveys).

The median best population estimate is calculated as the median value between mean minimum and mean maximum number of individuals.

	Minimum population size estimate			Maximum population size estimate			Best population estimate		
	Mean minimum	Minimum minimum	Maximum minimum	Mean maximum	Minimum maximum	Maximum maximum	Median	Minimum	Maximum
Very High	992	558	1488	1984	1116	2976			
High	1116	558	1116	2232	1116	2232			
Medium	1339.2	496	2976	2678.4	992	5952			
Low	347.2	0	1736	694.4	0	3472			
TOTAL	3794.4	1612	7316	7588.8	3224	14632	5691.6	1612	14632

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