Ecology of the spotted-tailed quoll
(Dasyurus maculatus), and its interactions
with eutherian predators

by
Alistair S. Glen

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# Table of contents

Abstract i

Acknowledgements vii

Chapter 1: General introduction

1.1. Introduction 1
1.2. Definitions 2
1.3. Interactions between native and introduced carnivores 4
1.4. Interactions among native carnivores 12
1.5. Interactions among introduced carnivores 15
1.6. Implications for prey populations 17
1.7. Implications for predator management 18
1.8. Conclusions 21
1.9. Aims 22

Chapter 2: A summary of the biology of the spotted-tailed quoll, red fox, wild dog and feral cat in Australia

2.1. Physical characteristics 24
  2.1.1. Spotted-tailed quoll 24
  2.1.2. Red fox 24
  2.1.3. Dingo 24
  2.1.4. Feral cat 25
2.2. Habitat and distribution 25
  2.2.1. Spotted-tailed quoll 25
  2.2.2. Red fox 26
  2.2.3. Wild dog 26
  2.2.4. Feral cat 27
2.3. Diet 27
  2.3.1. Spotted-tailed quoll 27
  2.3.2. Red fox 27
Chapter 3: Study area

3.1. Location, topography and land use 34
3.2. Vegetation 35
3.3. Climate 35
3.4. Vertebrate fauna 36

Chapter 4: Abundance, life history and population dynamics of spotted-tailed quolls

4.1. Introduction 37
4.2. Methods 38

4.2.1. Trapping and handling of quolls 38
4.2.2. Analysis of data 39

4.2.2.1. Demography 39
4.2.2.2. Comparative trap success 41
4.2.2.3. Morphometrics 41

4.3. Results 42

4.3.1. Demography 42
4.3.2. Comparative trap success 44
4.3.3. Morphometrics 45
4.3.4. Injuries and parasites 46
4.4. Discussion

4.4.1. Demography

4.4.2. Comparative trap success

4.4.3. Morphometrics

4.4.4. Injuries and parasites

4.4.5. Conclusions

Chapter 5: Diet of the spotted-tailed quoll

5.1. Introduction

5.2. Methods

5.2.1. Collection of scats

5.2.2. Scat analysis

5.2.3. Data analysis

5.2.3.1. Dietary diversity

5.2.3.2. Seasonal variation

5.2.3.3. Variation in diet due to sex and body-size

5.3. Results

5.3.1. Seasonal variation in diet

5.3.2. Diets of male and female quolls

5.3.3. Effect of quoll body size on diet

5.4. Discussion

5.4.1. Seasonal variation in the diet

5.4.2. Influence of sex and body size on diet

5.4.3. Conclusions

Chapter 6: Movement, home range and microhabitat use of quolls

6.1. Introduction

6.2. Methods

6.2.1. Radio-tracking

6.2.2. Spool-and-line tracking

6.2.3. Data analysis

6.3. Results

6.3.1. Trapping
6.3.2. Radio-tracking
6.3.3. Den use
6.3.4. Spool-and-line tracking
6.3.5. Effects of fire on habitat use
6.4. Discussion
   6.4.1. Home ranges
   6.4.2. Den use
   6.4.3 Microhabitat use
   6.4.4. Conclusions

Chapter 7: Interactions between quolls and eutherian predators
7.1. Introduction
7.2. Methods
   7.2.1. Dietary overlap
   7.2.2. Spatial resource use
   7.2.3. Population viability analysis
7.3. Results
   7.3.1. Diet
   7.3.2. Spatial resource use
   7.3.3. Population viability analysis
7.4. Discussion
   7.4.1. Dietary overlap
   7.4.2. Spatial overlap
   7.4.3. Interference competition
   7.4.4. Population viability analysis
   7.4.5. Conclusions

Chapter 8: General discussion: Why are there so many spotted-tailed quolls in north-eastern New South Wales?
8.1. Introduction
8.2. Availability of prey
8.3. Quality and spatial extent of habitat
8.4. Density of competitors
References
Abstract

The spotted-tailed quoll (*Dasyurus maculatus*) is an endangered marsupial carnivore endemic to eastern Australia. Formerly abundant across much of eastern mainland Australia and Tasmania, *D. maculatus* now has a highly fragmented distribution and is rarely recorded west of the Great Dividing Range. Several factors are likely to have contributed to the decline of the species, the most obvious being the destruction and alteration of habitat. However, the ongoing effects of introduced predators, which may prey upon and/or compete with spotted-tailed quolls, are also thought to be a major agent of decline.

Concern has been raised in recent years that poison baits used to control pest animals such as red foxes (*Vulpes vulpes*) and wild dogs (*Canis lupus dingo* and *C. l. familiaris*) may pose a threat to spotted-tailed quolls. However, if introduced predators themselves represent a threat to *D. maculatus*, then their control might potentially benefit quoll populations. This thesis investigates the ecology of the spotted-tailed quoll in a localised area of high abundance in Marengo and Chaelundi State Forests, north-eastern New South Wales. Information is presented on population dynamics, diet, movements and spatial organisation of the species. Finally, evidence for interactions between spotted-tailed quolls and sympatric eutherian predators is collected and evaluated. Indices of dietary overlap between species are presented, and the home ranges and microhabitat use of different species are compared. The possible effects of competition on spotted-tailed quoll populations are also investigated using population viability analysis.

Chapter 1 provides a theoretical review of ecological interactions between mammalian carnivores, placed in the context of examples from within and outside Australia. Mammalian carnivore populations are often intensively managed, either because the carnivore in question is endangered, or because it is viewed as a pest and is subjected to control measures, or both. Most management programmes treat carnivore species in isolation. However, there is a large and emerging body of evidence to demonstrate that populations of different carnivores interact with each other in a variety of complex ways. Thus, the removal or introduction of predators to or from a system can often affect other species in ways that are difficult to predict. Wildlife managers must consider such interactions when planning predator control programmes. Integrated
Abstract

predator control will require a greater understanding of the complex relationships between species.

In many parts of the world, sympatric species of carnivores have coexisted over an evolutionary time scale so that niche differentiation has occurred, and competition is difficult to observe. Australia has experienced numerous introductions during the past 200 years, including those of the red fox and the feral cat (*Felis catus*). These species now exist in sympatry with native mammalian predators, providing ecologists with the opportunity to study their interactions without the confounding effects of coevolution.

Despite an increasing body of observational evidence for complex interactions among native and introduced predators in Australia, few studies have attempted to clarify these relationships experimentally, and the interactions remain largely unacknowledged. A greater understanding of these interactions would provide ecologists and wildlife managers world-wide with the ability to construct robust predictive models of carnivore communities, and to identify their broader effects on ecosystem functioning.

Chapters 2 and 3 provide an introduction to the biology of the study animals and the area in which the project was conducted. Information on physical characteristics, distribution, habitat, diet, life-history and behaviour is provided for the spotted-tailed quoll, red fox, wild dog and feral cat in Australia.

Conservation management of the spotted-tailed quoll has been hindered by a paucity of information on the dynamics of wild populations. In Chapter 4, I investigate the population dynamics of spotted-tailed quolls in Marengo and Chaelundi State Forests, where density is conservatively estimated at 0.3 km\(^{-2}\). Sixty-one individual quolls were captured on 331 occasions over 22 months. As well as presenting data on abundance, density and survival, I investigate the timing and rate of reproduction, and present morphometric data for comparison with those of quolls from other areas. Population models are employed to investigate patterns in the survival of quolls in the study area, and to explore some possible factors that produce these patterns. Intense wildfires caused short-term reductions in captures of males, suggesting emigration. The exceptionally high abundance of *D. maculatus* identifies the study area as vital to the conservation and future study of the species.
In Chapter 5, the diet of spotted-tailed quolls in Marengo and Chaelundi State Forests is investigated by faecal analysis. Medium-sized mammals (500 - 6,999 g) formed the bulk of the faecal content, both in terms of volume and frequency of occurrence. The most frequently consumed vertebrates were the greater glider (*Petauroides volans*), rabbit (*Oryctolagus cuniculus*), bandicoots (*Perameles nasuta* and/or *Isoodon macrourus*), red-necked pademelon (*Thylogale thetis*), ringtail possum (*Pseudocheirus peregrinus*) and brushtail possum (*Trichosurus vulpecula* and/or *T. caninus*). Insects were also eaten frequently, but birds and reptiles occurred relatively infrequently in the diet. Seasonal variation in diet was marked, with insects and reptiles being consumed more frequently, and mammals less frequently, in summer than in winter. This seasonal pattern was also mirrored by the relative volumes of mammals and insects consumed. The extremely high proportion of mammalian prey in the diet identifies *D. maculatus* as a hypercarnivore, or meat specialist. The importance of tree hollow-nesting mammals in the diet indicates that preservation of hollow-bearing trees should aid the conservation of *D. maculatus*. Future dietary studies of the species should sample over extensive time periods, and involve concurrent monitoring of prey populations.

Radio-tracking of spotted-tailed quolls (Chapter 6) revealed that home ranges were extensive, with males occupying large, overlapping ranges [Minimum Convex Polygon (MCP) up to 757 ha], and females smaller, non-overlapping territories (MCP up to 175 ha). Quolls were partly arboreal, although most activity occurred on the ground or on fallen logs. Hollow logs were most frequently used as dens, but rock crevices, burrows, tree hollows and artificial structures were also used. Individual quolls were located in up to nine different dens and, with the exception of maternal dens, rarely sheltered in the same location on successive days. The large home ranges of the spotted-tailed quoll, and the non-overlapping nature of female ranges, necessitate very large areas of habitat to support viable populations. Fallen timber, used extensively for shelter and in travelling, may serve to enhance the quality of habitat for the species, and should be retained by forest and wildlife managers.

Chapter 7 examines the degree of overlap in resource use (dietary and spatial) between spotted-tailed quolls and eutherian carnivores in sympatry, and investigates mechanisms of niche partitioning between the species. Evidence for interspecific aggression is also
considered. Finally, the possible effects of interspecific competition on the viability of quoll populations are investigated. Analysis of scats from quolls, foxes and wild dogs revealed extensive dietary overlap between all three species, indicating the potential for exploitation competition. Medium-sized mammals were the most important prey for all three predators. Using Pianka's index, dietary overlap between quolls and foxes was 0.712. Overlap between quolls and wild dogs was 0.657, while that between foxes and dogs was 0.943. These values are extremely high in comparison to carnivore guilds from Africa and South America. However, some significant differences were found between the diets of the three species. For example, quolls consumed arboreal prey (particularly greater gliders), and foxes and dogs preyed on rabbits, significantly more often than their counterparts. This vertical niche partitioning, as well as consumption of different size classes of secondary prey, is likely to facilitate coexistence. Remains of spotted-tailed quolls were found in two dog scats, and cat hair in one dog scat collected in the study area during a previous survey in 1984, possibly indicating intraguild predation by dogs.

Extensive spatial overlap was also observed between quolls, foxes, feral cats and wild dogs. Overlap was confirmed by data from radio-tracking, trapping, scat collection and opportunistic sightings. Despite dietary evidence for vertical niche partitioning, quolls made little use (1%) of arboreal microhabitats, suggesting that habitat is unlikely to be divided vertically between quolls and eutherian predators. Despite the extensive spatial overlap, it is possible that species avoid direct encounters, either through avoidance at a very fine spatial scale, or through temporal niche partitioning. Interference competition may also be alleviated by the climbing ability of quolls, which could provide a means of escape in direct encounters with other predators.

Population viability analysis (PVA) indicated that quoll populations may be vulnerable to extinction when faced with high densities of competitors. Modelled reductions in carrying capacity (simulating the effects of exploitation competition) had a strong negative effect on the population's probability of survival. Modelled increases in mortality (simulating the effects of interspecific killing) produced a similar effect, indicating that quolls may be vulnerable to interference competition from larger predators. The effect was particularly strong when juvenile mortality was increased. PVA also showed that various combinations of decreased carrying capacity and
increased adult or juvenile mortality produced an additive effect, leading to greatly increased probability of extinction.

Chapter 8 explores the question of why spotted-tailed quolls remain abundant in parts of north-eastern New South Wales, while populations in many other areas have declined or disappeared. Based on observations presented in Chapters 1 - 7, a number of possible explanations for this pattern are discussed. These include availability of prey, quality and spatial extent of habitat, density of competitors, and relatively small home range size.

The abundance of mammalian prey such as red-necked pademelons, possums and greater gliders is very high in Marengo and Chaelundi State Forests. In addition, the arboreal habits of greater gliders make them relatively inaccessible to ground-based predators, perhaps enhancing their availability to spotted-tailed quolls. As well as prey availability, a number of habitat features may contribute to the high abundance of *D. maculatus* in the study area. The high availability of fallen timber, which is used extensively by quolls for denning and movement, may enhance the quality of the structural habitat, as may the abundant rocky outcrops characteristic of the area.

Although it is difficult to judge objectively the quality of habitat for spotted-tailed quolls, the spatial extent of habitat is more easily measured, and is also highly important. Very large areas of continuously forested habitat remain in north-eastern New South Wales, with the potential to accommodate large numbers of quolls, even given the non-overlapping nature of female home ranges. Large areas also reduce edge-effects and facilitate dispersal, which protects against inbreeding and stochastic events such as fire.

Low densities of competitors may also be important. Foxes are absent from, or occur at low densities in, many parts of north-eastern New South Wales. Given the similarity in diet between foxes and spotted-tailed quolls, and the propensity of foxes for aggression towards other carnivores, their scarcity may be a major contributing factor to the local abundance of quolls.
Abstract

Based on the results of radio telemetry (Chapter 6), female spotted-tailed quolls in Marengo State Forest may have smaller home ranges than those in areas studied previously, although this result is inconclusive. If female home ranges are indeed smaller in north-eastern New South Wales, this may help to account for the higher population densities in this region.

The results of this study illustrate the importance of maintaining high densities of hollow-bearing trees, which may help to support prey populations for *D. maculatus*. Wildlife managers must continue to implement policies which conserve common, as well as rare or threatened species, as these are often integral to ecosystem function. Managers should also seek to maintain an abundance of fallen timber in areas where spotted-tailed quolls occur, as this will enhance the structural quality of habitat by providing den and shelter sites, and movement pathways for quolls.

Future research should aim to clarify the effects of competition between spotted-tailed quolls and eutherian carnivores on quoll populations. Fox removal experiments should be conducted as a matter of highest priority, and should seek to measure the response of quolls at the individual and/or population level to the removal of foxes. Interactions among other mammalian carnivores must also be better understood if biodiversity and ecosystem function are to be maintained or restored. Predator manipulation experiments should seek to clarify interactions between foxes, feral cats and wild dogs in a variety of habitats.
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inability to grasp the basic concepts of any of these things. Finally, a million thanks to my parents Margaret and Jim for constant support.
Chapter 1: General Introduction: Complex interactions among mammalian carnivores in Australia, and their implications for wildlife management

1.1. Introduction
The deleterious effects of introduced mammalian carnivores in Australia are well documented. The red fox (*Vulpes vulpes*) and the feral cat (*Felis catus*) have been implicated in the decline and extinction of a vast array of native fauna, especially mammals, since European settlement (e.g. Rolls 1969; Burbidge and McKenzie 1989; Dickman 1996a,b; Smith and Quin 1996). In addition, foxes, dingoes (*Canis lupus dingo*) and feral dogs (*C. l. familiaris*) are significant predators of livestock and are therefore major pests of the grazing industry (Rolls 1969; Saunders et al. 1995; Glen and Short 2000; Fleming et al. 2001).

Studies on the impacts of introduced predators on Australia’s native wildlife have focused primarily on direct predatory impacts (e.g. Kinnear et al. 1988, 1998, 2002; Priddel 1989; Mahon 1999). However, several authors have suggested that introduced predators may also impact upon native species through competition for resources such as food, territories and den sites (e.g. Edgar and Belcher 1995; Morris et al. 1995; Dickman 1996a,b), or through the introduction and spread of diseases and parasites (e.g. Caughley 1980; Dickman 1996a,b; Molsher 1999). In addition, emerging evidence suggests that introduced predators may themselves be limited by competition and/or predation from other members of the mammalian carnivore guild (e.g. Marsack and Campbell 1990; Short and Smith 1994; Newsome et al. 1997; Molsher 1998, 1999; Molsher et al. 1999; Newsome et al. 2001).

There is a considerable body of theoretical and empirical work addressing interactions within trophic guilds outside Australia (e.g. Paine 1966; Polis et al. 1989; Doncaster 1992; Estes 1996; Holt and Polis 1997; Palomares and Caro 1999; Fedrani et al. 2000, Creel 2001; Gosselink et al. 2003; Jácomo et al. 2004). However, little research has been conducted in systems where one or more predators have been recently introduced. In Australia, where cats and foxes are relative newcomers in ecological terms, systems have probably not yet reached new stable states, and the potential for further decline among their native competitors and prey is therefore very real. Indeed, the dingo was
introduced to the Australian mainland some 3,500 - 4,000 years ago (Gollan 1984; Corbett 1995b) and co-occurred with the thylacine (*Thylacinus cynocephalus*) for perhaps 500 years before the latter disappeared. Even then, mainland extinction of the thylacine coincided with shifts in human hunting technology (Johnson and Wroe 2003). Given the ecological and economic impacts of introduced carnivores in Australia, an understanding of their effects, and of the processes that limit their populations, is clearly essential.

Wildlife managers often target one species at a time for management, neglecting to consider the indirect effects that their actions may have on other pest species. For example, removal of a predator may release other pest species from predation or competition. This review is a first step in being able to predict such effects, and is therefore of potential importance for wildlife managers. In addition, the Australian situation is of special interest from a theoretical point of view. Over an evolutionary timescale, competition often causes species to shift to exploit separate niches, so that its effects are no longer observable (Arthur 1982), except in unusual situations where competition is ‘suspended’ (Dickman 1986a). Where one or more species of competitor is a recent arrival, a window of opportunity exists to study competition before such adaptation occurs (Clode and Macdonald 1995; Blackwell and Linklater 2003).

Here, I review the evidence for complex interactions among native and introduced mammalian carnivores in Australia, and discuss this in the context of examples from other continents. The implications for management of vertebrate pests both within and outside Australia are also discussed.

### 1.2. Definitions

**Competition:** Competition may occur within or between species, when individuals deprive others of resources, thus reducing their growth, survivorship or fecundity (Begon *et al.* 1986). The mechanisms of competition can be broadly classified into exploitation or interference, although these can be divided more finely (Schoener 1983). Exploitation competition occurs when organisms use resources, thus depriving others of those resources (Fig. 1a). By contrast, interference competition occurs when individuals are directly antagonistic towards others (e.g. by fighting or production of chemical deterrents), thereby excluding them from a contested resource (Schoener 1983; Sih *et
The effects of interference competition may be particularly significant among carnivores due to their physical and behavioural adaptations for killing (Dickman 1991; Creel et al. 2001).

Intraguild predation: I follow the definition of Polis et al. (1989), which describes intraguild predation as “the killing and eating of species that use similar, often limiting, resources and are thus potential competitors.” This definition excludes cases of interspecific killing in which the victim is not consumed. Thus, intraguild predation constitutes both predation and extreme interference competition (Fig. 1c).

Trophic cascade: Numerous definitions, some general and some more specific, have been offered for trophic cascades. The term refers to predator-prey interactions whose effects extend (or cascade) down through more than one level in a food web so that plant biomass is ultimately affected by changes in predator abundance, via a series of intermediate links (Paine 1980; Pace et al. 1999; Schmitz et al. 2000) (Fig. 1d). Polis et al. (2000) recognised two levels of trophic cascades. Species-level cascades occur within a subset of the community so that changes in predator numbers affect one or a few plant species. Community-level trophic cascades are more complex and profound, causing plant biomass to be redistributed throughout the system.

Mesopredator release: This describes an increase in the abundance of subordinate predators following the removal of a dominant predator which previously held the subordinate species in check (Soulé et al. 1988). Such an occurrence may constitute one link in a larger trophic cascade.

Apparent competition: This is most commonly a situation in which two or more alternate prey species limit each other’s abundance, not because they compete directly for resources, but because each prey species helps to maintain the density of shared predators, thereby indirectly maintaining predation pressure on the other (Holt 1977) (Fig. 1e). An alternative form of apparent competition was described by Connell (1990) as involving three species within the same trophic level (Fig. 1f).

Keystone species: Originally, this term referred to a predator that facilitated the coexistence of potentially-competing prey species. By preying upon and hence...
suppressing the dominant competitor, the keystone predator indirectly allowed the subordinate competitors to persist (Paine 1966; 1969) (Fig. 1g). The term has come to be used much more broadly, and now refers to a species that has disproportionately large effects on the community or ecosystem relative to its own abundance (Heywood 1995; Power et al. 1996). Thus, a keystone species need not be a predator, but may exert strong effects through a variety of processes such as pollination, seed dispersal or alteration of the abiotic environment (Power et al. 1996).

*Indirect commensalism:* This describes a situation in which a dominant predator or competitor suppresses a subordinate one, indirectly benefiting competitors of the subordinate species (Fig. 1h).

*Native and introduced predators:* For the purposes of this discussion, the dingo, having existed in Australia for some 3,500 - 4,000 years prior to European settlement (Gollan 1984; Corbett 1995b), is treated as native. This reflects the management objectives of conservation agencies, which seek to conserve the dingo as part of Australia’s natural heritage. The cat and the fox arrived much more recently in Australia (Rolls 1969; Abbott 2002), and are defined as introduced.

1.3. *Interactions between native and introduced carnivores*

Introduced predators may impact on native ones via intraguild predation (Fig. 1c), introduction or spread of disease, or by competition for resources (Fig. 1a,b). Wiens (1989) outlined types of evidence that indicate interspecific competition. Where the distributions of two species appear to be mutually exclusive, this may be taken as weak evidence of competition. A stronger case is presented if overlap in resource use is demonstrated, and an even stronger case if it can be shown that the use of resources by one species reduces their availability to the other. Finally, if one or both species is negatively affected by the presence of the other (e.g. in terms of reduced abundance, growth or fecundity), and alternative hypotheses are not consistent with observed patterns, a convincing case exists for competition (Wiens 1989). Unequivocal evidence can be obtained from well-designed removal studies, in which reciprocal removal of putative competitors results in increased abundance and resource use of the remaining species. There is sufficient evidence from existing studies to present a strong case for the existence of competition between native and introduced predators in Australia.
Chapter 1: General introduction

a) Exploitation competition

b) Interference competition

c) Intraguild predation

d) Trophic cascade

e) Apparent competition
    
    *via* a shared predator

g) Apparent competition within
    
    a single trophic level
g) Keystone predation

h) Indirect commensalism

Fig. 1. Illustrated examples of a number of simple and complex interactions. Solid arrows denote direct effects; broken arrows denote indirect effects and signs (+, -, 0) indicate effect on species. a) exploitation competition, b) interference competition, c) intraguild predation, d) trophic cascade, e) apparent competition via a shared predator, f) apparent competition within a single tropic level, g) keystone predation (removal of the dingo from this system would cause mesopredator release of foxes and cats), h) indirect commensalism. Species names used in each example represent documented or postulated examples of the respective interactions in Australia. Adapted from Connell (1990) and Morin (1999).
Chapter 1: General introduction

Numerous authors have noted the potential for competition from cats and foxes to impact upon Australian native mammalian predators. These suggestions are often speculative, and based on the high degree of overlap in resource use observed between introduced predators and their native counterparts. For example, it has been posited that quolls (*Dasyurus* spp.) are likely to experience competition from cats for food and den sites (Dickman 1996a,b; Jones and Barmuta 1998; Molsher 1999). Quolls are the most similar Australian genus to cats in terms of diet, and are sympatric with cats throughout their distributions (Dickman 1996a). (Four species of quoll occur in Australia, and a further two in New Guinea). Molsher (1999) found that the diet of spotted-tailed quolls (*Dasyurus maculatus*) in central-western New South Wales overlapped sufficiently with the diet of cats to suggest potential for exploitation competition. Quolls also have overlapping habitat and den requirements with those of cats (Godsell 1982; Dickman 1996a; Oakwood 2002).

Niche overlap also occurs between quolls and foxes, which consume similar prey (e.g. Alexander 1980; Triggs *et al.* 1984; Mansergh and Belcher 1992), and probably have similar preferences for dens and shelter sites (Johnson and Roff 1982; Godsell *et al.* 1984; Mansergh and Marks 1993; Watt 1993; Edgar and Belcher 1995; Coman 1995). Belcher (2000) noted that the ability of the spotted-tailed quoll to climb trees and rock faces may provide some niche differentiation between this species and foxes. Such vertical partitioning could provide a refuge from predators or competitors. For example, Nellis (1989) reported that black rats (*Rattus rattus*) persisted on a Caribbean island following the introduction of the Indian mongoose (*Herpestes auropunctatus*) by switching to arboreal habitats, while bridled quail doves (*Geotrygon mystacea*) changed from nesting on the ground to nesting in low trees. However, if quolls are forced in the presence of foxes to restrict their activity to arboreal or rocky habitats, this may severely limit their access to potential prey and shelter sites, thus causing them to persist at lower densities.

Individual eastern (*Dasyurus viverrinus*), northern (*D. hallucatus*) and spotted-tailed quolls use large numbers of dens, and rarely if ever share dens with conspecifics except when mating (Godsell *et al.* 1984; Watt 1993; Oakwood 2002; Belcher and Darrant 2004). Indeed, competition for dens may be a limiting factor for eastern quolls (Godsell 1982). It is likely, therefore, that a large number of suitable den sites is required for an
area to support high densities of these species. If the choice of den sites is restricted by competition from, or the need to avoid, introduced predators, this could have a marked effect on the population densities of quolls, as was the case for the arctic fox (*Alopex lagopus*) following invasion of its range by red foxes (Hersteinsson *et al.* 1989; Kaikusalo and Angerbjörn 1995).

As well as observations of niche overlap, further evidence of impact comes from instances where the historical pattern of decline of native predators has coincided with the arrival of cats and foxes (Jones *et al.* 2003). For example, the decline of the western quoll (*Dasyurus geoffroii*) in central Australia coincided with the arrival of foxes (Johnson and Roff 1982), as did the decline of the eastern quoll in South Australia (Wood-Jones 1923). The rate of decline in quolls has been much slower in fox-free areas (the northern tropics and Tasmania) than that observed elsewhere in Australia (Oakwood 1997; Jones *et al.* 2003). Similarly, Rolls (1969) noted that declines of the eastern and spotted-tailed quolls occurred shortly after the release of cats, and Dwyer (1983) proposed that the New Guinea quoll (*Dasyurus albopunctatus*) may have declined since the introduction of cats to its range. However, Johnson *et al.* (1989) claimed that cats may not have caused declines of quolls, noting a long period of coexistence prior to the arrival of foxes. The impacts of cats appear to be inconsistent, but can act in concert with a range of other variables such as alteration of habitat, leading in some instances to decline or extinction of native taxa (Oakwood 2000; Burbidge and Manly 2002).

In addition to the speculative arguments presented above, direct evidence for the impacts of introduced predators comes from increases in the abundance of native predators following the removal of foxes. Morris *et al.* (1995) reported increased abundance of the western quoll following poison baiting for foxes, with no concurrent increase in an adjacent, unbaited area. These authors attributed the observed response to reduced competition for food and reduced predation, particularly on young quolls.

Several authors have recorded intraguild predation (Fig. 1c) or competitive killing of native mammalian predators by cats and foxes. For example, Serena *et al.* (1991) and Morris *et al.* (2003) cited predation by foxes and cats as a major source of mortality for the western quoll. Körtner and Gresser (2002) recovered carcasses of two spotted-tailed
quolls that had been partially eaten by foxes, and Banks (1997) found hair from a spotted-tailed quoll in fox faeces. Similarly, Oakwood (2000) found that predation by cats, as well as by native predators, was a major source of mortality for the northern quoll. Cats and foxes also prey upon the mulgara (*Dasycercus cristicauda*), which is itself a predator of small mammals and therefore a potential competitor of cats and foxes (Mahon 1999; Dickman 2003).

On a global scale, Palomares and Caro (1999) found that the red fox was second among the canids (after the grey wolf, *Canis lupus lupus*) as a killer of other carnivores. For example, red foxes in Europe have been observed to prey directly on arctic foxes (Frafjord *et al.* 1989) and pine martens (*Martes martes*) (Lindström *et al.* 1995). The effects of competitive aggression by red foxes can be significant, particularly where they act in concert with other factors. For example, on islands or at the edge of their distribution, populations of arctic foxes may be driven to extinction by the red fox (Bailey 1992; Hersteinsson and Macdonald 1992).

The dingo is the largest terrestrial carnivore in Australia and, unlike its smaller marsupial counterparts, appears to assert predatory and competitive dominance over both cats and foxes. Numerous studies report direct predation by dingoes on foxes and cats. Marsack and Campbell (1990) observed four instances of dingoes feeding on fresh fox carcasses, saw one dingo carrying a freshly killed fox, and also witnessed one unsuccessful attempt at predation. During the same study, fox remains were present in the guts of 6.1% of 49 dingoes sampled, and 2.4% of 82 dingo faeces. Cat remains were also found in the gut of one dingo (2%), and in one faecal sample (1.2%). Consumption of cats by dingoes has also been reported by Newsome *et al.* (1983), Lundie-Jenkins *et al.* (1993), Thomson (1992c), Corbett (1995b) and Paltridge (2002). In addition, Pettigrew (1993) reported that an adult cat fitted with a radio collar was killed by a dingo. This pattern is mirrored in North America where coyotes (*Canis latrans*) kill and eat both bobcats (*Felis rufus*) and grey foxes (*Urocyon cinereoargenteus*) (Fedriani *et al.* 2000).

As well as killing cats and foxes, dingoes may also have exploitative effects (Fig. 1a), particularly when food is limited (Lundie-Jenkins *et al.* 1993; Corbett 1995b; Dickman 1996a). Dietary overlap is considerable, with rabbits (*Oryctolagus cuniculus*) being a
staple prey for all three species where they are available (Catling 1988; Corbett 1995b; Saunders et al. 1995; Molsher et al. 1999; Mitchell and Banks 2005). However, in some circumstances, dingoes can benefit cats by providing a source of carrion. For example, during a drought in central Australia, cats regularly scavenged carcasses killed by dingoes (Paltridge et al. 1997). Although paradoxical, this situation is not uncommon in other systems. Macdonald (1987), Dickman (1992a), Creel (2001) and Switalski (2003) illustrate a number of similar examples from Europe, Africa and North America in which dominant competitors kill or steal prey from subordinate ones, but the subordinate predator may also benefit by scavenging carcasses killed by the dominant one.

There is abundant evidence from the patterns of distribution of dingoes, foxes and cats to suggest that dingoes can suppress populations of their smaller competitors. Perhaps the most compelling evidence is that of Newsome et al. (2001), who measured the relative abundance of foxes on either side of the dingo fence, which excludes dingoes from much of south-eastern Australia while high densities remain to the north and west of the fence. Indices of fox abundance based on spotlight counts and spoor counts at waterholes were 20.6 and 7.1 times higher respectively in the absence than in the presence of dingoes. Cats were at similarly low densities on either side of the fence (Newsome et al. 2001).

Using a passive activity index, Newsome et al. (1997) found an inverse relationship between dingo and fox activity in Kosciuszko National Park and Nadgee Nature Reserve in south-eastern Australia. Given that both species occupy similar habitats, this may reflect a relationship between the densities of the two species, resulting either from avoidance [foxes often avoid dingoes at shared resources such as watering points (Lundie-Jenkins et al. 1993)], or from killing of foxes by dingoes. Alternatively, animals may alter their level of activity or use of roads according to the presence of their confamilials. Further investigation is required to clarify this relationship (Newsome et al. 1997).

In central Australia’s Tanami Desert, foxes were rare or absent until recently, possibly due to exclusion by dingoes. Control of dingoes has been followed by invasion of the area by foxes (Short et al. 2002). Lundie-Jenkins et al. (1993) also reported the absence
Chapter 1: General introduction

of foxes from their central Australian study area until dingoes were removed by poisoning. A single fox was then believed responsible for the extinction of a local population of endangered rufous hare-wallabies (*Lagorchestes hirsutus*). A similar situation has occurred in North America, where expansion in the distribution of coyotes has been attributed to the decline of the grey wolf (Mech 1970).

In addition to these specific instances, many authors have made the general observation that foxes are scarce where dingoes are abundant, or *vice versa* (e.g. Thompson 1983; Jarman *et al.* 1987; Johnson *et al.* 1989; Smith and Quin 1996; McArae 2004). However, the occurrence of the two species is not mutually exclusive, and Catling and Burt (1995) noted that fresh dingo and fox tracks were often recorded side by side. It is possible that foxes tolerate dingoes more readily in densely vegetated forest areas, such as those studied by Catling and Burt (1995), because of the greater ease of avoidance or evasion once detected where structural refugia are available (e.g. Finke and Denno 2002).

It has also been noted that cats can increase in density following the removal of dingoes (Lundie-Jenkins *et al.* 1993; Pettigrew 1993; Christensen and Burrows 1995). Using data presented by Catling and Burt (1994), Dickman (1996a) calculated that there was a negative correlation between the abundance of dingoes and feral cats in southern New South Wales. In contrast, Smith and Quin (1996) found that patterns of distribution suggested tolerance of cats by dingoes. The relationship between the two species is likely to be affected by extraneous factors. For example, interactions may be stronger in open habitats where it is difficult for cats to avoid dingoes (Pettigrew 1993; Dickman 1996a; Edwards *et al.* 2002). A similar dichotomy was reported in south-east Africa, where kleptoparasitism by spotted hyaenas (*Crocuta crocuta*) on African wild dogs (*Lycaon pictus*) was more frequent in open than in densely vegetated habitats (Creel 2001).

There is also evidence to suggest that small native predators in Australia may face competition from introduced species. For example, considerable niche overlap has been observed between insectivorous dasyurids in the genus *Antechinus* and the introduced black rat, which has similar dietary and habitat preferences to those of *Antechinus* (Cox 1997; Cox *et al.* 2000). Competitive interactions have been demonstrated between the insectivorous dunnart (*Sminthopsis griseoventer boullangerensis*) and the introduced
house mouse (*Mus domesticus*), with populations of the former species increasing up to fourfold when numbers of the mouse were reduced (Dickman 1992b).

### 1.4. Interactions among native carnivores

There is evidence of past and present competitive interactions among a range of Australian mammalian predators. This includes patterns of distribution, historic and prehistoric patterns of decline, morphological evidence, and ecological comparisons of sympatric native carnivores, as well as observations of direct interaction between species.

Dingoes are thought to have caused the pre-historic extinction on the Australian mainland of the thylacine and the Tasmanian devil (Burbidge and McKenzie 1989; Corbett 1995b; Smith and Quin 1996; Jones *et al.* 2003, but see also Johnson and Wroe 2003). Corbett (1995b) described two possible mechanisms by which dingoes may have facilitated the demise of thylacines and Tasmanian devils; the superior adaptability hypothesis and the disease hypothesis. The former states that the social structure of dingoes conferred on them a competitive advantage over their less socially cohesive rivals. Packs of predators should enjoy greater success than individuals in hunting large prey and protecting carcasses from competitors (e.g. Eaton 1979; Corbett 1995b). The disease hypothesis posits that dingoes introduced a pathogen (possibly toxoplasmosis) to Australia which decimated populations of thylacines and Tasmanian devils. However, there is no direct evidence implicating dingoes in the arrival of any new pathogens (Corbett 1995b), and such suggestions therefore remain speculative.

The extent to which the dingo now serves as an ecological analogue of the thylacine and Tasmanian devil is a matter of contention. As a scavenger of large carcasses, the devil is likely to have been replaced to a large extent by the dingo, which is a generalist predator and scavenger (Johnson and Wroe 2003). However, the former role of the thylacine is less clear as the species was extirpated before its ecology was studied. Jones and Stoddart (1998) concluded that the thylacine was most likely a predator of medium-sized vertebrates. However, Johnson and Wroe (2003) argue that the greater body size and wider gape of the thylacine relative to the dingo identify the species as a hunter of large prey.
Chapter 1: General introduction

The relationships between dingoes and the four Australian species of quolls are complex and poorly understood. The differences in body size between the taxa and the partially arboreal habits of the quolls are likely to provide a degree of niche separation. However, a number of studies provide evidence of interference competition (Fig. 1b) and/or intraguild predation between the two taxa. For example, in the northern tropics of Australia, dingoes were a major source of mortality for northern quolls, although carcasses were left uneaten (Oakwood 2000). These observations suggest extreme and asymmetrical interference competition. In addition, remains of spotted-tailed quolls have been identified in the scats of dingoes and domestic dogs (Brunner and Wallis 1986), perhaps indicating intraguild predation, although it is also possible that the remains were scavenged. As well as predation, Belcher (1995) suggested that spotted-tailed quolls may suffer kleptoparasitism from dingoes. Conversely, Edgar and Belcher (1995) stated that discarded dingo kills provide additional food for quolls. Quolls could also benefit from the presence of dingoes if dingoes suppress populations of cats or foxes (Fig. 1h). Similarly in Fennoscandia, arctic foxes apparently benefited from the presence of wolves by scavenging from their kills, and because wolves may have suppressed numbers of the red fox prior to their own decline (Hersteinsson et al. 1989). Further examples are presented by Mech (1970) and Hersteinsson and Macdonald (1982).

In studies of sympatric dasyurid carnivores in Tasmania, Jones (1997, 1998) and Jones and Barmuta (1998, 2000) found considerable evidence of interspecific competition. Tasmanian devils, spotted-tailed quolls and eastern quolls showed character displacement in the strength of the canine teeth and size of the temporalis muscle, suggesting that competition has occurred among these guild members over an evolutionary time scale (Jones 1997). That competition still occurs was evidenced by dietary overlap, inverse patterns of relative abundance, and interactions at carcasses, which indicated hierarchical dominance (Jones 1998; Jones and Barmuta 2000).

Dietary overlap among species was dependent on sex and age class. Thus, female and sub-adult Tasmanian devils showed significant overlap with male spotted-tailed quolls, and female spotted-tailed quolls overlapped with male eastern quolls. The degree of overlap was also affected by seasonal variations in the diets (Jones and Barmuta 1998). Where dietary overlap was greatest, habitats were partitioned. This caused different
prey to be encountered, thereby reducing competition; a situation termed niche complementarity (Jones and Barmuta 2000). For example, between adult male spotted-tailed quolls and adult devils, strong vertical partitioning of habitat was found, and the diet of adult male quolls contained a much higher proportion of arboreal prey than that of adult devils (Jones and Barmuta 2000).

Interactions between Tasmanian devils and spotted-tailed quolls at carcasses revealed that adult devils are dominant and can displace quolls from a carcass (Jones and Barmuta 2000). The vulnerability of spotted-tailed quolls to kleptoparasitism increases if they kill prey too large to consume quickly (Jones and Barmuta 2000). Unlike exploitation competition, interference of this kind can have a severe impact on the subordinate competitor even when live prey are abundant (Creel 2001).

Spotted-tailed quolls are the least abundant of the three sympatric carnivores in Tasmania, with densities five times lower than those of the Tasmanian devil (Jones and Barmuta 1998). These authors suggested that the low abundance of spotted-tailed quolls may have resulted from a combination of exploitation and interference competition, as well as possible predation by owls and devils. Hair of spotted-tailed quolls and eastern quolls was found in devil faeces, but it was not known whether this reflected intraguild predation or scavenging by devils (Jones and Barmuta 1998). An opportunity currently exists to evaluate this hypothesis of competition, as Tasmanian devil populations have crashed over large areas due to an outbreak of an unidentified disease (Jones 2003).

Among the smaller native predators, competitive interactions have been demonstrated among species of Antechinus, and between A. stuartii and the common dunnart (Sminthopsis murina). In a series of field experiments, Dickman (1986b,c, 1988) showed that controlled removal of the larger (50 g) dusky antechinus (A. swainsonii) triggered increases in juvenile survival and population size of the smaller (20 g) agile antechinus (A. agilis), as well as shifts in its arboreal activity, ground-level movements, habitat use and diet. These shifts allowed the agile antechinus to exploit resources formerly used by its larger congener and, in particular, to gain access to rich terrestrial microhabitats that contained its preferred invertebrate prey. In contrast, removals of A. agilis had limited effects on the demography and resource use of the dusky antechinus, suggesting that competition was strongly asymmetrical. In the case of A. stuartii (35 g)
and *S. murina* (20 g), Fox (1982) observed shifts in the habitats used by the smaller species in the presence of the larger, and later showed that the two species overlapped strongly in their diets (Fox and Archer 1984). In staged encounters between the two species in captivity, the dunnart has been shown to avoid the antechinus, and interference appears to be the mechanism by which competition occurs (Righetti *et al.* 2000). Few other examples of competition among small native predators have been described (Dickman 1984).

### 1.5. Interactions among introduced carnivores

There is abundant experimental and anecdotal evidence pointing towards competitive interactions between foxes and cats in Australia. This evidence comprises patterns in relative abundance, overlap in resource use, changes in the abundance, diet or habitat use of cats following removal of foxes, and occasional observations of possible intraguild predation.

Exploitation competition is likely to occur between foxes and cats, particularly when food is limited (Dickman 1996a). Both are opportunistic predators (Coman 1973; Jones and Coman 1981) and have overlapping diets (Triggs *et al.* 1984; Catling 1988; Molsher 1999; Molsher *et al.* 1999; Risbey *et al.* 1999). In addition, Molsher (1999) noted overlap in the home ranges and habitat use of cats and foxes, and concluded that there was a high potential for exploitation competition. Both Molsher (1999) and Risbey *et al.* (1999) suggested that foxes are the dominant competitor and limit populations of cats.

Patterns of distribution further suggest exclusion of cats by foxes (Smith and Quin 1996), and a number of studies have reported increased numbers of cats following the removal of foxes. For example, Short *et al.* (1995) reported a substantial increase in the abundance of cats after meat baits were used to remove foxes. Subsequently, Risbey *et al.* (2000) obtained spotlight counts of cats before and after fox removal, with concurrent monitoring in an untreated area. Spotlight counts of cats tripled in the baited area, but did not change in the unbaited area. Christensen and Burrows (1995) also reported an increase in cats of more than fourfold in the twelve months following fox and dingo removal in central Australia. However, cats also increased more than twofold in an unbaited area during the same period. Above-average rainfall probably contributed
to the increases (Christensen and Burrows 1995; Burrows et al. 2003). A similar result was obtained in North America by Engeman et al. (2000), who found increased bobcat activity when coyote numbers were reduced.

Molsher (1999) studied the diet, home range and habitat use of cats following fox removal. Cats consumed significantly more carrion following fox removal, suggesting that foxes had previously limited cats’ access to carcasses by interference. Habitat use by cats also changed as fox numbers were reduced, with cats making more frequent use of open habitats, which contained high densities of rabbits (Molsher 1999). Where foxes were left uncontrolled, the home ranges of cats and foxes overlapped. However, there was no overlap in the core areas of the home ranges of cats and foxes, and six of eight cats were trapped outside fox core areas (Molsher 1999). This suggests that cats avoided the areas most frequently used by foxes; a result that was supported by temporal analysis of radio telemetry data. Simultaneous radio-tracking of cats and foxes showed that cats kept significantly further from foxes than they did from each other. Foxes also tended to keep further from cats than from each other, but this difference was not significant. Anecdotal observations of interactions between the two species suggested that they tolerated each other at distances of 50 m or more. At closer distances, displacement or aggression occurred, the fox usually being dominant. These observations suggest that cats actively avoid foxes, but not vice versa (Molsher 1999).

These results are consistent with patterns found in the United States for coyotes and red foxes. Harrison et al. (1989) trapped nine foxes outside the territories of coyotes and a further two within a 2 km buffer around core coyote territory, but no foxes were trapped in coyote core areas. Radio telemetry revealed that fox home ranges were located in the spaces between coyote ranges, with some overlap, and only occasionally were foxes radio-located in core coyote ranges. Further, within areas of spatial overlap between coyotes and foxes, there was considerable temporal separation. Coyotes were the dominant predator, displacing foxes from areas of preferred habitat (Harrison et al. 1989). Exclusion of foxes by coyotes has also been documented by Voigt and Earle (1983), Sargeant et al. (1987) and Gosselink et al. (2003). Similarly, Johnson and Franklin (1994) found strong spatial separation in the home ranges of grey (Dusicyon griseus) and culpeo foxes (D. culpaeus) in southern Chile, attributing the observed pattern to interference competition by culpeo foxes.
Chapter 1: General introduction

Several studies have also revealed evidence of competitive killing or consumption of cats by foxes. For example, Molsher (1999) reported that three of eight cats whose cause of death could be determined had been killed by foxes. Due to decomposition, it could not be determined whether any of the carcasses had been partially consumed by foxes. However, during the same study, Molsher (1999) found no cat remains in 598 fox scats and stomachs. Conversely, Risbey et al. (1999) found a cat’s paw in the gut of a fox. The absence of insects or their larvae suggested that the cat had not been consumed as carrion, but had probably been subject to intraguild predation (Risbey et al. 1999). Cat remains have also been found in the diets of foxes by Coman (1973), Brunner et al. (1991) and Paltridge (2002).

1.6. Implications for prey populations

Clearly, the various interactions that occur between mammalian predators can have significant effects on their behaviour, distribution and abundance. In turn, these can lead to profound effects on prey populations. For example, Risbey et al. (2000) investigated the response of small mammal and reptile populations to different levels of cat and fox activity. Where both foxes and cats were controlled, small mammal captures doubled. Where foxes were controlled but cats were not, small mammal captures declined by 80% over five years, and where foxes and cats were left uncontrolled, no consistent trend was observed in small mammal captures (Risbey et al. 2000). These authors concluded that populations of small mammals were limited by cat predation, and the effect was stronger when foxes were removed. Cats may have increased in abundance after fox removal through mesopredator release (sensu Soulé et al. 1988) (Fig. 1g). Alternatively, the spotlight counts used to assess the predator populations may have reflected increased activity of cats rather than increased abundance. Whichever explanation is correct, the result was decimation of prey populations. Similarly, de Tores et al. (1998) found evidence of increased predation by cats on native prey, including the endangered brush-tailed bettong (Bettongia penicillata), following fox control. Comparable results have been reported in North America, where local extinctions of coyotes appear to have caused mesopredator release of foxes, skunks and domestic cats, leading to decline or local extinction of their prey (Estes 1996).
Dingoes may also have an indirect positive effect on populations of some native prey by limiting densities of cats and foxes. For example, Pettigrew (1993) suggested that the net effect of dingoes on populations of the endangered greater bilby (*Macrotis lagotis*) was positive because, although dingoes prey occasionally on the bilby, they suppress populations of cats and foxes more strongly. Further evidence in support of this notion comes from Smith and Quin (1996), who studied the historical decline of conilurine rodents in Australia. These authors found a significant negative correlation between the abundance of dingoes and the number of local conilurine extinctions. Further, conilurine species whose ranges fall largely inside the range of the dingo have contracted less than those in whose ranges dingoes are scarce, whereas contractions and local extinctions were positively correlated with the abundance of foxes. In areas with few foxes, cats were also strongly implicated in local conilurine declines (Smith and Quin 1996). However, loss or modification of habitat may also have contributed to conilurine declines. Similarly, Short and Smith (1994) observed that in areas of north-eastern New South Wales where endangered medium-sized mammals such as the parma wallaby (*Macropus parma*) persist, dingoes are often abundant and foxes scarce. Such observations point towards the dingo as a potential keystone species (Fig. 1g). However, controlled and replicated experiments involving the removal or introduction of dingoes are required to confirm this.

1.7. Implications for predator management

The evidence reviewed above shows that the effects of one predator are unlikely to operate in isolation, but will usually influence, and be influenced by, the suite of co-occurring predators in the system. Removal of one predatory species (such as occurs typically during pest management programmes) may lead directly or indirectly to increases in another, and the effects upon prey species may ultimately be negative. Thus, a number of authors have stressed the importance of integrated pest control, arguing that managing each pest species in isolation can be ineffective or even counter-productive. Risbey *et al.* (1999) speculated that control of cats could benefit native prey populations at Shark Bay, whereas fox control could lead to competitive release of cats and therefore increased predation on small mammals, birds and reptiles. Similar suggestions have been made by Martin *et al.* (1996) and Newsome *et al.* (1997).
Chapter 1: General introduction

Management strategies need to consider the complex inter-relationships between sympatric predators and their prey, and many Australian authors have recommended integrated pest control programmes in which foxes, cats and rabbits are controlled in a co-ordinated fashion (e.g. Newsome 1990; Lundie-Jenkins et al. 1993; Dickman 1996a; Smith and Quin 1996; Molsher 1999). The introduced rabbit is inextricably linked to the abundance of dingoes, cats and foxes, for which it is a staple prey (Catling 1988; Saunders et al. 1995; Corbett 1995b). Thus, although it is itself not a predator, the rabbit warrants inclusion in discussions of predator management, and will be considered here.

Rabbits often support populations of cats and foxes, thereby contributing to the suppression of native prey (Pech et al. 1992; 1995; Saunders et al. 1995; Dickman 1996b; Newsome et al. 1997). This situation constitutes apparent competition (sensu Holt 1977) (Fig. 1e) between rabbits and native herbivores. For example, rabbits are thought to have supported populations of foxes and cats in the Tanami Desert in central Australia, leading in turn to increased predation on the endangered rufous hare-wallaby (Lundie-Jenkins et al. 1993). Rabbits may also facilitate increases in cat populations following fox control (Risbey et al. 2000). By allowing predators to persist at high densities even after native prey have been driven to scarcity, rabbits can facilitate the extinction of native prey populations; a situation termed “hyperpredatory extinction” (Smith and Quin 1996).

Clearly, the rabbit is of great importance in sustaining predator populations in many parts of Australia. Not surprisingly then, there have been many instances where the control of rabbits has apparently contributed to reductions in cat and fox populations. For example, in South Australia’s Flinders Ranges, the introduction of rabbit calicivirus in 1995 decimated rabbit populations, and probably contributed to subsequent reductions in cat and fox numbers (Holden 1999; Holden and Mutze 2002). Conversely, crashes in rabbit populations (for example, due to drought) have led in some instances to intensified predation on alternative native prey (Newsome et al. 1989). Thus, a simple “bottom-up” approach, whereby the primary prey (rabbits) are controlled in order to reduce densities of predators, may lead to a period of increased predation on secondary prey (Johnson et al. 1989). Where threatened populations of native prey exist, such a situation could potentially cause local extinction. Once again, this emphasises the importance of an integrated approach in which rabbits and introduced
predators are controlled simultaneously. Such was the case in Western Australia, where rabbits were historically controlled by poison baiting. Foxes, which fed on the poisoned rabbit carcasses, were killed by secondary poisoning. In the early 1970s, the myxoma virus was introduced to control rabbits, and poison baiting ceased. Fox numbers soared and marsupial populations crashed (Newsome 1993). Similarly, poisoning of rabbits in New Zealand has caused secondary poisoning of introduced predators including stoats (Mustela erminea), ferrets (Mustela furo) and cats (Alterio 1996).

Control of rabbits is desirable not only to increase the effectiveness of predator control programmes. Rabbits are themselves a serious agricultural and ecological pest in Australia, causing damage to pasture and native flora, and possibly competing with livestock and native herbivores alike (Williams et al. 1995). Control of mammalian predators without concurrent rabbit control has the potential to cause explosions in rabbit densities (Banks et al. 1998; Banks 2000), with subsequent negative impacts on vegetation and wildlife. This is an example of a species-level trophic cascade, as defined by Polis (1999) and Polis et al. (2000) (Fig. 1d).

Where integrated pest control is not practicable, managers must consider whether it is appropriate to implement control programmes for individual pest species. This will be dependent on the suite of other species present, and the purpose of conducting the pest control. In some cases, it may be preferable to conduct no pest control, rather than embark on an expensive exercise that may fail to reduce (or may even increase) the damage caused by releasing other pest species from competition or predation (Johnson et al. 1989; Dickman 1996a; Courchamp et al. 1999).

As well as presenting some challenges for wildlife managers, interactions among predators may also provide useful alternative approaches to pest control. For example, introduction of dingoes (or cessation of dingo control) may provide indirect benefits to biodiversity through the suppression of cats, foxes and rabbits (Johnson et al. 1989; Newsome 1990; Lundie-Jenkins et al. 1993; Short and Smith 1994). However, such a strategy would require that pest species were at low densities to begin with; either naturally or through intervention (Newsome 1990).
Palomares et al. (1995) and Palomares and Caro (1999) also noted that conserving larger predators can aid in the control of smaller ones. For example, conserving the Spanish lynx (*Lynx pardinus*) should reduce the effects of the red fox and the Egyptian mongoose (*Herpestes ichneumon*) on prey populations. An analogous situation occurs in California, where coyotes exclude the introduced red fox from their home range, but do not exclude the endangered San Joaquin kit fox. Therefore coyotes may slow or prevent invasion of kit fox habitat by the red fox (Ralls and White 1995).

Although the focus of the present review is on mammalian carnivores, it should be noted that avian predators will also often be involved in competitive and predatory interactions with terrestrial ones. For example, the wedge-tailed eagle (*Aquila audax*) is a predator of medium-large vertebrates including rabbits and small macropods (Brooker and Ridpath 1980; Richards and Short 1998). As such, it is likely to compete for food with cursorial predators. *A. audax* also preys upon cats and foxes (Brooker and Ridpath 1980), thereby exerting intraguild predation. Conservation of large raptors may therefore be beneficial in suppressing rabbits, cats and foxes.

1.8. Conclusions

It is clear from the evidence reviewed here that interactions within the mammalian carnivore guild are common, widespread and can be profound in their effects. While the strength of competitive and other interactions between species may have abated in many situations due to coevolution, areas remain where recent invasions or introductions have occurred and new equilibria have not been reached. The comparatively recent arrival of one or more predator(s) provides an opportunity for ecologists to study the effects of competition without the confounding influence of coevolution. In Australia, two such recent arrivals, the red fox and the feral cat, occur widely and appear to interact with each other and with native carnivores in a variety of complex ways. Australia therefore harbours a wealth of opportunities to develop and test theories of species interactions (Blackwell and Linklater 2003).

A further generality which becomes apparent from this review is that interactions between carnivore species vary with context. Simple pairwise interactions may be strongly influenced by extraneous factors such as habitat type, with open habitats apparently affording greater opportunity for antagonism. Interactions are also affected
Chapter 1: General introduction

by the suite of co-occurring predators. It is intuitively appealing for the observer to search for simple patterns in the relationships between pairs of species. Although some generalisations can be drawn from this approach, these will rarely explain all observed interactions. For example, the exclusion of foxes by dingoes is apparent from observations of their broad-scale distribution, but exceptions to this rule are easily found on a local scale (e.g. Catling and Burt 1995). It is likely that the interaction is real, but that its strength depends on such factors as habitat type, degree of human interference and the distribution and abundance of prey species.

In conclusion, although there is abundant evidence of complex interactions among mammalian carnivores, in the vast majority of systems, these are poorly understood. The bulk of our knowledge is based on observational studies, or at best on experimental studies with minimal replication. There is an urgent need for clarification of these relationships through detailed examination and rigorous experimental testing. For the wildlife manager, it is essential that complex interactions are given greater consideration when planning predator control programmes. The need for integrated control, as opposed to treatment of each species in isolation, is imperative, and this must be driven by a greater understanding of the complex relationships between species.

1.9. Aims

The broad aim of this thesis is to study the ecology of the spotted-tailed quoll, and to investigate its interactions with other mammalian carnivores. More specifically, the objectives are to:

1) study the population dynamics and life history of spotted-tailed quolls in Marengo and Chaelundi State Forests, an apparent hot-spot of activity for the species in New South Wales,

2) describe the diet of quolls, and investigate any differences due to season, sex or size class of quolls,

3) study the home ranges, denning behaviour and microhabitat use of quolls, and

4) investigate evidence for interactions between sympatric quolls and eutherian carnivores, such as overlap in resource use or direct interference.
Chapter 1: General introduction

The thesis is concluded by a brief discussion of the implications of the findings for management and conservation of the spotted-tailed quoll, as well as some suggestions for future research.
Chapter 2: A summary of the biology of the spotted-tailed quoll, red fox, wild dog and feral cat in Australia

2.1. Physical characteristics

2.1.1. Spotted-tailed quoll

The spotted-tailed quoll (*Dasyurus maculatus maculatus*) is the largest of the four species of *Dasyurus* extant in Australia. Size varies considerably, and sexual dimorphism occurs, with males weighing almost twice as much as females. Mean mass at maturity is 3.5 kg for males and 1.8 kg for females, and maximum size is approximately 7 kg and 4 kg for each sex respectively (Jones *et al.* 2001). A smaller subspecies, *Dasyurus maculatus gracilis*, is currently recognised in northern Queensland (Edgar and Belcher 1995; Burnett 2001), although recent genetic analysis calls this distinction into question (Firestone *et al.* 1999).

Pelage ranges from ginger to dark brown above, marked with numerous white spots which, in contrast to other species of *Dasyurus*, extend onto the tail. The ventral fur is pale in colour (Edgar and Belcher 1995; Jones *et al.* 2001). The dentition of *D. maculatus* is well adapted to a carnivorous diet, with large canines and molars that are well suited for shearing meat. Strong jaw musculature, a long snout and a wide gape further enable the spotted-tailed quoll to kill large prey in relation to its own body size (Jones *et al.* 2001).

2.1.2. Red fox

The red fox (*Vulpes vulpes*) is a medium-sized canid, with males ranging in size from 4.7 - 8.3 kg, and females from 4.0 - 6.8 kg. The fur is reddish brown above, often with some black markings. The chin, chest and belly are white (Coman 1995). The tail is characteristically bushy, and often has a white tip. The red fox has a long snout, wide gape and typical canid dentition, adapted to a mainly carnivorous diet with long, sharp canines and scissor-like carnassials for cutting flesh (Macdonald 1987).

2.1.3. Dingo

The dingo (*Canis lupus dingo*) is a large canid, ranging in weight from 9.6 - 24.0 kg, with a mean of approximately 15 kg (Corbett 1995a,b; Fleming *et al.* 2001). Sexual
dimorphism occurs, with males being approximately 15% heavier than females on average (Corbett 1995b).

The majority of dingoes are ginger in colour with white feet and a white tail tip. However, black-and-tan individuals are also relatively common, particularly in southern Australia. These animals are predominantly black, with areas of pale brown on the cheeks, ears and legs. A very small percentage of dingoes may be uniformly black or white (Corbett 1995b). The dentition of dingoes is similar to that of the domestic dog (Canis lupus familiaris), although dingoes possess larger canines and carnassials (Corbett 1995b). Here and in most Australian studies, dingoes, feral dogs and their hybrids are collectively referred to as wild dogs (Fleming et al. 2001).

2.1.4. Feral cat
The feral cat (Felis catus) is a medium-sized predator, with males ranging in weight from 3.8 - 6.2 kg and females from 2.5 - 4.4 kg (Newsome 1995). Feral cats are anatomically identical to domestic cats, which belong to the same species. Rather than a phylogenetic distinction, feral cats differ from domestic ones in that they exist in free-living, self-perpetuating populations with little or no reliance on humans (Moodie 1995). The most common coat colours among feral cats are tabby, ginger and black, although other variations may also occur (Brothers et al. 1985; Newsome 1995).

The dentition of cats is typical of a carnivore, with long canines and scissor-like carnassials (Ewer 1973; Shively and Beaver 1985). Cats have a comparatively blunt face, lacking the elongated snout of the canids (Radinsky 1981; Van Valkenburgh and Ruff 1987). The sharp, retractable claws of cats provide an additional means of capturing and subduing prey (Ewer 1973).

2.2. Habitat and distribution
2.2.1. Spotted-tailed quoll
Dasyurus maculatus occurs in a variety of wooded habitats ranging from rainforest to open woodland, as well as coastal heath (Edgar and Belcher 1995). Although wet forest types have previously been regarded as the most favourable habitat (Jones et al. 2001), recent studies have recorded high densities of spotted-tailed quolls in dry sclerophyll forest and in dry cypress (Callitris) woodland (Claridge et al. 2005).
Chapter 2: Biology of the spotted-tailed quoll, red fox, wild dog and feral cat

*Dasyurus maculatus maculatus* is distributed from southern Queensland to Tasmania (Edgar and Belcher 1995; Jones *et al.* 2001). On mainland Australia, it occurs mainly on and to the east of the great dividing range, although records also exist from the western slopes and plains of New South Wales (NPWS 1999). The species formerly occurred throughout southern Victoria and in the south-east of South Australia, but has contracted from much of this area. The remaining distribution is now fragmented, largely due to land clearing. *D. maculatus gracilis* is restricted to north-eastern Queensland (Edgar and Belcher 1995). The spotted-tailed quoll is listed as endangered under the *Environment Protection and Biodiversity Conservation Act* (1999), and is threatened by destruction of habitat, as well as the possible impacts of introduced predators (Mansergh 1983b; Maxwell *et al.* 1996; Chapter 1). Inappropriate use of poison baits for pest control may also pose a threat to populations of the spotted-tailed quoll (Belcher 1998; Glen 2001; Glen and Dickman 2003a,b).

### 2.2.2. Red fox

Globally, the red fox is distributed throughout much of Europe, Asia, Africa and North America (Macdonald 1987). Within Australia, the species is found in all habitats, including desert (Mahon *et al.* 1998), alpine (Bubela *et al.* 1998), coastal (Meek and Saunders 2000), agricultural (Saunders *et al.* 1995) and urban areas (Marks and Short 1996). No habitat preference is apparent, provided there is sufficient food, refuge and, in arid areas, water (Coman 1995). The species is distributed across all of mainland Australia, with the exception of the northern tropics. Foxes were absent from Tasmania until a number of individuals were introduced in 2000. At the time of writing, it is not known whether the fox will successfully establish in Tasmania (N. Mooney pers. comm.).

### 2.2.3. Wild dog

Dingoes are distributed throughout mainland Australia, with the exception of areas in the south-east and south-west, from which they are excluded by dingo-proof fences (Corbett 1995a; Glen and Short 2000). Dingoes are also absent from Tasmania (Corbett 1995a). However, feral dogs often occur in the areas from which dingoes are absent, so that wild dogs collectively occur in all areas of Australia. As with the fox, wild dogs occur in all habitat types, including urban areas (Brunner *et al.* 1991), forested ranges
(Harden 1985; Barker et al. 1994), desert (Marsack and Campbell 1990), alpine (Newsome et al. 1997) and coastal plains (Thomson 1992a).

2.2.4. Feral cat

Feral cats are present throughout Australia in all habitats, and are able to survive without free drinking water, obtaining sufficient moisture from their prey (Newsome 1995). Although feral cats can be found in all areas, some habitat types support higher densities of cats than others. For example, Edwards et al. (2002) found higher densities of cats in mulga woodland than in open habitat, possibly because dense cover suits the ambush hunting style of cats, and provides cover from dingoes.

2.3. Diet

2.3.1. Spotted-tailed quoll

The diet of the spotted-tailed quoll consists primarily of vertebrate prey. Small macropods, possums, gliders, bandicoots, rabbits, birds, snakes, lizards and rodents are frequently killed, and larger animals such as feral pigs, cattle and large macropods may be consumed by scavenging (Belcher 1995; Edgar and Belcher 1995; Jones et al. 2001). Invertebrate prey are also commonly consumed, including insects and crayfish. Small amounts of plant matter found in scat samples are thought to be consumed incidentally (Jones et al. 2001). Diet varies depending on the sex and age of the quoll, with adult males consuming mostly medium-sized mammals, and females consuming more small mammals, birds and invertebrates (Jones and Barmuta 1998).

2.3.2. Red fox

The red fox is an opportunistic predator with a highly varied diet that includes mammals, birds, reptiles, amphibians, fish, invertebrates, vegetation and human refuse (Coman 1973; Brunner et al. 1991). Mammalian prey vary in size from rodents and antechinus (Triggs et al. 1984; Lunney et al. 1990) to juvenile eastern grey kangaroos (Banks et al. 2000), and larger animals may be consumed as carrion (Coman 1995; Saunders et al. 1995). Sheep are a major food source for foxes in rural areas (Saunders et al. 1995), and rabbits are a staple prey where available (Coman 1973; Bayly 1978; Catling 1988; Lunney et al. 1990; Risbey et al. 1999). Semi-arboreal species such as ringtail possums are important prey in some forested areas (Triggs et al. 1984). In areas where these preferred prey are scarce or absent, foxes may compensate by consuming...
other foods such as carrion (e.g. Lapidge and Henshall 2001) or invertebrates (e.g. Mahon 1999; Paltridge 2002). Seasonal variation occurs in the diet in some areas, where fruits and insects are more important in summer, and mammals in winter (Coman 1995).

2.3.3. Wild dog

Dingoes and feral dogs are principally predators of medium-to-large mammalian prey such as kangaroos, wallabies, rabbits, sheep and cattle (Corbett 1995b). However, prey may vary enormously in size, from insects to buffalo (Corbett 1995a). Diet varies considerably between regions in Australia. For example, in the forested coastal ranges of New South Wales, swamp wallabies and red-necked wallabies predominate (Robertshaw and Harden 1985; Lunney et al. 1990). In the Nullarbor region of southwestern Australia, rabbits and red kangaroos are most commonly consumed (Marsack and Campbell 1990). Cattle are frequently eaten as carrion in central Australia, particularly during drought, whereas dusky rats and magpie geese are the most common prey in the northern tropics (Corbett 1995b).

Small and medium-sized prey are usually killed by wild dogs hunting alone, whereas large prey are taken by packs of dogs hunting co-operatively. Reptiles, invertebrates and vegetation are all consumed infrequently in most areas (Corbett 1995b), although Paltridge (2002) reported that reptiles were of high importance in the diet of dingoes in the Tanami Desert.

2.3.4. Feral cat

Feral cats are opportunistic predators whose diet is generally dominated by mammals (Jones and Coman 1981; Triggs et al. 1984). However, depending on seasonal and local availability, other taxa such as reptiles, birds and invertebrates are also commonly consumed (Bayly 1978; Paltridge et al. 1997; Molsher et al. 1999; Paltridge 2002). Rabbits are of high importance in the diet where available (Catling 1988; Molsher et al. 1999). Cats living in close proximity to human settlement often consume large amounts of human refuse (Hutchings 2003).
2.4. Reproduction and life history

2.4.1. Spotted-tailed quoll

The spotted-tailed quoll is a seasonal breeder that mates in winter. The pouch, containing six teats, becomes well-developed and conspicuous during the breeding season (Fleay 1940). Mating occurs between April and July, followed by a gestation period of three weeks, after which a litter of up to six (mean = 5) young is born (Edgar and Belcher 1995; Jones et al. 2001). The newborn young are 7 mm in length and hairless (Fleay 1940). The young are continually attached to the teats until approximately seven weeks of age, at which time they are partially-furred and begin to open their eyes (Fleay 1940). From this age, the young are left in a maternal den while the mother forages. However, they are still dependent on the mother’s milk, and only begin to eat solid food brought by the mother when they reach 14 weeks. The young are weaned and fully independent by 18 weeks, at which time they are about 30% of adult size (Fleay 1940; Settle 1978). Sexual maturity is attained within one year, although full size is not reached until the age of two (Fleay 1940). D. maculatus is a relatively short-lived species, surviving 3 - 6 years in captivity (Jones et al. 2001). Individuals in the wild have been recorded to live for up to five years (Belcher 2000).

2.4.2. Red fox

Red foxes are monoestrous, seasonal breeders, producing litters of up to ten (mean = 4) cubs, usually in August or September. This follows a gestation period of around 7.5 weeks (McIntosh 1963; Saunders et al. 1995). The cubs are born inside a maternal den, and feed entirely on the mother’s milk for four weeks before making a gradual transition to solid food (Saunders et al. 1995).

Both sexes become sexually mature at 9 - 10 months of age, and females subsequently enter oestrus annually in early winter. Males are fertile from May to September, the testes usually being inactive at other times of the year (McIntosh 1963; Saunders et al. 1995).

2.4.3. Wild dog

Perhaps the most significant difference between the dingo and other wild dogs is that dingoes are monoestrous, whereas other dogs can breed twice within a year given sufficient resources (Corbett 1995b; Fleming et al. 2001). Following a gestation period
of 61 - 69 days, dingoes usually give birth during winter, except in the tropics, where births may occur year-round. Litters consist of 1 - 10 pups (mean = 5) (Fleming et al. 2001). Females reach sexual maturity at two years of age, and males at 1 - 3 years (Fleming et al. 2001).

Domestic dogs and hybrids may breed at any time of the year, and gestation is slightly shorter (58 - 65 days) than in the dingo (Corbett 1995b). Litter size varies depending on the breed of the dog, but the average is around five (Spira 1988 in Fleming et al. 2001).

2.4.4. Feral cat

*F. catus* may breed at any time of year, although kittens are most commonly born in spring or summer (Jones and Coman 1982a). Females can produce two or more litters in a single year when conditions are favourable (Algar and Smith 1998). The female has 5 pairs of teats, and litters usually consist of 4 - 6 young. Gestation is 56 - 63 days (Ulmer et al. 1971). Females become sexually mature at 10 - 12 months, and males at 12 - 14 months (Jones and Coman 1982a).

2.5. Behaviour

2.5.1. Spotted-tailed quoll

Spotted-tailed quolls are predominantly solitary and nocturnal, although some foraging also occurs during daylight hours (Edgar and Belcher 1995; Belcher 2000). Shelter during resting hours is provided by a den, which may be situated in a hollow tree or log, rock crevice, cave, subterranean burrow or artificial structure (Godsell et al. 1984; Watt 1993; Belcher 2000; Belcher and Darrant 2004; Körtner et al. 2004). Individual quolls use multiple dens throughout their home range (Watt 1993; Belcher and Darrant 2004).

Home ranges of *D. maculatus* are highly variable in size, and are much larger for males than for females. For example, Belcher and Darrant (2004) reported mean home range sizes of 1,755 ha for males and 495 ha for females. The home ranges of male spotted-tailed quolls overlap significantly more than those of females (Belcher and Darrant 2004; Körtner et al. 2004; Claridge et al. 2005), as is the case in western (Serena and Soderquist 1989) and northern quolls (Oakwood 2002).
Chapter 2: Biology of the spotted-tailed quoll, red fox, wild dog and feral cat

Spotted-tailed quolls are agile climbers and have been observed hunting in the forest canopy (Jones et al. 2001) and inside hollow trees (Belcher 2000). However, the species is only partially arboreal and spends the majority of the time at ground level or travelling along fallen logs (Jones et al. 2001).

Communication between spotted-tailed quolls is aided by the use of communal defecation sites or latrines, which have a function in scent marking (Belcher 1994; Kruuk and Jarman 1995; Claridge et al. 2004). The precise reasons for this behaviour are poorly understood, but an apparent peak in visitation to latrines during the breeding season (Belcher 1994) suggests that scent marking conveys information related to reproductive status. However, latrines are used throughout the year (Kruuk and Jarman 1995) and therefore cannot be associated with reproduction alone. Other possible functions include territorial marking or, more probably, signalling of social rank. Scent marking could also be used by an individual to advertise its claim on a particular resource patch (Kruuk and Jarman 1995).

Spotted-tailed quolls vocalise infrequently, but do possess a repertoire of sounds including a loud, high-pitched screech and a cat-like hiss signalling aggression (Fleay 1940), as well as a variety of sounds associated with mating and rearing of young (Settle 1978; Croft 1982).

2.5.2. Red fox

Red foxes are predominantly nocturnal (Saunders et al. 1993). Like D. maculatus, foxes shelter by day in dens, which are frequently in hollows at the base of trees, excavations among tree roots or under rock outcrops, in hollow logs or in the disused burrows of other species (Mcintosh 1963).

The home ranges of foxes are extremely variable in size, depending largely on the density and distribution of resources in the area (Saunders et al. 1995). For example, foxes in resource-rich urban environments may have home ranges of less than 0.5 km² (Saunders et al. 1993), whereas foxes in arctic tundra utilise home ranges as large as 34.2 km² (Jones and Theberge 1982). Home ranges recorded in Australia range from 0.6 km² in coastal habitat (Meek and Saunders 2000) to 24.5 km² in the arid zone (Mahon 1999).
Depending on availability of resources, foxes may be solitary or live in social groups consisting of several related females and one adult male. Within such groups, a clear social hierarchy is maintained and usually only the dominant vixen produces offspring. Subordinate vixens, who are either siblings or offspring of the dominant one, assist with the rearing of young. Subordinate vixens occasionally produce young of their own, but these are usually killed (Macdonald 1979a, 1987).

Communication among red foxes is mediated by a wide repertoire of vocal, olfactory and visual cues. Vocalisations include barking, whining and ‘gekkering’ to signify aggression, social dominance or territorial claim, as well as a range of sounds involved in the rearing of young (Macdonald 1987). Scent marking with urine and faeces is used to convey such information as reproductive status and ownership of territories. Scent marks are often associated with visually prominent features such as grass tussocks, rocks and fence posts (Macdonald 1979b, 1987).

2.5.3. Wild dog
Wild dogs are social animals and aggregate into packs. At any given time, packs may be loosely or closely associated, depending on the availability of different prey types. Large prey such as cattle are generally hunted by a pack of dogs working cooperatively, whereas smaller prey are usually hunted by single dogs. Pack structure is maintained while dogs are hunting solitarily, and communication over long distances is facilitated by howling and scent marking (Corbett 1995b).

Wild dog packs, which typically consist of a dominant breeding pair and their offspring, occupy a shared home range. Packs are territorial, and in many areas there is little overlap between the home ranges of neighbouring packs (Thomson 1992d). However, home ranges may overlap at important resources such as water holes. In these situations, temporal separation occurs between different packs (Corbett 1995b). Home ranges vary greatly in size, depending on the availability of resources. For example, Harden (1985) reported a mean home range of 27 km$^2$ in the forested ranges of eastern New South Wales, Thomson and Marsack (1992) reported means of 56 km$^2$ for females and 86 km$^2$ for males in the Fortescue area of Western Australia, and home ranges of up to 270 km$^2$ occur in central Australia (Eldridge et al. 2002).
Chapter 2: Biology of the spotted-tailed quoll, red fox, wild dog and feral cat

Scent marking with urine or faeces occurs on objects such as grass tussocks, shrubs, and rocks, often along roads and trails. These cues are used to mark territorial boundaries, and to communicate information such as social status or breeding condition (Corbett 1995b).

Wild dogs are crepuscular, having peaks of activity around dusk and dawn, but may be active at any time of the day (Harden 1985). Dens are typically located in enlarged burrows of other animals, in caves or hollow logs, or under piles of debris or spinifex grass (Thomson 1992b; Corbett 1995b; Fleming et al. 2001).

2.5.4. Feral cat

Feral cats are predominantly solitary (Brothers et al. 1985), although areas of high resource availability may support groups of cats living socially (Macdonald and Apps 1978; Macdonald 1983, Denny et al. 2002). In such situations, individuals may assist in rearing the young of others (Macdonald and Apps 1978).

Cats can be active at any time of day, and activity times may vary according to season (Fitzgerald and Turner 2000). However, Jones and Coman (1982b) reported a predominantly nocturnal pattern of activity, with peaks around sunrise and sunset.

Home ranges of feral cats are variable in size, depending on resource availability. For example, in semi-arid north-western Victoria, Jones and Coman (1982b) reported home ranges of 0.7 - 2.7 (mean 1.7) km$^2$ for female cats, and 3.3 - 9.9 (mean 6.2) km$^2$ for males. In central Australia, the mean home range of male feral cats was 22.1 km$^2$ (Edwards et al. 2001). Shelter sites include rabbit warrens, hollow logs and thickets of dense vegetation (Jones and Coman 1982b; Brothers et al. 1985).

Scent marking with urine is commonly employed by cats, particularly adult males (Macdonald and Apps 1978). The exact function of such scent marks is unclear, but may be related to territorial marking, communication of social status or signalling of breeding status. Feral cats also possess a repertoire of vocalisations related to aggression, mating and rearing of young (Bradshaw and Cameron-Beaumont 2000).
Chapter 3: Study area

3.1. Location, topography and land use

The study was conducted in Marengo and Chaelundi State Forests, approximately 40 km north-west of Dorrigo in north-eastern New South Wales (30° 07'S, 152° 23'E) (Fig. 3.1). The area encompassed by traps in the present study was approximately 35 km². However, this area is part of a large tract of contiguous forest which extends over 100 km from north to south, encompassing a number of state forests, national parks and nature reserves. The area is characterised by large granite outcrops, and elevation ranges from 900 - 1300 m.

![Map showing the location of the study site and the distribution of quoll traps. NP = National Park; NR = Nature Reserve.](image)

The predominant land use on the study site is selective harvesting of native timber. However, cattle are also grazed over much of the area. Directly adjacent to Marengo State Forest are Guy Fawkes River National Park and Mount Hyland Nature Reserve,
Chapter 3: Study Area

both of which are conservation reserves, and are not subject to grazing or timber harvesting.

3.2. Vegetation

Vegetation in the area is dominated by open, dry sclerophyll forest. The dominant canopy species are New England blackbutt (*Eucalyptus campanulata*), silvertop stringybark (*E. laevispina*), New England peppermint (*E. novaanglica*) and manna gum (*E. nobilis*). This vegetation type is characterized by a grassy understorey with numerous herbs and forbs. Dominant species include *Lomandra longifolia*, *Poa sieberiana*, *Pteridium esculentum*, *Imperata cylindrica* and *Themeda australis*. Occasional stands of grass trees (*Xanthorrhoea* spp.) and areas of heath also occur.

Gullies and creek lines in the area are typically covered by subtropical and temperate rainforest species such as black booyong (*Heritiera actinophyllum*), sassafras (*Doryphora sassafras*), yellow carabeen (*Sloanea woollsii*) and laurels (*Cryptocarya* spp.). Stands of brush box (*Lophostemon confertus*) occur on the edges of these rainforest areas and around the more open drainage features.

In the centre of the study site is a cleared area (approximately 4 km²) of private leasehold land on which cattle are grazed. This area, known as the Marengo Plain, is covered by a variety of grasses but is dominated by *Lomandra longifolia* and *Poa sieberiana*. Patches of blackberry (*Rubus* sp.) also occur. Several stands of eucalypts remain scattered within this clearing such as wattle-leaved peppermint (*Eucalyptus acaciiformis*) and snowgum (*E. pauciflora*). Little or no understorey exists within these remnants.

Two wildfires affected parts of the study area in January and October 2003. Both fires were of high intensity, leaving parts of the area devoid of vegetation cover at both the understorey and canopy levels.

3.3. Climate

The climate of the study area is characterised by warm summers (average temperature range 15 - 26° C) and cold winters (average temperature range 0 - 12° C). Mean annual rainfall is 1600 - 2000 mm (Bureau of Meteorology unpublished data).
3.4. **Vertebrate fauna**

Marengo and Chaelundi State Forests support a high diversity and abundance of vertebrate fauna. Rodents and small dasyurids are abundant (B. Tolhurst, P. D. Meek pers. comm.), as are medium-sized mammals such as red-necked pademelons (*Thylogale thetis*), wallabies (*Wallabia bicolor* and *Macropus rufogriseus*) and gliders (*Petaurus australis* and *Petauroides volans*) (A. Glen pers. obs.). In addition to the study species, a number of threatened taxa occur in the area, including the Hastings River mouse (*Pseudomys oralis*), rufous bettong (*Aepyprymnus rufescens*), long-nosed potoroo (*Potorous tridactylus*), parma wallaby (*Macropus parma*), powerful owl (*Ninox strenua*), glossy black-cockatoo (*Calyptorhynchus lathami*) and koala (*Phascolarctos cinereus*) (A. Glen pers. obs.), making the area one of high conservation significance.
Chapter 4: Abundance, life history and population dynamics of spotted-tailed quolls

4.1. Introduction

Much of what is known about the life history of spotted-tailed quolls comes from observations of captive animals (e.g. Fleay 1940; Settle 1978; Green and Scarborough 1990). From these, it is known that *D. maculatus* is a seasonal breeder, with mating occurring in autumn and winter, and young being born after three weeks’ gestation in mid-late winter. However, few studies have investigated the biology of spotted-tailed quoll populations in the wild (see below for exceptions). In consequence, there is scant information on the abundance and density of the species in different parts of its distribution, the timing of breeding across the species’ considerable latitudinal range, or the rates of turnover in wild populations. Such information is essential for the management and conservation of the species.

Previous studies on quolls in northern New South Wales have focused primarily on the potential impacts of poison baiting for wild canids (Körtner *et al.* 2003; Körtner and Watson in press), although useful demographic data were obtained in conjunction with these experiments (Körtner *et al.* 2004). Wild populations of *D. maculatus* have also been studied in southern New South Wales and Victoria (Belcher 2003; Dawson 2005), and in Tasmania (Jones and Barmuta 1998, 2000). Burnett (2001) investigated populations of the northern spotted-tailed quoll (*D. maculatus gracilis*) in northern Queensland. An improved understanding of the species’ population dynamics is a priority for the effective conservation management of *D. maculatus* (Mansergh and Belcher 1992; Maxwell *et al.* 1996).

The aim of this chapter is to provide a descriptive analysis of the quoll population in Marengo and Chaelundi State Forests. As well as presenting data on abundance, density and survival, I investigate the timing and rate of reproduction, and present morphometric data for comparison with those of quolls from other areas. Population models are employed to investigate patterns in the survival of quolls in the study area, and to explore some possible factors affecting survival, including the effects of wildfire.
4.2. Methods

4.2.1. Trapping and handling of quolls

Trapping for quolls was conducted monthly between January 2003 and October 2004, with the exception of February 2003. Quolls were captured in wire cage traps (30 x 30 x 60 cm, Mascot Wireworks, Sydney) baited with chicken wings. Captured animals were protected from rain and wind by black plastic sheeting which was wrapped around each trap, and were provided with coconut fibre for insulation. Up to 40 traps were set at intervals of 500 m near the sides of roads (Fig. 3.1), and were placed alongside logs, stumps or boulders. The precise location of each trap was recorded using a global positioning system (GPS) (Garmin etrex®).

Trapping was conducted for four nights each month, and traps were checked in the early hours of the morning. Captured animals were assessed visually to ensure that they were not injured or distressed before being left in the cage with additional chicken wings. This additional feeding was a condition of the research licence, and was intended to ensure that captured animals did not suffer energetic deprivation or malnutrition due to the interruption of their usual foraging. The animals were left to consume the additional food while the remainder of the traps were checked, and were then processed and released at the point of capture.

Quolls were transferred from the trap into a cloth bag without sedation before being weighed with a spring balance. The animals were sexed, and measurements were taken of short-pes (measured from the heel to the distal end of the middle pad on the hind foot, excluding the toes), tail-length, head length and scrotal width, where applicable. The nature and location of any injuries, distinguishing marks or external parasites were noted, and each animal was implanted with a subcutaneous microchip (Destron Fearing Corp., Saint Paul) between the shoulder blades for future identification. For females, breeding condition was determined by assessing the pouch. Females were classed as showing no breeding activity if the folds of the pouch were undeveloped and fully-furred, and the teats were not enlarged. The pouch was considered to be developed when the folds were well-defined and there was a loss of fur from the area, accompanied by a reddening of the skin. Lactation was inferred when the flesh below the teats was swollen and reddened, indicating vascularisation and the presence of milk. Elongated teats within a bare pouch area were taken to indicate that a female had
recently been suckling. Where pouch young were present, these were individually sexed and their stage of development assessed according to the degree of hair growth. However, three litters were not sexed because the mothers became stressed when the pouch was investigated, and the animals were therefore released. The sex ratio observed on the first encounter with each litter was taken to indicate sex ratio on attachment to the teats, immediately after birth. To assess pre-weaning mortality, pouch young were re-counted on each subsequent encounter. When young had left the pouch and were deposited in maternal dens, further mortality was inferred if the number of elongated teats in the mother’s pouch declined. Although this is probably a reliable method of assessing mortality of pouch young (Dickman 1986b), mortality could be underestimated if surviving young continue to use all teats.

4.2.2. Analysis of data

4.2.2.1. Demography

The size of the population was estimated for each trapping period as the number of animals known to be alive (KTBA, Krebs 1966), as a lack of recaptures during some trapping periods precluded the use of other population estimators. The maximum longevity of quolls could not be determined due to the relatively short duration of the study. The density of quolls in the area was estimated by dividing the mean number of quolls KTBA by the effective trapping area. The effective trapping area was defined as all uncleared land within a radius of 1,310 m of any trap. This radius was chosen because it was the mean value for longest recorded distance moved by individual female quolls at the site (Chapter 6). For estimation of trapping area, I assumed that all quolls within this area were trappable and, using the programme DENSITY 2.1 (Efford 2003), calculated the effective trapping area to be 55 km$^2$.

Estimates of survival between each consecutive trapping period were obtained by Cormack-Jolly-Seber (CJS) modelling using the programme MARK 4.1 (White and Burnham 1999). This method was not used to produce closed population estimates, and was therefore robust to the low numbers of recaptures during some trapping periods. The survival estimates were used to test three a priori hypotheses. Firstly, it was postulated that survival would be lower among males than females. The greater mobility of males (Chapter 6) might lead to some individuals dispersing from the study area, and may also lead to greater male mortality, for example due to being killed on roads.
Secondly, it was postulated that the energetic demands of the winter breeding season would lead to reduced survival during the months immediately after breeding. For males, the post-breeding period was defined as the three months following mating, i.e. August - October. For females, post-breeding was defined as the three months immediately after young reach independence, i.e. December - February. The third hypothesis was that survival would have been reduced by two wildfires that occurred during the study, either because quolls were killed directly by the fires, or because a subsequent lack of food or shelter caused mortality or emigration. Based on the findings of Dawson (2005), I also expected survival of male quolls to be affected more strongly by fire than that of females. In order to test these hypotheses, six models were constructed in MARK 4.1. These were named as follows: 1) null model, 2) gender, 3) post-breeding, 4) fire, 5) fire-gender, and 6) fire-gender II.

In the null model, survival was expected not to vary significantly over time or between sexes. The gender model tested the hypothesis that survival differed between male and female quolls. The post-breeding model tested the scenario that survival in both sexes was lower in the post-breeding period than at other times of year, while the fire model compared survival in the two periods immediately after each wildfire with that at other times. The fire-gender model tested the assumption that post-fire survival would differ between male and female quolls. Finally, the fire-gender II model tested the assumption that the recapture probabilities of males and females were affected differently by fire. All six models were run using the mark-recapture data to determine how well each model explained the observed patterns of survival. For each model, MARK calculated Akaike’s Information Criterion (AICc), which is a measure of parsimony. The lower the AICc, the more readily a given model fits the available data. Alternative models were compared by calculating the difference between their AICc values (known as ΔAICc), and their Akaike weight, which is a measure of the relative likelihood of each model. The best supported model was considered to be the one with the lowest ΔAICc and the highest Akaike weight (Buckland et al. 1997). To confirm that the data conformed to the assumptions of the models, a goodness-of-fit test was conducted using parametric bootstrapping with 100 simulations.
4.2.2.2. Comparative trap success
To investigate any seasonal effects on trap success, trapping results were divided into four seasons, based on the breeding biology of the species: mating (May - Jul), pouch young (Aug - Sep), maternal den (Oct - Nov) and non-breeding (Dec - Apr). Data from 2003 and 2004 were pooled, and the capture rates in each season were compared using a chi-square contingency test.

As well as seasonal differences in trap success, it was postulated that quolls may be attracted to a trap by the odour of their conspecifics. To determine whether traps that had recently caught a quoll had a higher success rate than those that had not, capture rates were compared between these two groups using a chi-square contingency test. To retain independence of data, repeated captures of an individual in the same trap were excluded. To determine whether the probability of recapture differed between male and female quolls, the frequency distribution of captures per individual of each sex was compared using a Kolmogorov-Smirnov two-sample test.

4.2.2.3. Morphometrics
Morphometric data were compared between male and female quolls to determine the extent of sexual dimorphism in the population. To minimise bias as a result of including juveniles in the analyses, quolls measuring less than 1,160 g (the mass of the smallest sexually mature female recorded) were excluded. It is likely that many animals above this size, particularly males, were not yet fully grown. However, there was no objective way to separate mature males from immature ones, as even the smallest male captured (740 g) had well developed testes. Although this approach is likely to underestimate the average size of mature quolls in the population, arbitrary decisions about the precise point of sexual maturity of males are avoided.

For each sex, the mean was calculated for body mass, head length, tail length and short-pes. For each of the linear dimensions, differences between males and females were investigated using Student’s t-tests. However, because variance in body mass was unequal between males and females, a t-test could not be used to compare these. Instead, a Mann-Whitney rank sum test was used to compare the medians. Relationships between body mass and each of the linear dimensions were investigated using the Pearson correlation coefficient (r). Scrotal width of males was tested for seasonal
differences using one-way ANOVA, following a Levine’s test to confirm homogeneity of variances.

4.3. Results

4.3.1. Demography

Sixty-one individual quolls were captured on 331 occasions during 2,545 trap nights, giving a trap success rate of 13%. There was a strong male bias in the captures, both in terms of number of individuals (41 male, 20 female) and raw number of captures (210 male, 121 female). However, the sex ratio of pouch young, based on 24 young from five litters, did not differ from parity (11 male, 13 female). The number of quolls KTBA varied between trapping sessions from 6 - 27 (mean = 16.8), but fluctuated around an approximate value of 20 for most of the study period (Fig. 4.1). The mean density of spotted-tailed quolls in the area was estimated at 0.3 km\(^{-2}\). The maximum time that any individual quoll was KTBA was 22 months (i.e. throughout the study period).

Fig. 4.1. Number of quolls known to be alive (KTBA) in each trapping period. Arrows indicate the occurrence of wildfires.

Some individuals of each sex became trap-prone, and were often captured in the same or neighbouring traps on three or four consecutive nights. The number of captures per individual did not differ between sexes ($D = 0.14$, $P = 0.94$). The maximum number of
captures for one individual was 26. Conversely, 20 individual quolls (13 male, 7 female) were captured on only one occasion. It is not known whether these individuals died, dispersed or simply avoided traps following their first capture.

Breeding was strongly seasonal, with the pouches of mature females becoming developed in May or June, and young being born in July or August each year. 64% of adult females bred each year, and mean litter size was 4.9 (range 3 - 6, s.d. = 1.4, n = 8). Precise dates of birth were not known as young appeared between trapping sessions but, based on size, were assumed to be 1 - 2 weeks prior to the first observation of each litter. Pouch young had begun to develop fur by around 6 - 8 weeks of age, and had left the pouch by 10 - 12 weeks. Mothers continued to lactate until young were around 16 - 18 weeks of age.

Pre-weaning mortality was estimated at 16.7% (n = 39 young). In two lactating females, the number of elongated teats declined during the period when young were left in the den, suggesting that one of the litter had died. However, one litter declined in size from six to five while still in the pouch, but all six teats remained elongated until weaning. Thus, it was assumed that shrunken teats provided only a minimal estimate of pre-weaning mortality.

A bootstrap goodness-of-fit test showed that the mark-recapture data met the assumptions of the CJS model, with only weak overdispersion (model deviance = 404.75, mean deviance of 100 bootstrap replicates = 405.73, P = 0.29, c = 1.037). As shown in Table 4.1, CJS modelling strongly supported the hypothesis that survival was reduced by wildfire, and furthermore, that the impact was strong for males but not for females. Weak support was obtained for the model proposing that survival declined in the post-breeding period. The null model and the gender model were also poorly supported, implying that survival was neither constant throughout the study period, nor different between male and female quolls overall. Finally, the fire x gender II model was poorly supported, indicating that the recapture probabilities of males and females did not differ in the post-fire periods.
Table 4.1. Cormack-Jolly-Seber (CJS) models describing survival and recapture of quolls at monthly intervals. Models are shown in descending order of parsimony. N = number of parameters; AICc = Akaike’s Information Criterion; ΔAICc = differences in AICc.

<table>
<thead>
<tr>
<th>Model Name</th>
<th>Survival (s)</th>
<th>Recapture (p)</th>
<th>N</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>Akaice Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fire-gender</td>
<td>Time</td>
<td>Time</td>
<td>23</td>
<td>554.5</td>
<td>0.0</td>
<td>0.8758</td>
</tr>
<tr>
<td>Fire</td>
<td>Time</td>
<td>Time</td>
<td>22</td>
<td>560.2</td>
<td>5.7</td>
<td>0.0519</td>
</tr>
<tr>
<td>Post-breeding</td>
<td>Time</td>
<td>Time</td>
<td>22</td>
<td>561.1</td>
<td>6.6</td>
<td>0.0323</td>
</tr>
<tr>
<td>Fire-gender II</td>
<td>Time</td>
<td>Fire + Gender</td>
<td>7</td>
<td>563.7</td>
<td>9.2</td>
<td>0.0089</td>
</tr>
<tr>
<td>Null</td>
<td>Time</td>
<td>Time</td>
<td>21</td>
<td>564.0</td>
<td>9.5</td>
<td>0.0077</td>
</tr>
<tr>
<td>Gender</td>
<td>Time</td>
<td>Time</td>
<td>22</td>
<td>564.2</td>
<td>9.7</td>
<td>0.0069</td>
</tr>
</tbody>
</table>

Mean monthly survival across both sexes throughout the study period was 88% (95% confidence interval = 83-91%). During the two post-fire periods, survival within the population as a whole was 77% (95% confidence interval = 66-85%), as opposed to 92% (95% confidence interval 86-95%) at other times. However, the fire-gender model revealed that this difference was due largely to reduced survival among male quolls, which declined in the post-fire periods to 62% (95% confidence interval = 46-76%). Survival among females in the post-fire periods was 90% (95% confidence interval = 73-97%). During the post-breeding period, survival within the population as a whole was 77% (95% confidence interval = 66-86%), as opposed to 92% (95% confidence interval = 86-95%) at other times.

4.3.2. Comparative trap success
Trap success varied markedly with season, ranging from 8.8% in the non-breeding period to 17.9% during the mating season (Table 4.2). A contingency test showed that this difference was significant ($\chi^2 = 29.69$, d.f. = 3, $P < 0.001$).

Traps that had recently captured a quoll appeared marginally more successful at catching new individuals than those that had not. Although the difference was not quite significant ($\chi^2 = 3.47$, $P = 0.063$); the power of the test was limited (0.45).
Chapter 4: Abundance, life history and population dynamics

Table 4.2. Capture rates of spotted-tailed quolls according to season.

<table>
<thead>
<tr>
<th>Season</th>
<th>Mating</th>
<th>Pouch young</th>
<th>Maternal den</th>
<th>Non-breeding</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of captures</td>
<td>132</td>
<td>81</td>
<td>44</td>
<td>74</td>
</tr>
<tr>
<td>No. of trap nights</td>
<td>739</td>
<td>667</td>
<td>299</td>
<td>840</td>
</tr>
<tr>
<td>Trap success (%)</td>
<td>17.9</td>
<td>12.1</td>
<td>14.7</td>
<td>8.8</td>
</tr>
</tbody>
</table>

4.3.3. Morphometrics

Male quolls ranged in body mass from 0.74 - 4.24 kg, and females from 0.92 - 2.44 kg. The mean physical dimensions of male and female quolls are summarised in Table 4.3. Males were significantly heavier than females (Mann-Whitney $U = 191.5$, $P < 0.001$). The ratio of sexual size dimorphism based on body mass was 1.65. Males were also significantly larger than females in terms of short-pes ($t = 8.47$, d.f. = 57, $P < 0.001$), head length, ($t = 3.17$, d.f. = 53, $P = 0.003$) and tail length ($t = 5.57$, d.f. = 57, $P < 0.001$). Body mass was strongly correlated with short-pes ($r = 0.57$, $P < 0.001$) and with tail length ($r = 0.45$, $P < 0.001$), but not with head length ($r = 0.18$, $P = 0.18$).

Table 4.3. Mean physical dimensions (± standard deviation) of male and female quolls in Marengo and Chaelundi State Forests. Maximum and minimum values for each dimension are given in parentheses.

<table>
<thead>
<tr>
<th>Dimension</th>
<th>Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body mass (kg)</td>
<td>2.8 ± 0.7 (1.4 - 4.2)</td>
<td>1.7 ± 0.3 (1.2 - 2.4)</td>
</tr>
<tr>
<td>Short-pes (mm)</td>
<td>62 ± 2 (53 - 68)</td>
<td>55 ± 2 (52 - 57)</td>
</tr>
<tr>
<td>Tail length (mm)</td>
<td>442 ± 31 (360 - 530)</td>
<td>386 ± 20 (335 - 450)</td>
</tr>
<tr>
<td>Head length (mm)</td>
<td>107 ± 10 (87 - 141)</td>
<td>93 ± 8 (79 - 112)</td>
</tr>
</tbody>
</table>

A seasonal pattern was evident in the scrotal widths of males (Fig. 4.2), which were larger during the mating season than at other times. One-way ANOVA showed that this seasonal variation was significant ($F = 14.48$, d.f. = 11, $P < 0.001$). A Levine’s test showed that the variances were homogeneous ($F = 0.889$, d.f. = 11, $P = 0.55$).
Fig. 4.2. Mean scrotal width (+ standard deviation) of male quolls for each month. Data for 2003 and 2004 were pooled.

4.3.4. Injuries and parasites

External parasites were prevalent in the population, with fleas recorded on 56% of individuals captured, ticks (including *Ixodes hirsti*; I. Vilcins pers. comm.) on 54%, and mites on 15%. Also prevalent was a skin condition which involved localised fur loss and inflammation. In severe cases, the affected areas developed pyodermas, or pus-filled bacterial infections. These symptoms were often centred around the hips, shoulders, rump, tail and face. Two particularly severe cases were recorded in which animals had lost approximately 50 - 60% of all body fur. Both of these individuals were adult males in extremely poor condition. Both had swollen, infected wounds on the face and were severely emaciated. One of these individuals died shortly afterwards. The carcass was recovered and subjected to *post mortem* examination by a veterinary surgeon (K. Riddle). The second animal was never re-encountered.

The *post mortem* examination revealed puncture-wounds and tearing around the mouth, consistent with a bite. Bruising of the temporo-mandibular joint had occurred, and an abscess had developed in the upper lip. These mouth injuries were likely to have prevented the animal from eating, resulting in severe emaciation. The animal’s body weight at time of death was 2.62 kg; a 38% reduction from his first recorded weight of
4.24 kg. Cysts infested with worms were also found on the outside of the stomach wall. Cause of death was cardio-pulmonary failure.

Relatively minor injuries were common among male quolls, although no injuries were recorded for captured females. Small puncture wounds consistent with bites were observed on the heads and necks of ten males (24%), and facial scars were also common. A further two males (5%) had a missing claw.

4.4. Discussion

4.4.1. Demography

Spotted-tailed quolls were highly abundant in Marengo and Chaelundi State Forests. The trap success rate of 13% in this study is the highest reported in any comparable study of the species spanning all seasons. The mean population density estimate of 0.3 km\(^{-2}\) is likely to be conservative, because the actual number of quolls present may have been higher than the number KTBA, which is by definition a minimal estimate of the population, and suffers from negative bias, particularly towards the beginning and end of a trapping study (Pocock et al., 2004).

The strong male bias in captures found here is consistent with previous studies (Settle 1978; Mansergh 1983a; Green and Scarborough 1990; Jones and Barmuta 1998; Belcher 2003; Körtner et al. 2004), but see also Burnett (2001). However, the sex ratio in the pouch was even, as has been reported in captive-bred populations (Settle 1978; Green and Scarborough 1990; C. Staples pers. comm.). Burnett (2001) also reported an even sex ratio among newborn *D. m. gracilis*.

Why were capture rates biased towards males, while the sex ratio in the pouch was even? The likely explanation is that males are not more abundant than females, but simply are more readily trapped (Settle 1978; Mansergh 1983a). Males have large, overlapping home ranges, while females have relatively small, virtually exclusive home ranges (Chapter 6). Thus, a trap placed at any given location might potentially be encountered by several males, but is unlikely to be within the home range of more than one or two females.
The estimated pre-weaning mortality of 16.7% in the present study is similar to that obtained by Burnett (2001) of 13%. However, both of these estimates were inferred from counts of elongated teats. This measure may underestimate mortality, as teats do not always return to normal size following the death of a juvenile (Merchant et al. 1984; this study). When Burnett (2001) estimated mortality of pouch young based on six litters of known fate, a much higher mortality rate of 27.2% was obtained. By monitoring litters while they were in the maternal den, Belcher (2003) reported a pre-weaning mortality rate of 50%.

The timing of breeding in northern New South Wales was consistent with that in other areas, including northern Queensland (Burnett 2001) and southern New South Wales and Victoria (Belcher 2003), suggesting little or no latitudinal trend. Winter breeding means that young reach independence in late spring or early summer when easily-caught prey such as insects and reptiles are generally most abundant (Belcher 1995, 2003).

CJS modelling strongly supported the a priori hypothesis that survival of quolls would decline following wildfire. More specifically, the modelling revealed that the sexes were affected differently, with males showing a marked reduction in survival, while that of females remained constant. This is consistent with the findings of Dawson (2005) following extensive wildfire in Kosciuszko National Park in southern New South Wales. Dawson (2005) concluded that males, being more mobile than females, emigrated from the burnt area, while females, which are territorial and show strong site fidelity (Firestone et al. 1999; Belcher and Darrant 2004; Chapter 6), were less likely to disperse. A similar explanation likely holds in the present study.

4.4.2. Comparative trap success

Capture rates of spotted-tailed quolls were markedly lower in the non-breeding period than at other times of year, and reached a peak in the mating season, probably reflecting the greater mobility of the animals (particularly males) at this time (Chapter 6). Belcher (2003) also noted this pattern in capture rates, and suggested that the breeding season is an ideal time to conduct trapping surveys for the species.
Although the capture success of traps that had recently caught a quoll was not significantly higher than that of other traps, the low power of this test means that the null result should be interpreted with caution. A strong trend was observed towards repeated captures in the same trap within a trapping period. This may be due to the attraction of quolls to the odour of their conspecifics. However, as the traps were not relocated between capture events, it is possible that this trend was an artefact of trap location. It is also possible that quoll odour may have persisted until later trapping periods, as traps were not washed. Given the importance of scent-marking in communication between quolls (Chapter 2), it seems likely that conspecific odour does increase trap success. An experimental comparison between randomly-placed clean traps and traps marked with quoll odour would serve to test this hypothesis.

4.4.3. Morphometrics

The mean body weights recorded in this study are similar to those recorded in other regions. For example, Jones and Barmuta (2000) reported mean body masses of 3.2 kg for male quolls and 1.7 kg for females in Tasmania. The sexual dimorphism ratio of 1.65 obtained in the present study falls within the extreme range for mammals, as defined by Ralls (1977). The strong correlations between body mass and short-pes, and body mass and tail length suggest that ratios of these measures might provide useful indices of body condition in quolls. The seasonal trend in scrotal width of quolls is consistent with other members of the Dasyuridae with promiscuous breeding (Woolley 1966; Dickman 1985; Dickman et al. 2001) and, possibly in some cases, sperm competition (Taggart et al. 1997, 2003). Genetic paternity testing of pouch young would serve to determine whether multiple paternity occurs within litters of *D. maculatus*, and therefore whether sperm competition is likely to occur.

4.4.4. Injuries and parasites

The prevalence of fleas and ticks in the quoll population in Marengo and Chaelundi State Forests is consistent with observations from other populations (e.g. Körtner et al. 2004). Skin lesions were also frequently observed by Körtner et al. (2004), who concluded that the likely cause was mites and/or flea larvae. Examination of quolls captured in the present study by a veterinary surgeon (B. Cowled pers. comm.) confirmed that the lesions were consistent with this explanation, although no larvae were identified.
Also commonly observed in the present study were superficial wounds around the heads and necks of male quolls. The majority of these were presumed to have resulted from fights with other male quolls. Aggression between males has been recorded in captivity (Fleay 1940; Settle 1978), and two males trapped together in the present study were observed fighting (Glen and Dickman 2005). In the case of the dead male subjected to post mortem examination, the physical wounds sustained in a fight appeared to have been the ultimate cause of death. It could not be determined, however, whether the bite to the jaw had been inflicted by a quoll or another predator such as a fox or dog.

4.4.5. Conclusions

Spotted-tailed quolls are highly abundant in Marengo and Chaelundi State Forests, and appear to occur at similarly high densities in other, restricted, parts of north-eastern New South Wales (Körtner et al. 2004). The results of population modelling show that the survival of male spotted-tailed quolls was strongly affected in the short term by wildfires, but recovered within a period of months. However, survival of females was unaffected, suggesting emigration of males, as opposed to actual mortality, as the cause. The rate of turnover in the population was relatively high, but overall abundance appeared stable throughout the study period.

The high abundance of quolls recorded in this study presumably results from numerous biotic and abiotic factors, including habitat quality, spatial extent of suitable habitat, and differences in the abundance of competitors and prey between this and other areas. These factors will be the subject of exploration in subsequent chapters.
Chapter 5: Diet of the spotted-tailed quoll

5.1. Introduction

The spotted-tailed quoll is principally a predator of mammals, but also feeds on insects, birds and reptiles (Belcher 1995; Jones 1997; Burnett 2001). The few studies that have investigated the diet of *D. maculatus* have been in southern New South Wales and Victoria (Belcher 1995, 2000; Dawson 2005), Tasmania (Jones 1997; Jones and Barmuta 1998) and northern Queensland (Burnett 2001). Between these northern and southern extremes is a vast latitudinal range from which little is known of the quoll’s diet. Differences in the biotic and abiotic environment across this wide range mean that the diet of quolls might be expected to differ between such broadly separated areas.

A clear understanding of the dietary resources needed by a species across its geographical range is essential to its conservation, particularly in the case of endangered species such as the spotted-tailed quoll. Clearly, animal populations may persist only where there are sufficient food resources to sustain them. Furthermore, quolls may require access to different food resources depending on their sex and size class, or depending on seasonal factors such as the energetic demands of breeding (e.g. Belcher 1995; Jones 1997; Burnett 2001). The aims of this chapter are to 1) investigate the diet of spotted-tailed quolls in north-eastern New South Wales, and compare the results to those from other locations, and 2) compare the diet between seasons, and between sexes and size classes of quolls. Finally, recommendations are made for management and conservation of the spotted-tailed quoll, and for future dietary studies.

5.2. Methods

5.2.1. Collection of scats

Scats were collected from trapped animals, from targeted searches of roads and known latrine sites, and opportunistically. Quoll scats were identified by appearance, size and odour. In some cases, the identification was confirmed during microscopic analysis by the presence of small numbers of grooming hairs. Scats which could not be identified with confidence were excluded from the analyses. For each scat, the date and location of collection were recorded.
Targeted searches were conducted along five road transects, each 1 km long, every month from January 2003 to February 2004. Because the transects were cleared monthly, scats collected were of known age and could be used for analysis of seasonal variation in diet. Similarly, scats from trapped animals and scats found opportunistically that were very fresh at the time of collection were included in seasonal comparisons. Scats were collected by these methods from January 2003 to October 2004.

When collecting from quoll latrine sites, care was taken not to remove all scats, or any that were very fresh and may therefore have contained important olfactory information. These precautions were to minimise disturbance to the quolls’ social organisation.

5.2.2. Scat analysis

All quoll scats were oven-dried at >80° C for 48 hours to kill any parasites (Brunner and Wallis 1986) before being broken apart using forceps. Prey remains were separated macroscopically into five categories: hair, feathers, scales, insects and other. The volume of each category was estimated by eye (to the nearest 5%) as a percentage of the total volume of the scat. Prey taxa were then identified by analysing hair, teeth, jaws, feathers or other identifiable structures, using keys and reference specimens. Hair analysis was conducted according to the methods of Brunner and Coman (1974). Hairs were identified to the lowest taxonomic level which could be achieved with confidence. Depending on the type of hair, and how much damage it had sustained in passing through the gut, some samples were able to be identified to species and some only to genus or family. In cases of uncertain identification, samples were sent to a specialist (B. Triggs) for confirmation.

Where more than one type of hair was visible in a sample, examples of all types were analysed to detect different prey within the one scat. Where all hair in a scat appeared to be from one animal, five random samples were taken and compared microscopically to reduce the possibility of overlooking different taxa within the one scat.

The diet was analysed both in terms of the relative volume attributed to each prey category, and in terms of their frequency of occurrence. Each of these measures has limitations. For example, the relative volumes in which prey categories occur in the scats may not reflect the volumes in which they were consumed. Indigestible material
such as hair, bone and insect exoskeleton will mostly pass through the digestive tract and appear in the scats, whereas soft material will be largely digested. Therefore, food items consisting largely of soft material will be under-represented in the scats in terms of volume (Macdonald 1987). Measuring frequency of occurrence is less affected by this problem. However, some prey may be consumed frequently, but in very small volumes. Describing diet by frequency alone would therefore over-estimate the importance of such food items (Corbett 1989). Thus, it is more useful to describe the diet in terms of both volume and frequency, while bearing in mind the limitations of each measure. Ideally, dietary analysis should also consider nutritional value, as foods consumed rarely or in small quantities may still be of high nutritional importance (Pinkas et al. 1971). However, such information was not available in this study. Although the word 'prey' is used here, some items in the diet (in particular, large mammals such as cattle) may have been consumed as carrion.

5.2.3. Data analysis
5.2.3.1. Dietary diversity
The diversity of prey in the scats was calculated using the Brillouin index. This is calculated according to the equation

\[
H = \frac{\ln N! - \sum \ln n_i!}{N}
\]

where \(H\) = diversity, \(N\) = total number of individual prey recorded, and \(n_i\) = number of individual prey items in the \(i\)th category (Brillouin 1956; Magurran 1988). Cumulative diversity \((H_k)\) was plotted against number of scats analysed \((k)\) in order to determine whether an asymptote had been reached, and therefore whether the diet of quolls in the study area had been adequately sampled. The order of the samples was randomised before plotting cumulative diversity to avoid any effect of seasonal succession of species in the diet.

5.2.3.2. Seasonal variation
The frequency of occurrence of different prey categories eaten was compared between seasons using the Fisher Exact Test. Seasonal differences in terms of volume were
investigated using non-metric multidimensional scaling (MDS) and global one-way analysis of similarities (ANOSIM), based on a Bray-Curtis similarity matrix (Clarke and Warwick 1994). These analyses are based on the rank order of similarities between samples, and do not make the assumption that data are normally distributed, or that variances or covariances are equal (Anderson and Underwood 1994). The results of MDS are presented as two-dimensional graphical representations of the relative similarities of each sample. The distance between points on the plot represents the magnitude of the difference between the two samples which they represent. Associated with each MDS analysis is a stress coefficient, which indicates how well the two-dimensional MDS corresponds to the rank-order distances contained in the similarity matrix. Stress values of less than 0.20 indicate strong correspondence, leading to an interpretable MDS pattern (Clarke 1993).

Data were not pooled between years as an initial test showed a significant difference in the diet between summer 2003 and summer 2004. Following the global test, differences between individual seasons were investigated by pairwise comparison. Where significant differences occurred between seasons, the prey categories most responsible for the difference were determined using similarity percentages (SIMPER) (Clarke and Warwick 1994).

5.2.3.3. Variation in diet due to sex and body-size

The frequency of occurrence of each prey category in the diet was compared between male and female quolls using the Fisher Exact Test. A similar comparison was made by dividing captured quolls into three size classes: small (<1,500 g), medium (1,500 - 2,499 g) and large (2,500 - 4,200 g). The frequency of occurrence of each prey category was subject to pairwise comparison between each size class using the Fisher Exact Test. The relative volumes of different prey categories for quolls of each sex and size class were compared using MDS and global one-way ANOSIM.

In order to compare the sizes of prey consumed by the different sexes and size classes of quolls, mammalian prey were classified into small (1 - 499 g), medium (500 - 6,999 g) and large (7 kg or more), based on the maximum weights for species listed in Menkhorst and Knight (2001). The frequency of occurrence of each prey size eaten was compared between sexes and size classes of quolls using the Fisher Exact Test.
5.3. Results

A total of 424 quoll scats was analysed, containing 37 prey taxa (Table 5.1). Mammals predominated in the diet, both in terms of the number of taxa detected, and in terms of frequency of occurrence. The most frequently consumed vertebrate species were the greater glider (Petauroides volans), rabbit (Oryctolagus cuniculus), bandicoots (Perameles nasuta and/or Isoodon macrourus), red-necked pademelon (Thylogale thetis), ringtail possum (Pseudocheirus peregrinus) and brushtail possum (Trichosurus vulpecula and/or T. caninus). Insects [in particular beetles (Coleoptera) and cicadas (Cicadidae)] were also frequently consumed. Birds and reptiles were found relatively infrequently in the diet.

In terms of volume, mammals again constituted the bulk of the scats (87.9%), followed by insects (8.3%), birds (1.5%), and reptiles (0.9%). Although very small amounts of vegetation were frequently found in scats, these invariably consisted of dry grass or leaf litter which had apparently been ingested incidentally with prey. No evidence was found of deliberate consumption of vegetation by quolls. The cumulative diversity ($H_k$) of the diet reached an asymptote at a sample size of approximately 90 scats (Fig. 5.1), indicating that a representative sample of the diet had been obtained.
**Chapter 5: Diet of the spotted-tailed quoll**

**Table 5.1.** Prey taxa identified in quoll scats from Marengo and Chaelundi State Forests. T = terrestrial, A = arboreal, F = flying, Aq = aquatic (after Lunney *et al.* 2000).

<table>
<thead>
<tr>
<th>Prey item</th>
<th>n</th>
<th>Frequency (%)</th>
<th>Habit</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small mammals</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Antechinus</em> spp.</td>
<td>24</td>
<td>5.7</td>
<td>T/A</td>
</tr>
<tr>
<td><em>Melomys</em> spp.</td>
<td>12</td>
<td>2.8</td>
<td>T/A</td>
</tr>
<tr>
<td><em>Rattus</em> spp.</td>
<td>4</td>
<td>0.9</td>
<td>T</td>
</tr>
<tr>
<td><em>Rattus lutreolus</em>, swamp rat</td>
<td>2</td>
<td>0.5</td>
<td>T</td>
</tr>
<tr>
<td><em>Rattus rattus</em>, black rat</td>
<td>1</td>
<td>0.2</td>
<td>T</td>
</tr>
<tr>
<td><em>Mus domesticus</em>, house mouse</td>
<td>2</td>
<td>0.5</td>
<td>T/A</td>
</tr>
<tr>
<td>Muridae, unidentified rodents</td>
<td>2</td>
<td>0.5</td>
<td>T/A</td>
</tr>
<tr>
<td>Chiroptera, unidentified bat</td>
<td>1</td>
<td>0.2</td>
<td>F</td>
</tr>
<tr>
<td>Medium-sized mammals</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Petauroidea volans</em>, greater glider</td>
<td>113</td>
<td>26.7</td>
<td>A</td>
</tr>
<tr>
<td><em>Oryctolagus cuniculus</em>, rabbit</td>
<td>55</td>
<td>13.0</td>
<td>T</td>
</tr>
<tr>
<td>Peramelidae, long-nosed and northern brown bandicoots</td>
<td>53</td>
<td>12.5</td>
<td>T</td>
</tr>
<tr>
<td><em>Thylagale thetis</em>, red-necked pademelon</td>
<td>51</td>
<td>12.0</td>
<td>T</td>
</tr>
<tr>
<td><em>Pseudocheirus peregrinus</em>, ring-tailed possum</td>
<td>38</td>
<td>9.0</td>
<td>T/A</td>
</tr>
<tr>
<td><em>Trichosurus</em> spp., common and mountain brushtail possums</td>
<td>26</td>
<td>6.1</td>
<td>T/A</td>
</tr>
<tr>
<td><em>Potorous tridactylus</em>, long-nosed potoroo</td>
<td>13</td>
<td>3.1</td>
<td>T</td>
</tr>
<tr>
<td><em>Tachyglossus aculeatus</em>, echidna</td>
<td>2</td>
<td>0.5</td>
<td>T</td>
</tr>
<tr>
<td><em>Macropus parma</em>, parma wallaby</td>
<td>1</td>
<td>0.2</td>
<td>T</td>
</tr>
<tr>
<td><em>Petaurus australis</em>, yellow-bellied glider</td>
<td>1</td>
<td>0.2</td>
<td>A</td>
</tr>
<tr>
<td><em>Dasyurus maculatus</em>, spotted-tailed quoll *</td>
<td>1</td>
<td>0.2</td>
<td>T/A</td>
</tr>
<tr>
<td>Large mammals</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Wallabia bicolor</em>, swamp wallaby</td>
<td>38</td>
<td>9.0</td>
<td>T</td>
</tr>
<tr>
<td><em>Bos taurus</em>, cattle</td>
<td>7</td>
<td>1.7</td>
<td>T</td>
</tr>
<tr>
<td><em>Macropus giganteus</em>, eastern grey kangaroo</td>
<td>4</td>
<td>0.9</td>
<td>T</td>
</tr>
<tr>
<td><em>Macropus</em> spp., eastern grey kangaroo or red-necked wallaby</td>
<td>4</td>
<td>0.9</td>
<td>T</td>
</tr>
<tr>
<td><em>Macropus rufogriseus</em>, red-necked wallaby</td>
<td>1</td>
<td>0.2</td>
<td>T</td>
</tr>
<tr>
<td><em>Sus scrofa</em>, pig</td>
<td>1</td>
<td>0.2</td>
<td>T</td>
</tr>
<tr>
<td>Reptiles</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reptilia, unidentified reptiles</td>
<td>24</td>
<td>5.7</td>
<td></td>
</tr>
<tr>
<td>Serpentia, unidentified snakes</td>
<td>2</td>
<td>0.5</td>
<td></td>
</tr>
<tr>
<td>Scincidae, unidentified skink</td>
<td>1</td>
<td>0.2</td>
<td></td>
</tr>
<tr>
<td>Agamidae, unidentified dragon</td>
<td>1</td>
<td>0.2</td>
<td></td>
</tr>
<tr>
<td>Birds</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aves, unidentified birds</td>
<td>30</td>
<td>7.1</td>
<td>F</td>
</tr>
<tr>
<td><em>Platycercus elegans</em>, crimson rosetta</td>
<td>1</td>
<td>0.2</td>
<td>F</td>
</tr>
<tr>
<td><em>Trichoglossus haematodus</em>, rainbow lorikeet</td>
<td>1</td>
<td>0.2</td>
<td>F</td>
</tr>
<tr>
<td>Insects</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Insecta, unidentified insects</td>
<td>50</td>
<td>16.6</td>
<td></td>
</tr>
<tr>
<td>Coleoptera, beetles</td>
<td>29</td>
<td>6.8</td>
<td>T/A</td>
</tr>
<tr>
<td>Cicadidae, cicadas</td>
<td>23</td>
<td>5.4</td>
<td>T/A</td>
</tr>
<tr>
<td>Hymenoptera, unidentified ant</td>
<td>1</td>
<td>0.2</td>
<td></td>
</tr>
<tr>
<td>Other</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Parastacidae, unidentified crayfish</td>
<td>5</td>
<td>1.2</td>
<td>Aq</td>
</tr>
<tr>
<td><em>Dasyurus maculatus</em>, quoll grooming hairs</td>
<td>60</td>
<td>14.2</td>
<td></td>
</tr>
</tbody>
</table>

* Sample contained a large volume of quoll hair, not consistent with grooming.
5.3.1. Seasonal variation in diet

The frequency of occurrence of different prey classes in the diet showed marked fluctuations over time (Fig. 5.2a). Insects were consumed significantly more frequently in summer than in winter during both years ($P < 0.001$), as were reptiles ($P < 0.001$ and $P = 0.008$ respectively). Mammals occurred significantly less frequently in summer than in winter 2004 ($P > 0.023$), but not in 2003. The frequency of occurrence of birds in the diet did not vary significantly with season.

The diet of quolls also showed marked seasonal variation in terms of the relative volumes of each prey category in the scats (Fig. 5.2b). MDS of the seasonal data yielded a stress coefficient of 0.02, indicating that the resulting ordination plot (Fig. 5.3) may be interpreted reliably. The plot shows considerable variation in the diet between seasons. A global one-way ANOSIM showed that this variation was significant (Global $R = 0.182$, $P = 0.001$). Pairwise comparison showed significant differences ($P < 0.05$) between a number of seasons. These are summarised in Table 5.2.
Fig. 5.2. Seasonal variation in the diet of quolls in terms of a) frequency of occurrence and b) volume (+ standard deviation) of respective prey classes.
Chapter 5: Diet of the spotted-tailed quoll

Fig. 5.3. MDS showing seasonal variation of quoll diet by volume for 2003 and 2004.

Table 5.2. Pairwise comparisons showing significant seasonal differences in the diet of quolls. All other seasonal comparisons did not reach significance at $P = 0.05$.

<table>
<thead>
<tr>
<th>Pairwise comparison</th>
<th>$R$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autumn 03 vs. Winter 03</td>
<td>0.184</td>
<td>0.001</td>
</tr>
<tr>
<td>Autumn 03 vs. Winter 04</td>
<td>0.036</td>
<td>0.01</td>
</tr>
<tr>
<td>Autumn 03 vs. Summer 03</td>
<td>0.217</td>
<td>0.001</td>
</tr>
<tr>
<td>Autumn 03 vs. Summer 04</td>
<td>0.34</td>
<td>0.001</td>
</tr>
<tr>
<td>Winter 03 vs. Spring 03</td>
<td>0.176</td>
<td>0.001</td>
</tr>
<tr>
<td>Winter 03 vs. Summer 03</td>
<td>0.655</td>
<td>0.001</td>
</tr>
<tr>
<td>Winter 03 vs. Summer 04</td>
<td>0.585</td>
<td>0.001</td>
</tr>
<tr>
<td>Winter 04 vs. Summer 03</td>
<td>0.404</td>
<td>0.001</td>
</tr>
<tr>
<td>Winter 04 vs. Summer 04</td>
<td>0.405</td>
<td>0.001</td>
</tr>
<tr>
<td>Spring 03 vs. Summer 03</td>
<td>0.118</td>
<td>0.03</td>
</tr>
<tr>
<td>Spring 03 vs. Summer 04</td>
<td>0.208</td>
<td>0.002</td>
</tr>
<tr>
<td>Summer 03 vs. Summer 04</td>
<td>0.073</td>
<td>0.02</td>
</tr>
</tbody>
</table>
In every pairwise comparison, SIMPER showed that differences in the volume of mammals were the greatest contributing factor to the overall differences observed, and that the volume of insects was the second greatest contributing factor.

5.3.2. Diets of male and female quolls

Scats collected from 16 female and 31 male quolls were included in this analysis (Table 5.3). No significant differences occurred between the diets of the two sexes in terms of frequency. A trend was apparent towards more frequent consumption of small mammals by females than by males, but the difference was not significant ($P = 0.239$).

Table 5.3. The diets of male ($n = 31$) and female ($n = 16$) spotted-tailed quolls in terms of frequency of occurrence (%) and volume (% mean ± standard deviation) of each prey category. $S =$ small, $M =$ medium, $L =$ large.

<table>
<thead>
<tr>
<th></th>
<th>Mammals</th>
<th>Birds</th>
<th>Reptiles</th>
<th>Insects</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$S$</td>
<td>$M$</td>
<td>$L$</td>
<td>Total</td>
</tr>
<tr>
<td>Frequency</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>12.9</td>
<td>83.9</td>
<td>16.1</td>
<td>90.3</td>
</tr>
<tr>
<td>Female</td>
<td>31.3</td>
<td>81.3</td>
<td>12.5</td>
<td>100</td>
</tr>
<tr>
<td>Volume</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>89 ± 5.4</td>
</tr>
<tr>
<td>Female</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>92.8 ± 12.2</td>
</tr>
</tbody>
</table>

In terms of relative volumes of each prey category, the diets of male and female quolls were broadly similar (Table 5.3). MDS produced an ordination plot with a stress value of 0.01 (Fig. 5.4). Although a small number of scats collected from males differed markedly from the remainder of the sample in containing a high proportion of insect remains, this plot suggests little difference between the diets of male and female quolls. This was confirmed by ANOSIM, which revealed no significant differences between the diets of the two sexes (Global $R = 0.09$, $P = 0.12$).
Chapter 5: Diet of the spotted-tailed quoll

Fig. 5.4. MDS comparison of the diets of male (M) \((n = 31)\) and female (F) \((n = 16)\) quolls by volume.

5.3.3. Effect of quoll body size on diet

Scats were analysed from eleven small, twenty medium-sized and fourteen large quolls (Table 5.4). Although there was a trend towards more frequent consumption of large prey by large quolls, no significant differences occurred between the diets of the different size classes.

Table 5.4. The diets of small \((< 1500 \text{ g})\) \((n = 11)\), medium \((1500 - 2499 \text{ g})\) \((n = 20)\) and large \((2500 - 4200 \text{ g})\) \((n = 14)\) spotted-tailed quolls in terms of frequency of occurrence (%) and volume (% mean ± standard deviation) of each prey category. S = small, M = medium, L = large.

<table>
<thead>
<tr>
<th>Quoll body mass (g)</th>
<th>Mammals</th>
<th>Birds</th>
<th>Reptiles</th>
<th>Insects</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>S</td>
<td>M</td>
<td>L</td>
<td>Total</td>
</tr>
<tr>
<td><strong>Frequency</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt; 1500</td>
<td>9.1</td>
<td>72.7</td>
<td>9.1</td>
<td>72.7</td>
</tr>
<tr>
<td>1500-2499</td>
<td>30</td>
<td>95</td>
<td>10-</td>
<td>100</td>
</tr>
<tr>
<td>2500-4200</td>
<td>14.3</td>
<td>71.4</td>
<td>21.4</td>
<td>92.9</td>
</tr>
<tr>
<td><strong>Volume</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt; 1500</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>78.6 ± 39.2</td>
</tr>
<tr>
<td>1500-2499</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>95.5 ± 11.2</td>
</tr>
<tr>
<td>2500-4200</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>91.1 ± 26.8</td>
</tr>
</tbody>
</table>
In terms of volume, a trend was apparent in which small quolls consumed less mammalian prey and more insects than medium-sized or large quolls (Table 5.4). However, MDS showed no clear differences between the size categories of quolls (Fig. 5.5). As in the case of Fig. 5.4, the three outlying points represent scats from male quolls that contained a high proportion of insect remains. ANOSIM also revealed no significant differences (Global R = 0.063, P = 0.10).

**Fig. 5.5.** MDS comparison of the diets of small (S), medium (M) and large (L) quolls by volume.

### 5.4. Discussion

The diet of spotted-tailed quolls in northern New South Wales is broadly similar to that reported from other regions of Australia, with mammals forming the bulk of the diet in volume and frequency of occurrence. Arboreal mammals, in particular the greater glider, were important components of the diet. Similarly, Belcher (2000) reported that greater gliders were the most important prey species in the diet of quolls from Badja and Tallaganda State Forests in southern New South Wales. Also important in the diet
Chapter 5: Diet of the spotted-tailed quoll

during the present study were rabbits, bandicoots and small macropods. This is consistent with the findings of Belcher (1995, 2000) Jones (1997), Jones and Barmuta (1998), Burnett (2001) and Dawson (2005), all of whom noted the importance of medium-sized mammals in the diet. Insects were frequently consumed by quolls in the present study, but constituted a relatively small proportion of the total volume. Finally, birds and reptiles constituted relatively small proportions of the diet, both in terms of volume and frequency. Not surprisingly, reptiles were absent from the diet during the colder months when they were presumably inactive.

5.4.1. Seasonal variation in the diet

As was reported by Belcher (1995), the importance of mammals in the diet was higher in winter than at other times of year. This presumably reflects the relative availability of prey, as other categories (particularly insects and reptiles) are probably difficult to find at this time. However, this period also coincides with the breeding season of quolls (Chapter 4). Both sexes of quoll might be expected to have greater energetic needs at this time; males due to their increased activity in search of mates (see Chapter 6), and females due to the metabolic demands of gestation and lactation. It is possible that these demands cause quolls to prey selectively on larger animals at this time, which might contribute to the predominance of mammals in the diet.

The importance of insects in the diet also fluctuated significantly, and to some extent appeared to offset the fluctuations in mammalian prey. Insects occurred more frequently, and in higher volumes, during the warmer months when mammals were consumed to a lesser extent. Some caution is warranted in interpreting this result however, as sampling occurred over less than two years. The results are therefore highly susceptible to fluctuations which may be unrelated to season. For example, an extremely high abundance of cicadas was observed at the study site during January 2004. Scats collected at this time showed a marked increase in the occurrence of insects, and some scats consisted entirely of insect remains. Thus, cicadas may be considered an opportune prey for quolls (sensu Newsome et al. 1983). This short period of intense predation on cicadas may have caused an inflated estimate of the importance of insects in the diet. Similarly, other seasonal differences summarised in Table 5.2 may be related to annual patterns, or may simply reflect stochastic variation.
5.4.2. Influence of sex and body size on diet

Jones (1997) found that the diet of spotted-tailed quolls in Tasmania varied significantly with body size, which was in turn a function of sex and age. Whereas the largest quolls (adult males) ate mainly medium-sized mammals, the smaller quolls (females and immature animals) consumed a higher proportion of small mammals. Although the present study showed no significant difference between the diets of male and female quolls, the power of these comparisons was limited by the small sample sizes. The observed trend towards greater consumption of small mammals by females than by males is consistent with the findings of Jones (1997).

Similarly, some trends were apparent in the diets of small, medium and large quolls. Small quolls appeared to eat more insects and less mammalian prey than larger quolls, both in terms of volume and frequency. In addition, large quolls consumed large mammalian prey more frequently than did small and medium-sized quolls. Although these results were not significant, the power of the comparisons was once again limited by small sample sizes.

A confounding factor in these comparisons is that the size of quolls is affected by their sex, with males being larger than females. Thus, any difference observed between males and females could be simply a result of size. Given sufficient data, this problem could be avoided by comparing the diets of males and females of comparable size.

5.4.3. Conclusions

This study provides the first insight into the diet of the spotted-tailed quoll in northern New South Wales, where the species remains locally abundant (Körtner et al. 2004; Chapter 4) despite declines across most of its former range (Maxwell et al. 1996). The apparent abundance of prey (in particular, medium-sized arboreal mammals) in Marengo and Chaelundi State Forests may partially explain the persistence of large numbers of quolls. North-eastern New South Wales is also of particular interest because the area supports an unusually high diversity of potential prey. The present study occurred within the ‘Macleay-McPherson’ overlap zone (Burbidge 1960), where the Torresian fauna of Australia’s tropical and sub-tropical north blends into the Bassian fauna of the temperate south-east (Crowther and Blacket 2003). This diversity of potential prey is reflected in the diet of quolls, with 37 taxa identified in the present
study compared to 23 in Victoria (Belcher 1995) and 27 in southern New South Wales (Dawson 2005).

The results obtained here indicate that the spotted-tailed quoll consumes a wide variety of prey. The extremely high proportion of mammalian prey in the diet identifies *D. maculatus* as a hypercarnivore, or meat specialist (*sensu* Van Valkenburgh 1999; Wroe *et al.* 2005). This term refers to specialised carnivores whose diets contain more than 70% flesh, as opposed to more generalist predators, whose diets may contain large proportions of invertebrates or plant material (Van Valkenburgh 1988, 1989, 1999; Holliday and Steppan 2004).

According to the definitions of Newsome *et al.* (1983), medium-sized mammals, in particular the greater glider, were the staple prey of quolls in Chaelundi and Marengo State Forests. Insects were a supplementary prey, fluctuating in importance in the diet. One family of insects, Cicadidae, represented an opportune prey, assuming great importance in the diet during a short period of high availability, but being absent at other times.

The importance of greater gliders in the diet suggests that land managers should seek to conserve gliders in order to sustain quoll populations. This will require maintenance of large numbers of hollow-bearing trees, which serve as denning sites for greater gliders. This is supported by the observations of Belcher (2000), who reported seeing quolls entering tree hollows on a number of occasions during daylight hours and preying upon gliders.

The marked fluctuations in diet recorded during the course of this study demonstrate the importance of sampling diet over an extended period. Samples collected over a brief period may provide biased estimates of the importance of particular prey, as seasonal differences would not be sampled. The analysis of seasonal data should ideally span a large number of years so that recurring seasonal patterns may be differentiated from other variations resulting from environmental stochasticity. Ideally, dietary studies should coincide with monitoring of prey abundance. Given the breadth of diet of the spotted-tailed quoll, simultaneous monitoring of all prey categories would be difficult. However, as noted above, the importance of medium-sized mammals in the diet has
now been confirmed over a broad geographical range. Future dietary studies should aim at least to monitor the relative abundance of these prey, using techniques such as spotlighting, or using indirect indices such as counts of warrens, tracks or other identifiable signs (e.g. Dawson 2005).
Chapter 6: Movement, home range and microhabitat use of quolls

6.1. Introduction

Despite a number of recent studies (Belcher and Darrant 2004, Körtner et al. 2004, Claridge et al. 2005), there remains a paucity of information about the habitat use and spatial organisation of the spotted-tailed quoll across its geographic range, which continues to impede appropriate conservation management. Jones et al. (2003) noted that habitat loss was a particular threat to the four Australian species of *Dasyurus*, and pinpointed loss of dens and other shelters, for example due to clearing, as a key problem. Habitat loss has also been identified as a threat to *D. maculatus* by Mansergh (1983b).

Western (*D. geoffroii*), northern (*D. hallucatus*) and spotted-tailed quolls all exhibit a pattern in which males occupy large home ranges, overlapping with a number of other males and females, while females occupy comparatively small, exclusive territories (Serena and Soderquist 1989; Oakwood 2002; Belcher and Darrant 2004; Körtner et al. 2004; Claridge et al. 2005). A similar pattern is also found in the carnivorous marsupial *Phascogale tapoatafa* (Soderquist 1995). The home range of an animal can be defined as ‘that area traversed by the individual in its normal activities of food gathering, mating and caring for young’ (Burt 1943). A territory, on the other hand, is often defined simply as ‘any defended area’ (Noble 1939). By these definitions, a home range need not necessarily be a territory, and a territory need not comprise all of an animal’s home range (Burt 1943).

Few reliable estimates of home range size in spotted-tailed quolls are available. Some estimates are based on very short periods of radio-tracking (e.g. Watt 1993), and are therefore likely to be underestimates. The most reliable published estimates are those of Belcher and Darrant (2004) and Claridge et al. (2005), who radio-tracked quolls in southern New South Wales and northern Victoria. Belcher and Darrant (2004) estimated the home ranges of male and female quolls using both the minimum convex polygon (MCP) and the kernel methods. Males had a mean home range of 1,755 ha (MCP) or 3,762 ha (kernel). Females had a mean home range of 496 ha (MCP) or 872 ha (kernel). Claridge et al. (2005) reported a mean home range size (MCP) of 992 ha for males, and 244 ha for females.
In addition to the above studies, which investigated movements at a relatively large scale, the behaviour of quolls has also been described at a finer spatial scale in Tasmania. Jones and Barmuta (2000) studied the use of different microhabitats by quolls, measuring the relative proportions of activity which occurred on the ground, in trees and in other microhabitat types. These authors found that spotted-tailed quolls were partly arboreal, and also made frequent use of fallen timber when moving. No study has documented the microhabitat use of quolls on the Australian mainland.

As summarised in Chapter 2, the types of dens used by spotted-tailed quolls have been described in a number of studies (Godsell et al. 1984; Watt 1993; Belcher 2000; Belcher and Darrant 2004; Körtnet et al. 2004). However, little detail has emerged regarding the number of dens used by individual quolls, or the proportional use of different den types.

The aim of this chapter is to investigate the home range, spatial organisation and microhabitat use of spotted-tailed quolls in north-eastern New South Wales. Such information is of both intrinsic and comparative interest, but also necessary for appropriate management to conserve the species and its habitat. More specific aims are to 1) describe the size and spatial organisation of quoll home ranges, 2) investigate the den use of quolls, and 3) quantify the relative use of different microhabitats by quolls, including the degree of arboreal activity. Two unplanned wildfires also occurred during the study, and thus provided an opportunity to evaluate how quolls respond to fire-induced damage to their habitat. I used a combination of methods to achieve these objectives, including live-trapping, radio telemetry and spool-and-line tracking.

6.2. Methods

Quolls were radio-tracked in Marengo State Forest, in the vicinity of the Marengo Plain (Chapter 3). The radio-collared animals were captured in cage traps, using the methods described in Chapter 4.

6.2.1. Radio-tracking

Radio collars were fitted to eight quolls (4 male, 4 female), and radio-tracking was conducted for six days each month between August 2003 and November 2004. Quolls were fitted with radio collars (Faunatech®, 150-151 MHz) weighing approximately 25
This was between 0.6% and 2.2% of the body weights of the individuals collared, and is therefore very unlikely to have interfered significantly with their activities or welfare. The collars were made of soft suede leather, and were designed to stretch gradually so that they would eventually become loose and fall off in the event that an animal could not be recaptured. Collared animals were repeatedly recaptured and assessed for any signs of injury or loss of condition caused by the tracking device.

The radio collars were equipped with a whip aerial and a 2-stage transmitter with a mortality function. If no movement occurred for a period of 12 hours, the pulse rate of the transmitter would double from 50 to 100 pulses per minute, indicating that the animal had either died or shed its collar.

Collared animals were located while active by triangulation using a hand-held 3-element Yagi antenna and a BIOTEL RX3 receiver. Where possible, a minimum of three bearings were taken by a single observer from separate locations using a sighting compass. The precise locations from which bearings were taken were recorded using a Global Positioning System (GPS) (Garmin etrex®). To minimise error due to movement of the animal, the three consecutive bearings were taken within as short a time as possible (usually <8 mins). Twenty-two locations (7.3%) were derived from only two bearings due to loss of the signal before a third bearing was recorded. Triangulation was conducted at various times between dusk and dawn.

During daylight while animals were at rest, they were approached on foot and their precise locations recorded by GPS. When dens or shelter sites were located, these were described qualitatively. Animals were occasionally active during the day (as judged from fluctuations in the strength of the radio signal). In these instances, locations were obtained by triangulation, as described above.

To minimise autocorrelation, individuals were usually located only twice in each 24-hour period; once at night and once in daylight. Where more than one location was recorded on the same night, these were usually separated by at least one hour. Although some degree of autocorrelation is virtually unavoidable (e.g. locations of Irish mountain hares (Lepus timidus) were autocorrelated even when sub-sampled at weekly intervals), data collected at infrequent intervals may greatly under-estimate home range sizes.
Thus, biologically meaningful data may be discarded if too great an emphasis is placed on statistical independence of radio-tracking data (Rooney et al. 1998).

As all but one of the radio-collared quolls were trap-prone individuals, and most triangulations were necessarily carried out from distances of several hundred metres, my presence is unlikely to have had any effect on the behaviour of the radio-collared animals. Similarly, Prosser et al. (2004) showed that the presence of an observer had no effect on the behaviour of habituated wood mice (Apodemus sylvaticus).

Location data derived from trapping were also included in analysis of home ranges. Where an animal was captured in the same trap more than once during a session, only the first capture was included in the analysis, as further captures at the same location could not be considered independent.

The accuracy of locations obtained by triangulation was tested by placing three transmitters at known locations (recorded by GPS) and then locating them by triangulation from distances of 150 - 800 m. The mean distance between the locations estimated by triangulation and the actual locations was calculated to give an estimate of error.

6.2.2. Spool-and-line tracking

Spools of nylon thread (Danfield Ltd.) were glued to the fur on the rumps of captured quolls, according to the methods of Jones and Barmuta (2000). The thread left a trail behind the animals as they moved, indicating their precise path. Thus, it was possible to record the movements of quolls on a very fine spatial scale. Spool-and-line tracking is widely used to monitor the movements of small and medium-sized animals (e.g. Miles et al. 1981; Cox et al. 2000), including spotted-tailed quolls (Jones and Barmuta 2000). Depending on the size of the individual quoll, tracking spools of 250, 500 or 750 m, weighing 6 - 18 g, were used. Quolls fitted with tracking spools were released at various times, ranging from late morning to shortly after dusk, thus sampling their diurnal and nocturnal behaviour. Although D. maculatus is predominantly nocturnal, I wished to sample diurnal behaviour because observations by Belcher (2000) suggest that quolls may climb trees during the day to take arboreal prey while they are inactive in nest hollows. Quolls were released during daylight hours on 13 occasions (yielding 174
location fixes), and at or after dusk on 12 occasions (yielding 332 location fixes). Quolls held until the following dusk were provided with additional food to avoid energetic or nutritional stress, and were placed in sheltered locations. Quolls were not held during winter, when there may have been a risk of hypothermia.

The first 40 m of each spool were discarded to avoid sampling the behaviour of fleeing animals immediately after release. Direct observations suggested that animals resumed ‘normal’ movement behaviour within this distance. Some individuals took shelter in hollow logs, resuming activity after an unknown period. Frequent changes of direction in many of the tracking spools suggested a ‘foraging’ movement pattern (sensu Jones and Barmuta 2000), which would not be consistent with a fleeing individual. In addition, 18 of the 25 tracking spools were fitted to individuals that had been captured previously, and were therefore accustomed to handling. It was therefore assumed that capture and handling had a minimal effect on the quolls’ subsequent behaviour. At intervals of 20 m along the tracking spool, I recorded microhabitat type (e.g. ground, log, rock, tree), and measured the height above ground using a tape measure. Vegetation cover was estimated visually (to the nearest 10%) within a one metre radius of the sampled location, at the elevation where the animal had been active.

6.2.3. Data analysis

Locations were derived from telemetry data by triangulation, using the programme Locate II (Nams 1990). Location data were mapped using the Animal Movement extension to Arc View (Hooge and Eichenlaub 1997). Home ranges were calculated for each individual quoll using both the 100% minimum convex polygon (MCP) method and the 95% and 50% kernel method. For consistency with Claridge et al. (2005), I considered that a home range was adequately defined when the last 5 location records increased the MCP area estimate by less than 5%. I estimated diurnal and nocturnal home ranges for each radio-collared quoll by calculating the 100% MCP area for all location data obtained during daylight and darkness respectively. Capture locations were included in the nocturnal range. I also compared diurnal and nocturnal activity in terms of microhabitat use. Chi-square contingency tests were used to investigate any differences in the proportion of activity in each microhabitat type, and Mann-Whitney rank sum tests to investigate any difference in mean vegetation cover or height above ground.
Chapter 6: Movement, home range and microhabitat use of quolls

Maximum distance travelled by individual quolls was estimated using location data derived from trapping and radio-tracking. For each individual that had been recorded in two or more locations, all recorded locations were mapped using the Arc View GIS programme, and the distance between the two most widely separated points was calculated. All error estimates presented are standard deviations (s.d.).

6.3. Results

6.3.1. Trapping

For the 41 individual male quolls trapped during the study (Chapter 4), capture locations revealed extensive spatial overlap. During trapping sessions of four nights, up to three males were captured in the same trap, and on one occasion in November 2003, two adult males were captured together (Glen and Dickman 2005). No male had a trapping history that did not indicate spatial overlap with at least one other male. In contrast, trapping records of females showed almost no spatial overlap between individuals. Two exceptions were recorded, both of which involved females captured on the perimeter of the known range of Female 1. One of these individuals was a sub-adult whose pouch was undeveloped, despite being trapped during the breeding season.

6.3.2. Radio-tracking

Radio collars remained in operation for between one week and six months before falling off or being removed. The mean number of independent locations recorded for each animal was 38 (range 13-74) (Table 6.1). The mean triangulation error in locating transmitters at pre-recorded locations was 67 m (range 29 - 110 m, s.d. = 41). Sufficient location data were obtained to adequately define the home range of two individual quolls, Male 1 (MCP 757 ha) and Female 1 (MCP 76 ha). Thus, the mean home range estimates produced here are likely to be underestimates. However, Female 1 had the smallest home range of all, suggesting that the estimates for the other three females may be regarded as indicative, if not definitive.

The mean home range estimate for female quolls was 133 ha, s.d. = 45 (100% MCP), or 188 ha, s.d. = 142 (95% kernel). Males had larger home ranges than females, with a mean area of 363 ha, s.d. = 299 (100% MCP), or 401 ha, s.d. = 247 (95% kernel). However, due to the small sample sizes obtained, it could not be determined whether
this difference was significant. Kernel estimates were generally slightly larger than MCP estimates because the kernel method includes a radius around each location record, including those on the edge of the recorded range.

Table 6.1. Home range estimates for radio-collared quolls in Marengo State Forest. (Number of location records in parentheses).

<table>
<thead>
<tr>
<th>Animal ID</th>
<th>100% MCP Area (ha)</th>
<th>95% Kernel Area (ha)</th>
<th>Diurnal Range (ha)</th>
<th>Nocturnal Range (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female 1*</td>
<td>76 (47)</td>
<td>99 (47)</td>
<td>21 (29)</td>
<td>54 (18)</td>
</tr>
<tr>
<td>Female 2</td>
<td>161 (32)</td>
<td>172 (32)</td>
<td>32 (13)</td>
<td>150 (19)</td>
</tr>
<tr>
<td>Female 3</td>
<td>175 (28)</td>
<td>394 (28)</td>
<td>123 (14)</td>
<td>141 (14)</td>
</tr>
<tr>
<td>Female 4</td>
<td>118 (44)</td>
<td>87 (44)</td>
<td>24 (15)</td>
<td>109 (29)</td>
</tr>
<tr>
<td>Male 1*</td>
<td>757 (74)</td>
<td>524 (74)</td>
<td>337 (19)</td>
<td>741 (55)</td>
</tr>
<tr>
<td>Male 2</td>
<td>108 (45)</td>
<td>143 (45)</td>
<td>62 (8)</td>
<td>61 (37)</td>
</tr>
<tr>
<td>Male 3</td>
<td>155 (13)</td>
<td>253 (13)</td>
<td>36 (3)</td>
<td>129 (10)</td>
</tr>
<tr>
<td>Male 4</td>
<td>433 (20)</td>
<td>684 (20)</td>
<td>- (1)</td>
<td>433 (19)</td>
</tr>
</tbody>
</table>

* = home range adequately defined.

No overlap was observed in the home ranges of radio-collared female quolls. However, males overlapped extensively with other quolls of both sexes (Fig. 6.1). Mean overlap of MCP home ranges in pairwise comparisons between males was 37.6% (range 6.2 - 87.8%, s.d. = 27.0). Maximum distance between recorded locations was significantly larger for males (mean = 2,367 m, s.d. = 1,285, n = 24) than for females (mean = 1,310 m, s.d. = 844, n = 9) (t = 2.278, P < 0.05), while the greatest distance between records for an individual male was 5,309 m, compared to 2,946 m for a female. The maximum distance for a male was recorded in June 2004. Immediately afterwards, the same individual moved a straight-line distance of 4,480 m in less than 48 hours.
Fig. 6.1. Estimated home ranges (100% MCP) of four male (narrow outline) and four female (bold outline) adult spotted-tailed quolls in Marengo State Forest.

Nocturnal ranges were larger for both males (mean 341 ha, s.d. = 312) and females (mean 114 ha, s.d. = 43) than were diurnal ranges (male mean 145 ha, s.d. = 167; female mean 50 ha, s.d. = 49) (Table 6.1; Fig. 6.2). Den sites were clustered within a relatively small portion of each individual’s home range.

Seven of the eight radio-collared quolls were recaptured repeatedly. Only one animal showed signs of skin abrasion from the collar, which was immediately removed. One animal was never recaptured, although the collar was later recovered, having stretched and fallen off. All but one of the radio-collared animals shed their collars before the end of the project. The final animal was recaptured, and the collar removed.
Fig. 6.2. Nocturnal (dark shading), diurnal (faint shading) and total (bold outline) MCP home ranges for each adult spotted-tailed quoll. Dots indicate den sites. (a) Female 1; (b) Female 2; (c) Female 3; (d) Female 4; (e) Male 1; (f) Male 2; (g) Male 3; (h) Male 4. Note difference in scale bars for the two sexes.
6.3.3. Den use

Thirty-eight quoll dens were located on 73 occasions by radio-tracking. Nineteen dens (50%) were in hollow logs, seven (18.4%) were in subterranean burrows (possibly dug by other species), five (13.2%) were in rock crevices, and four (10.5%) were in hollows in standing trees. Of the remaining three dens (7.9%), one was a shallow scrape in the ground at the base of a boulder, another was under a road bridge, and the third was in a pile of timber off-cuts and soil created by logging machinery. Quolls fled their dens before being located on two occasions (2.7%).

Individual quolls were located in up to nine different dens. Eleven dens (including three maternal dens) were known to be used on more than one occasion. No two quolls were observed to share a den at the same time. However, on one occasion, a female quoll was tracked to a den once occupied by a male who was known to have died. Six dens appeared to have secondary entrances, although it was not possible to confirm that these were connected to the den chamber. The chambers of three dens were visible from the outside, and these contained nesting material such as dried grass and ferns. One of these dens was used by a male quoll in December, suggesting that nesting material was unlikely to be a feature only of maternal dens.

6.3.4. Spool-and-line tracking

Twenty-five quolls (19 male, 6 female) were tracked over an accumulated distance of 10,140 m. Most activity was recorded on the ground (61%) or on top of fallen logs (37%). Very little arboreal activity was recorded (1%), and the maximum height to which a quoll climbed a tree was 3 m. A small proportion of activity was also recorded on top of raised rocks or boulders (1%) (Table 6.2). No quolls climbed standing trees in the 20 m intervals between the sampling points, indicating that the method used is unlikely to have underestimated arboreal activity. Mean height travelled above ground was 28 cm (range 0 - 300 cm, s.d. = 47.2), while mean vegetation cover traversed was 26% (range 0 - 100%, s.d. = 22).

Quolls were significantly more active on top of fallen logs during the day than at night ($\chi^2 = 4.02, P = 0.045$), although activity on the ground did not vary significantly ($\chi^2 = 2.33, P = 0.127$). The low numbers of observations in other microhabitat types
precluded statistical testing. No difference occurred between day and night in terms of mean height travelled above ground ($U = 44894$, $P = 0.615$), or mean vegetation cover that was used ($U = 43319$, $P = 0.613$).

Table 6.2. Microhabitats used by quolls fitted with tracking spools.

<table>
<thead>
<tr>
<th>Microhabitat</th>
<th>Ground</th>
<th>Log</th>
<th>Standing tree</th>
<th>Rock or boulder</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overall activity</td>
<td>61%</td>
<td>37%</td>
<td>1%</td>
<td>1%</td>
</tr>
<tr>
<td>Nocturnal</td>
<td>57%</td>
<td>43%</td>
<td>0%</td>
<td>0%</td>
</tr>
<tr>
<td>Diurnal</td>
<td>64%</td>
<td>34%</td>
<td>1%</td>
<td>1%</td>
</tr>
</tbody>
</table>

6.3.5. Effects of fire on habitat use

Two wildfires which affected parts of the study area in January and October 2003 provided some opportunistic observations of quolls' responses to fire in the short-to-medium term. Both fires were of high intensity, leaving extensive areas devoid of cover at the canopy and understorey levels (A. Glen pers. obs.). The presence of fresh scats in these areas indicated the continued presence of quolls less than three weeks after fire. In addition, three quolls were trapped in burnt areas within three weeks of the fires, and one quoll fitted with a tracking spool travelled approximately 600 m through freshly-burnt habitat which was devoid of understorey. Finally, one female quoll radio-collared after October 2003, but who was known to be resident in the area before the fire, was regularly located either active or resting in dens within the burnt area.

6.4. Discussion

6.4.1. Home ranges

Spotted-tailed quolls in Marengo State Forest exhibited similar spatial organisation to those in southern New South Wales and Victoria (Belcher and Darrant 2004; Claridge et al. 2005) in that females appeared to occupy exclusive territories, which were smaller than the home ranges of males. Only minimal overlap between females was apparent from trapping records, and one of the two recorded cases of overlap involved an immature animal. Overlap in home range has been reported between mature and sub-adult female $D. maculatus$, and is thought to occur between mothers and their immature offspring (Belcher and Darrant 2004; Claridge et al. 2005).
The home ranges of male quolls overlapped extensively with those of females, and of other males. This is consistent with a system in which the distribution of females is determined largely by the availability of patchy resources such as prey and den sites, and reinforced by interactions among the females themselves, while the distribution of males is driven principally by access to females (Trivers 1972; Emlen and Oring 1977; Clutton-Brock and Harvey 1978; Macdonald 1983; Oakwood 2002; Belcher and Darrant 2004). When females are widely spaced in exclusive territories, it is impossible for one male to guard, and maintain exclusive access to, a large number of mates. Thus, males must roam over wide areas in order to encounter several females, and cannot devote sufficient effort to exclude potential competitors (Clutton-Brock and Harvey 1978).

These results confirm that spotted-tailed quolls occupy large home ranges, and that small, isolated reserves are unlikely to support viable populations. As females appear to be territorial, persistence of a population is likely to require very large areas of suitable habitat, which can accommodate large numbers of non-overlapping female ranges. The home ranges of female quolls in Marengo appear to be much smaller than those in southern New South Wales and Victoria (Belcher and Darrant 2004; Claridge et al. 2005). This difference may contribute to the relatively high abundance of quolls recorded in north-eastern New South Wales (Körntner et al. 2004; Chapter 4).

The maximum distances between location records of individual quolls in this study were also consistent with previous results (Körntner et al. 2004; Claridge et al. 2005) in that males moved significantly further than females. The mean distances in this study were similar to those recorded by Körntner et al. (2004) of 2,686 m for males, and 1,506 m for females. I also found evidence for increased roaming in males during the breeding season, as would be expected as males seek to maximise their number of potential mates. The longest recorded distance between location records (5,309 m) was for a male who was captured during the mating season in June 2004 well outside the area where he had been previously recorded. Less than 48 hours later, he was recaptured in the area where he was more frequently encountered, having travelled a straight-line distance of 4,480 m.
Chapter 6: Movement, home range and microhabitat use of quolls

This study is the first to compare the diurnal and nocturnal home ranges of spotted-tailed quolls. With the exceptions of Female 3 and Male 2, quolls ranged over substantially larger areas at night than during the day. It is unlikely that this observation is simply an artefact of larger sample sizes obtained at night. For example, Female 1 had a nocturnal home range more than twice the size of her diurnal range, despite being located more times during the day than at night. Dens were not evenly distributed across the home ranges of each quoll, suggesting that the animals usually return to a core area at the end of each night’s activity. This pattern is unlikely to reflect the availability of possible den sites, as hollow logs were present throughout the study area (A. Glen pers. obs.). In this case, tracking methods that sample diurnal locations only (e.g. radio-tracking from a helicopter) may be biased towards this core area, thus underestimating home range. Future studies should aim to sample both the diurnal and nocturnal activity of quolls. Home range estimates in the present study may also have been biased towards relatively sedentary individuals, as most of the radio-collared animals were trap-prone. The fact that some males were trapped repeatedly while others were encountered only once suggests that some males may be more nomadic than others.

6.4.2. Den use

In contrast to the reports of Belcher and Darrant (2004) and Körtner et al. (2004), quolls in the present study rarely fled their dens when approached. Thus, I was able to obtain and describe a representative sample of the types of dens used by quolls. Hollow logs were most frequently used as dens, despite the high availability of rocky outcrops. Indeed, one female was tracked to two maternal dens, both of which were inside hollow logs within 80 - 150 m of rocky dens in which she had been previously recorded. This is in contrast to the observations of Belcher (2000) in Tallaganda State Forest in southern New South Wales, where quolls most frequently used rocky dens.

One female quoll was observed to move her litter from one maternal den to another, across a distance of approximately 300 m. Similarly, Belcher and Darrant (2004) reported that females may move their litters between several maternal dens before they are weaned. Other than maternal dens, quolls of both sexes usually changed dens each day, as was reported also by Körtner et al. (2004). The exception was one female who used the same den four times in six days shortly before the 2004 breeding season.
Chapter 6: Movement, home range and microhabitat use of quolls

However, after giving birth to a litter in the following month, she was not found in this den again.

6.4.3. Microhabitat use

The results of spool-and-line tracking revealed that, although the spotted-tailed quoll is a partly arboreal species (Settle 1978; Edgar and Belcher 1995; Jones et al. 2001), only 1% of the recorded activity of quolls in Marengo occurred in trees. A large portion of the recorded activity (39%) occurred above ground level, predominantly on fallen logs (37%). Quolls appeared to use these as pathways while travelling, and frequently jumped from one log to another, covering up to 140 m without returning to the ground. Presumably, logs provide a convenient route along which quolls can travel with little resistance from dense vegetation, and with minimal noise. Extensive use of logs by *D. maculatus* was also reported by Jones and Barmuta (2000) in Tasmania.

Despite the large proportion of time spent on logs, I rarely recorded activity high above the ground. Quolls climbed standing trees on three occasions, to a maximum height of 3 m. On these occasions, the quoll climbed the trunk of the tree and returned to the ground without venturing onto the branches. These results are in contrast to those of Jones and Barmuta (2000) in Tasmania, who recorded *D. maculatus* climbing to a height of 8.5 m, and Burnett (2001) who frequently observed northern spotted-tailed quolls (*D. m. gracilis*) foraging in the forest canopy, occasionally moving directly from one tree to another. These differences may be partly due to variation between the study sites in biotic factors such as habitat structure, prey availability and presence of ground-dwelling competitors (e.g. Tasmanian devils). It is also possible that the smaller size of the northern subspecies confers greater agility in the canopy.

The low proportion of arboreal activity was surprising, given that arboreal prey are important in the diet of quolls in this and other locations (Belcher 2000; Jones and Barmuta 2000; Chapter 5). However, as stated earlier, no quolls climbed standing trees in the 20 m intervals between the sampling points, indicating that my method is unlikely to have underestimated arboreal activity. Based on the observations of Belcher (2000), a possible explanation is that spotted-tailed quolls are able to detect
the nest hollows of greater gliders by smell, without leaving the ground. Trees may therefore be climbed infrequently unless a nest hollow has been detected. If this is the case, quolls may be able to encounter arboreal prey frequently without foraging extensively in trees.

Microhabitat use by quolls in Marengo differed little between day and night, with the exception that quolls made more extensive use of fallen timber during the day. It is possible that logs are used primarily as a convenient means of travel, and that quolls deviate from these convenient paths more frequently when foraging. Thus, the difference observed here may reflect a higher proportion of activity dedicated to foraging at night than during the day.

My results also indicate that *D. maculatus* can be resilient to disturbance of its habitat by fire. The extensive use by quolls of recently and intensely burnt areas indicates that they are not limited to areas covered by canopy or understorey. However, no quoll was observed to have its entire home range burnt. It is possible that a more widespread fire may have forced some individuals to alter their home ranges.

6.4.4. Conclusions

The results obtained here confirm that spotted-tailed quolls occupy extensive home ranges. This is common among predators whose diets, like that of the spotted-tailed quoll (Belcher 1995; Jones and Barmuta 1998; Belcher 2000; Burnett 2001; Chapter 5), consist predominantly of flesh (Gittleman and Harvey 1982). As a hypercarnivore (Wroe *et al.* 2005; Chapter 5), *D. maculatus* occupies home ranges much larger than might be expected for a generalised mammal of its size (Gittleman and Harvey 1982). Very large areas of habitat are likely to be required in order to support a viable population of spotted-tailed quolls, especially given the non-overlapping nature of female home ranges.

Also evident from this study is the value of fallen timber as a structural habitat component. Although *D. maculatus* may not be strictly dependent on fallen timber, hollow logs were the most commonly used dens in this study, and are also used extensively while travelling (Jones and Barmuta 2000; this study). This suggests that retention of fallen timber should be a management priority in areas where spotted-
tailed quolls occur. The forestry practice of leaving timber off-cuts *in situ* should continue (or be introduced where it is not current practice), and removal of fallen timber (e.g. for firewood) should be carefully limited.

Future study should aim to achieve more reliable estimates of the home ranges of spotted-tailed quolls. The results of this and previous studies (Belcher and Darrant 2004; Claridge *et al.* 2005) illustrate the difficulty of obtaining such estimates using radio telemetry, either from the ground or from aircraft. However, as emerging technology continues to improve, satellite telemetry (e.g. Ballard *et al.* 1998) may provide the opportunity to track the movements and habitat use of quolls with greater accuracy and reliability.
Chapter 7: Interactions between quolls and eutherian predators

7.1. Introduction

Competition between mammalian predators can have a strong influence on their abundance and distribution. For example, African wild dogs are more abundant in the absence than in the presence of lions and spotted hyaenas (Creel 2001; Creel et al. 2001), and red foxes have extirpated populations of arctic foxes through competitive interference (Hersteinsson et al. 1989; Kaikusalo and Angerbjörn 1995). Dominant competitors may exclude subordinate ones from some microhabitats (e.g. Dickman 1988), or even from larger areas, such that little or no spatial overlap occurs between the species (e.g. Harrison et al. 1989). If competition occurs between spotted-tailed quolls and eutherian predators, such inverse relationships might be expected between the abundances and distributions of these species. Catling and Burt (1997) found that the highest abundances of spotted-tailed quolls in north-eastern New South Wales occurred in areas (including Chaelundi State Forest) where foxes were absent. On a regional scale, D. maculatus was also more abundant and widespread in northern New South Wales than in the south, where foxes were ubiquitously abundant (Catling and Burt 1994, 1997). Despite their intuitive appeal, correlations such as these present only weak evidence for competition. As discussed in Chapter 1, more convincing evidence comes from patterns of overlapping resource use, while conclusive evidence may be obtained only from appropriate manipulative experiments (MacNally 1983; Wiens 1989).

Does the resource use of spotted-tailed quolls overlap with that of eutherian predators? Many authors have studied the diets of foxes and wild dogs, revealing that these species are opportunistic predators which, like D. maculatus (Chapter 5), consume mainly mammals, and supplement their diets with varying proportions of birds, reptiles, invertebrates and vegetation (e.g. Coman 1973; Bayly 1978; Triggs et al. 1984; Catling 1988; Lunney et al. 1990; Paltridge 2002; Saunders et al. 2004). Considerable overlap has been reported between the diets of foxes and wild dogs in sympatry (e.g. Triggs et al. 1984; Paltridge 2002; Mitchell and Banks 2005). However, no previous study has analysed and compared the diets of sympatric quolls, foxes and wild dogs. Given the broad similarity in the diets of these three species in separate locations, it is likely that considerable niche overlap occurs in areas where they coexist. A further advantage of studying the diets of sympatric predators is that instances of intraguild predation may be detected (e.g. Palomares and Caro 1999).
As well as having similar diets, species may occupy niches that overlap in terms of spatial resources (Johnson et al. 1996). For example, guild members may hunt or forage in similar habitats, or use similar structural features in which to shelter and raise young. In such cases, species may partition resources spatially or temporally (e.g. Harrison et al. 1989; Johnson and Franklin 1994). Existing knowledge of spotted-tailed quolls, foxes, feral cats and wild dogs indicates overlap in the habitat use of all of these species (e.g. Catling and Burt 1994, 1997). In addition, structures such as hollow logs and rock crevices may be used by some or all of these predators as den sites (McIntosh 1963; Thomson 1992b; Corbett 1995a; Belcher and Darrant 2004; Körtner et al. 2004; Chapter 6). By studying the movements and shelter use of sympatric species, the degree of spatial overlap may be ascertained. Further, by fitting animals with mortality-sensing radio collars, instances of intraguild predation or interspecific killing may be detected (e.g. Körtner et al. 2004). Given the difficulty of obtaining data on behaviour, resource use and abundance of mammalian predators in the field, useful insights may also be gained using modelling. Population viability analysis (PVA) in particular is of great value in predicting the likelihood of population persistence under various scenarios of competition or predation.

The aims of this chapter are to 1) quantify the degree of overlap in resource use between sympatric quolls, foxes, feral cats and wild dogs in the study area, 2) investigate possible mechanisms of niche partitioning (dietary or spatial), 3) examine any evidence for interspecific aggression or killing among mammalian carnivores in the study area, and 4) explore, via modelling, the possible effects of interspecific competition on the viability of quoll populations.

7.2. Methods

7.2.1. Dietary overlap

The diets of spotted-tailed quolls, foxes and wild dogs were investigated by scat analysis, using the methods described in Chapter 5. Scats of each species were identified based on shape, size and odour. Identification was confirmed in some cases by the detection of small numbers of grooming hairs during microscopic analysis. However, as scats can be misidentified even by an experienced observer (Davison et al. 2002), scats of uncertain origin were excluded from analyses. Scats of eutherian
predators were collected from the same road transects described in Chapter 5, which
were cleared on a monthly basis between January 2003 and February 2004. Opportunistic collection of scats continued until October 2004. For each predator
species, the cumulative diversity of prey items was plotted against sample size to
determine whether sufficient scats had been analysed to accurately describe the diet.
Diversity was calculated using the Brillouin index (Brillouin 1956). Dietary overlap
between each pair of species was calculated using Pianka’s index (Pianka 1973),
according to the equation

\[ O_{jk} = \frac{\sum p_{ij} p_{ik}}{\left( \sum p_{ij}^2 \sum p_{ik}^2 \right)^{0.5}} \]

where \( O \) is the index of overlap, \( j \) and \( k \) are the species being compared, and \( p_i \) is the
frequency of occurrence of the \( i \)th food type. The value of this index ranges from zero,
signifying no overlap, to one, signifying complete overlap (Pianka 1973). This index
was chosen to allow direct comparisons of the degree of overlap in similar studies of
carnivores elsewhere (e.g. Ray and Sunquist 2001; Jácomo et al. 2004). All prey taxa
were included in calculating the indices of overlap. Differences in the frequency
of occurrence of prey types between predators were investigated by pairwise comparison
using chi-square contingency tests with sequential Bonferroni adjustments (Quinn and
Keough 2002). For this purpose, food types were divided into seven categories: small
mammals (1 - 499 g), medium-sized mammals (500 - 6,999 g), large mammals (7 kg or
more), insects, birds, reptiles and vegetation. Mammalian prey were assigned to size
categories according to the maximum weights listed by Menkhorst and Knight (2001). I
also conducted interspecific comparisons of the frequency of occurrence of arboreal
mammals (which were the staple prey of quolls) and rabbits (which were the staple prey
of foxes and wild dogs). Differences in the diets of quolls, foxes and wild dogs in terms
of volume were investigated using non-metric multidimensional scaling (MDS) and
global one-way analysis of similarities (ANOSIM), based on a Bray-Curtis similarity
matrix (Clarke and Warwick 1994).

Additional data on the diets of foxes and wild dogs in the area (P. Fleming unpublished;
R. Harden and J. Robertshaw unpublished) were also analysed. The former analysed
scats of foxes and dogs collected from Chaelundi State Forest, Guy Fawkes River National Park and nearby areas between 1990 and 1993. The latter analysed dog scats collected in Chaelundi and Marengo State Forests, and adjacent areas of Guy Fawkes River National Park, in November 1984. Both sets of results were expressed as the frequency of occurrence of each prey category identified. Because of the length of time elapsed between the collection of these scats and the present study, data were not pooled, but the additional data were used for comparative purposes.

7.2.2. Spatial resource use

Use of space by predators was investigated by radio telemetry, trapping, collection of scats, and opportunist sightings of animals. The microhabitat use of quolls was also investigated by spool-and-line tracking (Chapter 6). Radio-tracking was conducted using the same methods and equipment for all species, as described in Chapter 6. Radio collars were fitted to eight quolls (4 male, 4 female), two feral cats (1 male, 1 female) and one male fox. Spatial overlap between individuals was assessed using minimum convex polygon (MCP) home ranges estimated for animals that were radio-collared over corresponding time periods. MCP and 95% kernel home range estimates were derived using the Animal Movement extension to ArcView (Hooge and Eichenlaub 1997).

Trapping for foxes and feral cats was conducted between October 2003 and October 2004 using Victor Soft Catch leg-hold traps. Each trap was secured by a 1 m length of chain to a post driven into the ground. Traps were set in shallow holes and covered with soil for concealment. A small square of foam rubber was placed under the trigger plate of each trap to prevent soil from lodging beneath the plate and blocking the trigger mechanism (Meek 1995). The foam also increased the force needed to trigger the trap, so that small non-target animals were less likely to be trapped. To minimise human odour, trapping equipment was washed with deodourising detergent and handled only with rubber gloves. A sheet of plastic was laid on the ground while setting the traps so that minimal human odour was left on the surrounding ground surface. Traps were baited with a range of olfactory lures including synthetic fermented egg, berry flavour essences and pieces of meat buried in a shallow scrape intended to mimic a fox cache. Traps were set on and around the Marengo Plain for a total of approximately 600 trap-nights.
Traps were checked in the early hours of each morning, and captured animals were initially restrained using a noose-pole. Animals were then covered by a cloth bag and restrained by hand before the noose was removed. The trapped limb was examined for any sign of injury before the animal was fitted with a radio collar, weighed using a spring balance, and then released. Capture locations were included in the analysis of home ranges. Quolls were captured in wire cage traps, as described in Chapter 4.

The locations of all predator scats were recorded at the time of collection using a global positioning system (GPS), as were the locations of any predator sightings. These data were used to confirm spatial overlap between species.

To determine whether vertical niche partitioning was likely to occur between quolls and eutherian predators, spool-and-line tracking was employed to investigate the degree of arboreal activity of quolls. This provides information that cannot easily be obtained from radio-tracking. Foxes, cats and wild dogs were not tracked in this way as they were captured too infrequently to provide meaningful results. However, these species (especially the canids) were assumed to be largely terrestrial. Thus, a high degree of arboreal activity in quolls could be taken to imply spatial separation.

### 7.2.3. Population viability analysis

A basic population model was constructed in the software package VORTEX 9.56 (Lacy et al. 2005), using ecological data collected from the present study, but complemented by information from previous studies of *D. maculatus* where necessary. The input values for each parameter of the basic model are shown in Table 7.1, along with the sources of information used. Following the recommendation of Lacy et al. (2005), environmental variation (EV) was set at zero in the basic model, as insufficient data were available to estimate EV. An initial population size of 27 was used as this was the maximum number of quolls known to be alive at any one time during the study (Chapter 4). A number of scenarios were then explored by varying the parameters of the basic model. Firstly, to model the effects of exploitation competition from eutherian predators, the model was run with incremental reductions in carrying capacity (K) ranging from K = 30 to K = 20.3. In this first scenario, exploitation was assumed to reduce food, shelter or other essential resources, but not to have additional effects that
could arise from interspecific intolerance or interference. Secondly, to model the effects of interspecific killing of juvenile quolls, the model was run with an increased level of juvenile mortality (50%). Thirdly, to test the potential effect of interspecific killing of adult quolls, adult mortality rates ranging from 60 - 80% were entered into the model. In these two latter scenarios, direct mortality was assumed to represent the effects of extreme interference competition or intraguild predation. As both kinds of interaction would result in quoll death, no attempt was made to model their effects separately. Finally, various combinations of reduced K and increased adult and juvenile mortality were simulated. For each scenario, the model was run for 100 iterations, and the population’s average probability of survival was plotted against time for a projected period of 100 years.

Table 7.1. Parameter inputs and information sources for the basic VORTEX population model for *Dasyurus maculatus*. (EV = environmental variation).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Scenario settings</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of years</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td>Number of iterations</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td>Extinction definition</td>
<td>Only 1 sex remains</td>
<td></td>
</tr>
<tr>
<td>Number of populations</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><strong>Species description</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inbreeding</td>
<td>n/a</td>
<td></td>
</tr>
<tr>
<td>Number of catastrophes</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td><strong>Reproductive system</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mating system</td>
<td>Polygynous</td>
<td>Assumed</td>
</tr>
<tr>
<td>Age at first offspring (years)</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>Max age of reproduction (years)</td>
<td>3</td>
<td>Assumed</td>
</tr>
<tr>
<td>Max progeny per year</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>Sex ratio in the pouch (% males)</td>
<td>50</td>
<td>1</td>
</tr>
<tr>
<td><strong>Reproductive rates</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% adult females breeding</td>
<td>64.3</td>
<td>1</td>
</tr>
<tr>
<td>EV in % breeding</td>
<td>0</td>
<td>Assumed</td>
</tr>
<tr>
<td>Offspring per female per year (mean ± s.d.)</td>
<td>4.9 ± 1.4</td>
<td>1</td>
</tr>
<tr>
<td><strong>Mortality rates</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Juvenile mortality (%)</td>
<td>40</td>
<td>1,3,4</td>
</tr>
<tr>
<td>Adult mortality (%)</td>
<td>60</td>
<td>1,2</td>
</tr>
<tr>
<td>SD in mortality due to EV</td>
<td>0</td>
<td>Assumed</td>
</tr>
<tr>
<td><strong>Mate monopolisation</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% males in breeding pool</td>
<td>50</td>
<td>Assumed</td>
</tr>
<tr>
<td><strong>Initial population size</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age distribution</td>
<td>Stable</td>
<td>Assumed</td>
</tr>
<tr>
<td>Initial population size</td>
<td>27</td>
<td>1</td>
</tr>
<tr>
<td><strong>Carrying capacity</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carrying capacity (K)</td>
<td>30</td>
<td>1</td>
</tr>
<tr>
<td>SD in K due to EV</td>
<td>0</td>
<td>Assumed</td>
</tr>
</tbody>
</table>

1This study, 2 Körner *et al.* (2004), 3 Burnett (2001), 4 Belcher (2003), 5 Fleay (1940).
Chapter 7: Interactions between quolls and eutherian predators

7.3. Results

7.3.1. Diet

Scat collection yielded 424 quoll scats, 207 fox, 73 dog, and 3 cat scats. The low number of cat scats, perhaps due to the species’ habit of burying its faeces, meant that no meaningful analysis of cat diet could be made. The dietary study was therefore restricted to quolls, foxes and wild dogs. Extensive overlap occurred between the diets of all three species.

The cumulative diversity (H_k) of foods in the diet of each species approached an asymptote at a sample size well below the number of scats analysed (Fig. 7.1), indicating that the sample sizes were adequate. Foxes had a more diverse diet than quolls, while dogs had the least diverse diet of the three species.

![Graph showing cumulative diversity (H_k) of fox, dog, and quoll diet with increasing sample size of scats (k).](image-url)
Chapter 7: Interactions between quolls and eutherian predators

A total of 43 food types was identified in the scats (Table 7.2). Twenty-two food types (51%) were common to the diets of all three predators. In terms of frequency of occurrence, medium-sized mammals dominated the diets of all three species; in particular rabbits, red-necked pademelons and bandicoots. Pairwise comparisons indicated extensive overlap in the diets of all three predators. Pianka’s index of dietary overlap between quolls and foxes was 0.712, while overlap between quolls and dogs was 0.657. Foxes and dogs showed the greatest similarity in diet, with a Pianka’s index of 0.943.

Despite the high degree of similarity (Fig. 7.2), there were significant differences between predators in the frequency of occurrence of some prey categories in the diets. Foxes consumed small mammals more often than did quolls ($\chi^2 = 44.6$, d.f. = 1, $P < 0.001$) or dogs ($\chi^2 = 10.3$, d.f. = 1, $P = 0.001$). Conversely, dogs consumed large mammals more often than did foxes ($\chi^2 = 34.0$, d.f. = 1, $P < 0.001$) or quolls ($\chi^2 = 20.9$, d.f. = 1, $P < 0.001$). Medium-sized mammals were consumed with similar frequency by all three predators. Insects were consumed more often by quolls than by foxes ($\chi^2 = 9.1$, d.f. = 1, $P = 0.003$) or dogs ($\chi^2 = 12.2$, d.f. = 1, $P < 0.001$). Foxes consumed birds more often than did quolls ($\chi^2 = 15.9$, d.f. = 1, $P < 0.001$). Both wild dogs ($\chi^2 = 49.2$, d.f. = 1, $P < 0.001$) and foxes ($\chi^2 = 42.5$, d.f. = 1, $P < 0.001$) consumed vegetation more often than did quolls.

Differences also occurred in terms of the most commonly eaten prey. Arboreal mammals were eaten more frequently by quolls than by foxes ($\chi^2 = 17.4$, d.f. = 1, $P < 0.001$) or wild dogs ($\chi^2 = 16.6$, d.f. = 1, $P < 0.001$). Conversely, rabbits were consumed more often by foxes ($\chi^2 = 63.6$, d.f. = 1, $P < 0.001$) and dogs ($\chi^2 = 47.4$, d.f. = 1, $P < 0.001$) than by quolls.
Chapter 7: Interactions between quolls and eutherian predators

Table 7.2. Frequency of occurrence (%) of prey taxa in the diets of spotted-tailed quolls (n = 424), foxes (n = 207) and wild dogs (n = 73) in Marengo and Chaelundi State Forests.

<table>
<thead>
<tr>
<th>Prey item</th>
<th>Quoll</th>
<th>Fox</th>
<th>Dog</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Small mammals</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Antechinus</em> spp.</td>
<td>5.7</td>
<td>9.7</td>
<td>2.7</td>
</tr>
<tr>
<td><em>Antechinus swainsonii</em>, dusky antechinus</td>
<td>0</td>
<td>1.0</td>
<td>0</td>
</tr>
<tr>
<td><em>Melomys</em> spp., grassland and fawn-footed melomys</td>
<td>2.8</td>
<td>9.7</td>
<td>6.8</td>
</tr>
<tr>
<td><em>Rattus</em> spp.</td>
<td>0.9</td>
<td>2.9</td>
<td>2.7</td>
</tr>
<tr>
<td><em>Rattus lutreolus</em>, swamp rat</td>
<td>0.5</td>
<td>2.4</td>
<td>0</td>
</tr>
<tr>
<td><em>Rattus rattus</em>, black rat</td>
<td>0.2</td>
<td>0.5</td>
<td>0</td>
</tr>
<tr>
<td><em>Rattus fuscipes</em>, bush rat</td>
<td>0</td>
<td>2.9</td>
<td>0</td>
</tr>
<tr>
<td><em>Mus domesticus</em>, house mouse</td>
<td>0.5</td>
<td>1.4</td>
<td>0</td>
</tr>
<tr>
<td>Muridae, unidentified rodents</td>
<td>0.5</td>
<td>2.4</td>
<td>1.4</td>
</tr>
<tr>
<td>Chiroptera, unidentified bat</td>
<td>0.2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Petaurus breviceps</em>, sugar glider</td>
<td>0</td>
<td>0.5</td>
<td>0</td>
</tr>
<tr>
<td><strong>Medium-sized mammals</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Petauroides volans</em>, greater glider</td>
<td>26.7</td>
<td>3.4</td>
<td>1.4</td>
</tr>
<tr>
<td><em>Oryctolagus cuniculus</em>, rabbit</td>
<td>13.0</td>
<td>41.0</td>
<td>46.6</td>
</tr>
<tr>
<td>Peramelidae, long-nosed and northern brown bandicoots</td>
<td>12.5</td>
<td>7.7</td>
<td>5.5</td>
</tr>
<tr>
<td><em>Thylogale thetis</em>, red-necked pademelon</td>
<td>12.0</td>
<td>12.0</td>
<td>16.4</td>
</tr>
<tr>
<td><em>Pseudocheirus peregrinus</em>, ring-tailed possum</td>
<td>9.0</td>
<td>3.4</td>
<td>1.4</td>
</tr>
<tr>
<td><em>Trichosurus</em> spp., common and mountain brushtail possums</td>
<td>6.1</td>
<td>4.3</td>
<td>1.4</td>
</tr>
<tr>
<td><em>Potorous</em> tridactylus*, long-nosed potoroo</td>
<td>3.1</td>
<td>2.9</td>
<td>1.4</td>
</tr>
<tr>
<td><em>Tachyglossus aculeatus</em>, echidna</td>
<td>0.5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Macropus parma</em>, parma wallaby</td>
<td>0.2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Petaurus australis</em>, yellow-bellied glider</td>
<td>0.2</td>
<td>0.5</td>
<td>0</td>
</tr>
<tr>
<td><em>Dasyurus</em> maculatus*, spotted-tailed quoll</td>
<td>0.2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Aepyprymnus rufescens</em>, rufous bettong</td>
<td>0</td>
<td>1.0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Large mammals</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Wallabia bicolor</em>, swamp wallaby</td>
<td>9.0</td>
<td>2.4</td>
<td>16.4</td>
</tr>
<tr>
<td><em>Bos taurus</em>, cattle</td>
<td>1.7</td>
<td>1.4</td>
<td>6.8</td>
</tr>
<tr>
<td><em>Macropus giganteus</em>, eastern grey kangaroo</td>
<td>0.9</td>
<td>2.4</td>
<td>8.2</td>
</tr>
<tr>
<td><em>Macropus</em> spp., eastern grey kangaroo or red-necked wallaby</td>
<td>0.9</td>
<td>0.5</td>
<td>1.4</td>
</tr>
<tr>
<td><em>Macropus rufogriseus</em>, red-necked wallaby</td>
<td>0.2</td>
<td>0.5</td>
<td>1.4</td>
</tr>
<tr>
<td><em>Sus scrofa</em>, pig</td>
<td>0.2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Reptiles</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reptilia, unidentified reptiles</td>
<td>5.7</td>
<td>1.0</td>
<td>1.4</td>
</tr>
<tr>
<td>Serpentina, unidentified snakes</td>
<td>0.5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Scincidae, unidentified skink</td>
<td>0.2</td>
<td>1.4</td>
<td>0</td>
</tr>
<tr>
<td>Agamidae, unidentified dragon</td>
<td>0.2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Birds</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aves, unidentified birds</td>
<td>7.1</td>
<td>18.8</td>
<td>11</td>
</tr>
<tr>
<td><em>Platycercus elegans</em>, crimson rosella</td>
<td>0.2</td>
<td>0.5</td>
<td>0</td>
</tr>
<tr>
<td><em>Trichoglossus haematodus</em>, rainbow lorikeet</td>
<td>0.2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Insects</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Insecta, unidentified insects</td>
<td>16.6</td>
<td>11.1</td>
<td>1.4</td>
</tr>
<tr>
<td>Coleoptera, beetles</td>
<td>6.8</td>
<td>3.9</td>
<td>6.8</td>
</tr>
<tr>
<td>Cicadidae, cicadas</td>
<td>5.4</td>
<td>1.4</td>
<td>1.4</td>
</tr>
<tr>
<td>Hymenoptera, unidentified ants</td>
<td>0.2</td>
<td>1.4</td>
<td>0</td>
</tr>
<tr>
<td><strong>Vegetation</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unidentified vegetation*</td>
<td>20.0</td>
<td>45.0</td>
<td>59.0</td>
</tr>
<tr>
<td>Seeds</td>
<td>0</td>
<td>0.5</td>
<td>0</td>
</tr>
<tr>
<td><strong>Other</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Parastacidae, unidentified crayfish</td>
<td>1.2</td>
<td>2.4</td>
<td>0</td>
</tr>
</tbody>
</table>

* May include plant material ingested incidentally with prey.
Chapter 7: Interactions between quolls and eutherian predators

Fig. 7.2. Frequency of occurrence (%) of each prey category in the diets of quolls, foxes and wild dogs.

Multidimensional scaling confirmed the high degree of dietary overlap between quolls, foxes and dogs in terms of volume of prey types in the diet, with samples from all three species overlapping extensively on the ordination plot (Fig. 7.3). The low stress value (0.04) associated with the plot means that it can be interpreted reliably. The closely-packed arrangement of the square symbols reflects the lower diversity in the diet of dogs compared to the other two predators. This is consistent with the lower diversity reflected in the Brillouin index for dogs (Fig. 7.1).
In terms of the relative volumes of prey categories, global one-way ANOSIM revealed no significant difference in the diets of quolls, foxes and dogs (Global $R = 0.027$, $P = 0.113$). However, pairwise comparison between the species showed a significant difference between the diets of quolls and foxes ($R = 0.04$, $P = 0.02$).

The scat samples analysed by R. Harden and J. Robertshaw (unpublished) and P. Fleming (unpublished) contained a similar range of prey taxa to those collected in the present study, although the relative proportions varied substantially between data sets (Table 7.3). Several species were also detected in the earlier surveys that did not appear in the scats collected in the present study, such as *Sminthopsis murina*, *Acrobates pygmaeus* and *Lepus capensis*. Of particular interest is the occurrence of spotted-tailed quoll hair in two dog scats, and cat hair in one dog scat collected by Harden and Robertshaw. From Fleming’s data, the Pianka’s index of overlap between the diets of foxes and wild dogs was 0.679.

![MDS plot showing the diets of quolls (Q), foxes (F) and wild dogs (D) in Marengo and Chaelundi State Forests.](image)
Chapter 7: Interactions between quolls and eutherian predators

Table 7.3. Comparison of the diets of foxes and wild dogs in and around Chaelundi State Forest in 1984\(^1\), 1990-1993\(^2\) and 2003-2004\(^3\). Figures for each taxon are frequency of occurrence (%).

<table>
<thead>
<tr>
<th>Prey item</th>
<th>Dog</th>
<th>Fox</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>H&amp;R</td>
<td>Fleming</td>
</tr>
<tr>
<td></td>
<td>(n = 92)</td>
<td>(n = 142)</td>
</tr>
<tr>
<td>Small mammals</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Antechinus spp.</td>
<td>4.4</td>
<td>0</td>
</tr>
<tr>
<td>Melomys spp.</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Rattus spp.</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Rattus lutreolus</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Rattus rattus</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Rattus fuscipes</td>
<td>15.2</td>
<td>0.7</td>
</tr>
<tr>
<td>Mus domesticus</td>
<td>0</td>
<td>0.7</td>
</tr>
<tr>
<td>Pseudomys sp.</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Muridae, unidentified rodents</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Petaurus breviceps</td>
<td>1.1</td>
<td>0.7</td>
</tr>
<tr>
<td>Acrobautes pygmaeus</td>
<td>2.2</td>
<td>0</td>
</tr>
<tr>
<td>Sminthopsis murina</td>
<td>2.2</td>
<td>0</td>
</tr>
<tr>
<td>Medium-sized mammals</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Petauroidea volans</td>
<td>1.1</td>
<td>0</td>
</tr>
<tr>
<td>Oryctolagus cuniculus</td>
<td>1.1</td>
<td>9.9</td>
</tr>
<tr>
<td>Lepus capensis</td>
<td>0</td>
<td>0.7</td>
</tr>
<tr>
<td>Peramelidae, bandicoots</td>
<td>5.5</td>
<td>0</td>
</tr>
<tr>
<td>Thylagale thesis</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Pseudocheirus pergerinus</td>
<td>8.7</td>
<td>0.7</td>
</tr>
<tr>
<td>Trichosurus spp.</td>
<td>3.3</td>
<td>21.8</td>
</tr>
<tr>
<td>Potorosus tridactylus</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Tachyglossus aculeatus</td>
<td>3.3</td>
<td>2.1</td>
</tr>
<tr>
<td>Macropus parma</td>
<td>3.3</td>
<td>0</td>
</tr>
<tr>
<td>Petaurus australis</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Aeopyrymnus rufescens</td>
<td>0</td>
<td>1.4</td>
</tr>
<tr>
<td>Ornithorhynchus anatinus</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Dasyurus maculatus</td>
<td>2.2</td>
<td>0</td>
</tr>
<tr>
<td>Felis catus</td>
<td>1.1</td>
<td>0</td>
</tr>
<tr>
<td>Large mammals</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wallabia bicolor</td>
<td>12.0</td>
<td>38.7</td>
</tr>
<tr>
<td>Bos taurus</td>
<td>1.1</td>
<td>1.4</td>
</tr>
<tr>
<td>Macropus giganteus</td>
<td>6.5</td>
<td>7.8</td>
</tr>
<tr>
<td>Macropus spp.</td>
<td>8.7</td>
<td>4.4</td>
</tr>
<tr>
<td>Macropus rufogriseus</td>
<td>17.4</td>
<td>2.1</td>
</tr>
<tr>
<td>Macropus robustus</td>
<td>1.1</td>
<td>3.5</td>
</tr>
<tr>
<td>Petrogale penicillata</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Sus scrofa</td>
<td>0</td>
<td>0.7</td>
</tr>
<tr>
<td>Ovis aries</td>
<td>0</td>
<td>2.1</td>
</tr>
<tr>
<td>Unidentified arboreal mammal</td>
<td>1.1</td>
<td>0</td>
</tr>
<tr>
<td>Reptiles</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Birds</td>
<td>2.2</td>
<td>2.8</td>
</tr>
<tr>
<td>Insects</td>
<td>0</td>
<td>1.4</td>
</tr>
<tr>
<td>Vegetation</td>
<td>1.1</td>
<td>0</td>
</tr>
</tbody>
</table>

\(^1\) R. Harden and J. Robertshaw (H&R) unpublished, \(^2\) P. Fleming unpublished, \(^3\) present study (Glen).
7.3.2. Spatial resource use

Radio collars fitted to the spotted-tailed quolls, feral cats and fox remained operative for between one week and six months. No wild dogs were captured during the study. As shown in Table 7.4, the mean number of independent locations recorded for each animal was 39 (range 13 - 74). As only two home ranges were considered to be adequately defined (i.e. the last 5 location records increased the MCP area estimate by less than 5%), the remainder are likely to be underestimates. Despite this, the home ranges of quolls were found to overlap extensively with those of eutherian predators (Fig. 7.4). This was confirmed by the locations of predator scats and sightings. Quoll, fox and dog scats were regularly found only a few metres apart, while three fox, nine cat and four dog sightings were recorded within the known home ranges of quolls. With the exception of quoll M2 and cat F1, the individuals with overlapping home ranges were known (either from radio-tracking or trapping data) to occupy the areas of overlap at the same time. Because most home range sizes were underestimated, and many more quolls were trapped in the study area than were radio-collared, no attempt was made to calculate mean percentage overlap between the home ranges of quolls and other predators. There was no mortality of radio-collared animals, and therefore no direct evidence of interspecific killing.

Table 7.4. Home range estimates for 8 radio-collared quolls, 2 feral cats and 1 fox in Marengo State Forest. F = female, M = male. The number of location records for each animal is given in parentheses.

<table>
<thead>
<tr>
<th>Animal ID</th>
<th>100% MCP Area (ha)</th>
<th>95% Kernel Area (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Quoll F1 (47)*</td>
<td>76</td>
<td>99</td>
</tr>
<tr>
<td>Quoll F2 (32)</td>
<td>161</td>
<td>172</td>
</tr>
<tr>
<td>Quoll F3 (28)</td>
<td>175</td>
<td>394</td>
</tr>
<tr>
<td>Quoll F4 (44)</td>
<td>118</td>
<td>87</td>
</tr>
<tr>
<td>Quoll M1 (74)*</td>
<td>757</td>
<td>524</td>
</tr>
<tr>
<td>Quoll M2 (45)</td>
<td>108</td>
<td>143</td>
</tr>
<tr>
<td>Quoll M3 (13)</td>
<td>155</td>
<td>253</td>
</tr>
<tr>
<td>Quoll M4 (20)</td>
<td>433</td>
<td>684</td>
</tr>
<tr>
<td>Cat M1 (47)</td>
<td>432</td>
<td>532</td>
</tr>
<tr>
<td>Cat F1 (25)</td>
<td>83</td>
<td>112</td>
</tr>
<tr>
<td>Fox M1 (55)</td>
<td>227</td>
<td>77</td>
</tr>
</tbody>
</table>

* Home range adequately defined.
There was some evidence for the use of similar den sites by quolls and foxes. As well as the 38 quoll dens described in Chapter 6, three dens belonging to the same radio-collared fox were also located. All three dens were in crevices among rock jumbles, which was a type of den structure commonly used by *D. maculatus*. Unlike quolls, the radio-collared fox did not change dens frequently, and was using the same den on all but two of the 26 occasions when he was located during the day. The radio-collared cats frequently fled their diurnal rest sites when approached and could not be located precisely. However, on one occasion, the radio-collared male cat was found resting in a dense pile of fallen timber.

As discussed in Chapter 6, spool-and-line tracking revealed that quolls made little use of standing trees. Three individuals climbed the trunks of standing trees to a maximum height of 3 m, and none of the 25 individuals tracked over a cumulative distance of
10,140 m ventured into the forest canopy. The mean height of quolls above the ground was 28 cm (range 0 - 300 cm, s.d. = 47.2).

7.3.3. Population viability analysis

The basic VORTEX model depicted a stable population over the short- to medium term, with an 88% probability of the population persisting 100 years. However, the probability of survival decreased sharply when carrying capacity was reduced to 23 or less (Fig. 7.5), simulating the effects of increased exploitation competition.

![Fig. 7.5. PVA showing mean probability of population survival for a range of carrying capacities (K): 1 Basic model; 2 K = 25.1; 3 K = 23; 4 K = 20.3.](image)

Increased mortality (simulating the effects of interspecific killing) also caused a sharp decrease in the probability of survival (Fig. 7.6). The population was especially sensitive to increases in juvenile mortality, while concurrent increases in both adult and juvenile mortality produced an additive effect (Fig. 7.7).
Chapter 7: Interactions between quolls and eutherian predators

Fig. 7.6. PVA showing mean probability of population survival under various levels of adult mortality ($M_a$). ¹ Basic model; ² $M_a = 70\%$; ³ $M_a = 80\%$.

Fig. 7.7. PVA showing mean probability of population survival under various levels of juvenile ($M_j$) and adult ($M_a$) mortality. ¹ Basic model; ² $M_j = 50\%, M_a = 60\%$; ³ $M_j = 50\%, M_a = 65\%$; ⁴ $M_j = 50\%, M_a = 70\%$.
Finally, when juvenile mortality was increased and carrying capacity decreased (simulating the combined effects of exploitation and interference competition), the probability of survival fell precipitously, approaching zero in the worst-case scenario (Fig. 7.8).

Fig. 7.8. PVA showing mean probability of survival for the population under the combined effects of increased juvenile mortality ($M_j$) and decreased carrying capacity ($K$).  

- Basic model;  
- $M_j = 50, K = 30$;  
- $M_j = 50, K = 27.2$;  
- $M_j = 50, K = 25.2$;  
- $M_j = 50, K = 23.1$;  
- $M_j = 50, K = 20.3$.

7.4. Discussion

The results of this study demonstrate extensive overlap in resource use between all four species of mammalian carnivores in Marengo and Chaelundi State Forests. As outlined by MacNally (1983) and Wiens (1989), extensive overlap in resource use helps to corroborate the relatively weak evidence for competition presented in Section 7.1, which comes from inverse relationships in abundance and distribution. Taken together, these two forms of evidence present a stronger (although still inconclusive) case for the existence of competition. Is the overlap in resource use measured here high in comparison to other carnivore guilds, and if so, what facilitates the coexistence of quolls, foxes, wild dogs and feral cats? I will explore these two questions in turn, firstly
in terms of dietary overlap, then in terms of spatial resources. Interference competition is then discussed, and finally the potential impacts of eutherian predators on the population viability of *D. maculatus* are considered.

### 7.4.1. Dietary overlap

The diets of spotted-tailed quolls, foxes and wild dogs in Marengo and Chaelundi State Forests were similar, not only in terms of the range of prey types consumed, but also their frequency of occurrence and relative volumes. In a similar dietary study between eight sympatric carnivore species in central Africa (Ray and Sunquist 2001), only four of 21 pairwise comparisons yielded a Pianka's index higher than 0.657; the lowest of the indices calculated in the present study. None had a Pianka's index as high as that calculated here for foxes and wild dogs of 0.943. In a dietary study of three sympatric canids in Brazil, Jácomo *et al.* (2004) calculated Pianka's indices ranging from 0.044 to 0.498. Compared to the Brazilian and central African guilds then, the level of dietary overlap observed in the present study is high. Among the three central African species with the highest dietary overlap, temporal and vertical niche partitioning occurred (Ray and Sunquist 2001).

Not surprisingly, the species found by Ray and Sunquist (2001) to have the highest degree of overlap were of comparable size. It is also noteworthy that these species were among the smallest in the guild. In general, large predators do not specialise on larger prey, but consume a wider range of prey sizes than smaller predators (Rosenzweig 1966; Wilson 1975; Gittleman 1985; Radloff and Du Toit 2004). Thus, the larger species in a guild will often utilise many of the same prey as the smaller predators, but also have access to larger prey that cannot readily be captured by the smaller predators. Similarly in the present study, wild dogs consumed large numbers of rabbits and red-necked pademelons, which were common prey of foxes and quolls, but also frequently consumed larger macropods such as swamp wallabies and eastern grey kangaroos.

The high degree of similarity found here between the diets of foxes and wild dogs is consistent with the findings of Mitchell and Banks (2005), who reported a Pianka's index of 0.91 in the central tablelands of New South Wales. However, a meta-analysis of previous dietary studies of foxes and wild dogs from similar areas suggested a much
lower Pianka’s index of 0.69. As in the present study, foxes ate small prey, and dogs large prey, more often than their counterparts (Mitchell and Banks 2005).

Despite the high level of similarity measured in the diets of predators in this study, competition may not occur unless resources are limiting (Schoener 1983). If resources are super-abundant, species may coexist with similar - or even identical - patterns of resource use. However, in this case there were a number of significant differences between species, which may facilitate their coexistence even if resources are limiting. A high degree of vertical niche partitioning was found between the diets of spotted-tailed quolls and canids. Greater gliders in particular were eaten very frequently by quolls, and infrequently by foxes and wild dogs. Greater gliders are strictly arboreal (Kehl and Borsboom 1984) and, as such, are probably quite inaccessible to canids, which have limited climbing ability. Spotted-tailed quolls, however, are adept climbers, and have been observed climbing trees to capture gliders while they are inactive in nest hollows (Belcher 2000). Thus, quolls probably had almost exclusive access to greater gliders, which were their staple prey. Similarly, Belcher (2000) proposed that spotted-tailed quolls were able to coexist with high densities of foxes in Victoria because of their ability to utilise arboreal as well as terrestrial prey. Other arboreal prey (brushtail and ringtail possums) were also eaten more frequently by quolls than by canids, although the disparity was less marked than for greater gliders. This presumably reflects the less strictly arboreal habits of these possums (e.g. Davey 1984; Gresser 1996).

In addition to the apparent vertical niche partitioning, each of the canids appeared to exploit a different size class of secondary prey. While medium-sized mammals were the staple prey of all three predators, foxes consumed small mammals, and dogs large mammals, significantly more often than their counterparts. Conversely, quolls consumed more insects than foxes or dogs. However, this was largely due to a sharp peak in the occurrence of insects during the summer months, while insects were rare or absent in the diet at other times (Chapter 5).

Both canids consumed vegetation significantly more often than did quolls. This may reflect the more omnivorous nature of these canids compared to D. maculatus. However, because it was not possible to determine how much of the vegetation in scats had been consumed incidentally with prey, this result must be interpreted with caution.
The final significant difference involved the consumption of avian prey, which occurred more often in the diet of foxes than in that of quolls. This is perhaps surprising in view of the partly arboreal habits of *D. maculatus*. Two avian species that are predominantly ground-dwelling, the superb lyrebird (*Menura novaehollandiae*) and the spotted quail-thrush (*Cinclosoma punctatum*), were common in the study area (A. Glen pers. obs.). Possibly, foxes were more adept than quolls at capturing birds at ground-level.

The dietary data collected by R. Harden and J. Robertshaw (unpublished) and P. Fleming (unpublished) revealed a similar range of prey to that sampled in the present study. However, there was considerable variation between the data sets in the relative proportions of each prey type eaten. For example, rabbits were much more common in the scats collected during the present study than in those collected previously. Such differences may reflect spatial variation in the abundance of prey at a local scale. Many of the scats collected in the present study were found on or near the Marengo Plain, where rabbits appeared much more abundant than in the surrounding forested areas (A. Glen pers. obs.). Temporal fluctuations in prey abundance may also have contributed to the differences.

Although the diet of cats was not sampled here, previous studies reviewed by Dickman (1996b) suggest some similarity to the diet of *D. maculatus*. Cats were common in the study area (A. Glen pers. obs; Forests NSW, DEC unpublished data), and may also have the potential to compete with quolls for food.

### 7.4.2. Spatial overlap

Radio-tracking showed extensive spatial overlap between spotted-tailed quolls, foxes and feral cats in the study area. This was confirmed further by the locations of predator scats and sightings, which also indicated spatial overlap between quolls and wild dogs. In some systems, coexistence between predator species is characterised by interspecific territoriality, with subordinate species mainly utilising areas outside the home ranges of dominant predators (e.g. Voigt and Earle 1983; Sargeant *et al.* 1987; Harrison *et al.* 1989; Johnson and Franklin 1994; Gosselink *et al.* 2003). Spatial avoidance at such a broad scale does not occur between spotted-tailed quolls and eutherian predators in Marengo State Forest. For example, the home range of one female quoll was contained almost entirely within that of a large male feral cat (Fig. 7.4), while three of the four
radio-collared male quolls had home ranges overlapping with that of the radio-collared fox. However, spatial overlap does not preclude the possibility that animals avoid direct encounters. Avoidance may still occur at a finer spatial scale. For example, Molsher (1999) found that foxes and feral cats with overlapping home ranges would tolerate each other at distances greater than 50 m, but cats normally fled to avoid aggression during closer encounters. Animals may also be active at different times of day (e.g. Konecny 1989; Kotler et al. 1993; Ray and Sunquist 2001), or they may partition the habitat vertically, while using the same two-dimensional area (e.g. Jones and Barmuta 2000; Ray and Sunquist 2001).

As well as competing for other spatial resources, species may contest suitable den or shelter sites. For example, red foxes compete for dens with arctic foxes (Hersteinsson et al. 1989; Kaikusalo and Angerbjörn 1995), and some skink species exclude each other from shelter sites in rock outcrops (Langkilde and Shine 2004). Red foxes are known to use similar den structures to those of quolls (McIntosh 1963; Belcher 2000; Belcher and Darrant 2004; Körtner et al. 2004; Chapter 6), and this was supported by the limited sample of fox dens located in the present study. Competition for dens might potentially be important in areas where shelter sites are limited, or foxes are abundant.

7.4.3. Interference competition

Evidence from previous studies confirms that northern (Oakwood 2000) and spotted-tailed quolls (Körtner et al. 2004) may be frequently killed by other predators such as feral cats, foxes and wild dogs. Similarly, the dietary data of Harden and Robertshaw presented here reveal the presence of spotted-tailed quoll hair in two dog scats, and cat hair in one scat. Such information may be indicative of intraguild predation by dogs, although it is also possible that these animals were scavenged.

Although there was no mortality among the radio-collared animals in the present study, the small number of collared animals means that interspecific killing was unlikely to be detected. The frequent den shifting of quolls (Oakwood 1997; Chapter 6) may serve to minimise the risk of predation. Similarly, greater gliders alternate between a number of nest hollows in order to avoid predators (Kehl and Borsboom 1984). Although there did not appear to be strong vertical partitioning of the habitat in this study, it remains possible that the climbing ability of quolls provides a means of escape in direct
Chapter 7: Interactions between quolls and eutherian predators

encounters with other predators, thereby reducing the severity of interference competition. For example, grey foxes climb trees to escape aggression from coyotes (Cypher 1993), and *Antechinus agilis* climbs to avoid direct encounters with *A. swainsonii* (Dickman 1991).

7.4.4. Population viability analysis

PVA showed that the spotted-tailed quoll population would be vulnerable to extinction if faced with high densities of competitors. The population was sensitive to changes in carrying capacity, which would result from exploitation competition. Based on a dietary overlap between quolls and canids of around 0.7 (Section 7.3.1), and assuming linearity in interaction strength, the modelled reduction in carrying capacity from 30 to 23 could result from the addition of around ten foxes or dogs. Unless quolls were able to adapt by shifting their dietary niche, a high probability of extinction would apply under these circumstances.

The spotted-tailed quoll population was also sensitive to increases in mortality, particularly of juveniles. Foxes and wild dogs are known to kill spotted-tailed quolls (e.g. Körtner *et al.* 2004), and juveniles are likely the most vulnerable. A situation in which juvenile mortality was increased to 50% or more would result in a high probability of extinction, while increased mortality of both adults and juveniles would lead to almost certain demise. Based on the results of Körtner *et al.* (2004), who lost 7% of radio-collared quolls to predation, increases in mortality of 10% or more are plausible in areas with a high abundance of canids. A situation in which interference and exploitation competition acted in concert would also lead to a very low probability of long-term survival. Similarly, Burnett and Marsh (2004) concluded from PVA that populations of *D. m. gracilis* were vulnerable to potential increases in mortality, or decreases in recruitment, caused by eutherian predators.

It should be noted that the population viability analyses conducted here may overestimate the risk to the quoll population in Marengo and Chaelundi State Forests, which was certainly much larger than the set of animals encountered in the limited trapping area. Also, PVA does not model density-dependent effects, such as compensatory increases in the survival or reproductive output of surviving quolls following competition-induced reductions in the population size. However, these
analyses are indicative of the potential impacts of competition on a hypothetical, isolated population of similar size.

7.4.5. Conclusions
The high degree of resource overlap measured here indicates the potential for exploitation competition, not only between quolls and eutherian predators, but also between the eutherian predators themselves. Coexistence in this predator assemblage is apparently facilitated by vertical niche partitioning of the diets of quolls and canids, and the exploitation by foxes and dogs of different size classes of secondary prey. If interspecific aggression occurs, this may to some extent be alleviated by the ability of quolls to climb trees to escape.

A network of direct and indirect interactions is likely to exist within the suite of predators (Chapter 1), and manipulation experiments are needed to tease out the pairwise relationships between the species. A useful approach may be to conduct intensive monitoring of small numbers of individual quolls and eutherian carnivores in sympatry. Rather than looking for effects of pest removal on quolls at the population level, individual habitat use, microhabitat use, diets, body condition, reproductive output and causes of mortality could be monitored before and after removal of putative competitors. If competition between quolls and other carnivores is indeed important, then few if any areas may exist that support an abundance of both. Unless several replicated areas can be found that support high densities of both quolls and potential competitors, monitoring at the individual level may be the only practicable way to test competition through removal experiments. Removing eutherian carnivores from areas where they are already scarce may have no measurable effect on quoll populations, while monitoring in areas of low quoll density would yield hopelessly small sample sizes. Removal experiments designed to investigate individual-level shifts in behaviour and resource use of quolls should be conducted as a matter of priority.
Chapter 8: General discussion: Why are there so many spotted-tailed quolls in north-eastern New South Wales?

8.1. Introduction

The aims of this thesis were to study the population dynamics, diet and spatial resource use of spotted-tailed quolls in Marengo and Chaelundi State Forests, and to investigate evidence for interactions between quolls and eutherian carnivores. During the course of the study I have shown that, despite the decline in abundance and distribution of spotted-tailed quolls since European settlement in Australia (Mansergh and Belcher 1992; Maxwell et al. 1996; Jones et al. 2001), localised areas remain in north-eastern New South Wales where the species persists in abundance (Körtner et al. 2003, 2004; Chapter 4). This high abundance affords the opportunity to investigate the ecology and life history of the species in detail, but also begs an important question: why are spotted-tailed quolls still abundant in these areas, while populations elsewhere have declined or disappeared? The answers to this question will be vital to the conservation and recovery of spotted-tailed quolls, and the information gleaned in this study suggests a number of possible explanations. These include the high availability of prey, quality and spatial extent of habitat, low densities of foxes, and small home ranges of female quolls in comparison to many other parts of New South Wales and Victoria. I will discuss each of these possible explanations in turn.

8.2. Availability of prey

In Chapter 5, we saw that spotted-tailed quolls in Marengo and Chaelundi State Forests took mammalian prey as a very high proportion of the diet. Medium-sized mammals constituted the bulk of the diet, and greater gliders in particular were a staple, occurring in over 25% of scats. Greater gliders were frequently seen during the course of the study, and their high abundance was confirmed by a number of spotlight surveys conducted in the area between 1998 and 2001 (Forests New South Wales unpublished data). The high abundance of greater gliders in the study area suggests that the retention of hollow trees during forestry operations is effective in maintaining large populations of hollow-nesting mammals. The importance of gliders in the diet of quolls emphasises the value of forestry practices that actively seek to maintain the abundance of common species, as well as to protect threatened species. Other arboreal prey such as brushtail and ringtail possums were also common in the diet of quolls in the area.
The importance of arboreal mammals such as greater gliders in the diet of quolls is probably due not only to their abundance, but also the fact that other mammalian predators, which lack the climbing ability of *D. maculatus*, are probably ineffective at exploiting this prey resource. Thus, it is not only the abundance, but the *availability* of prey that is likely to be important. Although other medium-sized mammals (e.g. rabbits) were also abundant in the study area, quolls did not eat these at such high frequency as they did greater gliders. Rabbits were heavily preyed upon by foxes and wild dogs (Chapter 7), and this may have reduced their availability to quolls. Greater gliders, on the other hand, were consumed infrequently by other mammalian predators, and may therefore have been more readily available to quolls.

This apparent reliance by quolls on greater gliders raises the possibility of competition between quolls and powerful owls. Predation by powerful owls can greatly reduce local abundance of greater gliders (Kavanagh 1988).

### 8.3. Quality and spatial extent of habitat

A number of biotic and abiotic features of the present study area suggest that it may represent very high quality habitat for *D. maculatus*. Firstly, an abundance of fallen timber contributes to the structural complexity of the habitat, and provides a high availability of potential den sites. Quolls were also shown to use fallen logs extensively when travelling (Chapter 6), as was the case for spotted-tailed quolls in Tasmania (Jones and Barmuta 2000). Similarly, rocky outcrops have been identified in previous studies of spotted-tailed (Belcher 2000) and northern quolls (Oakwood 1997, 2002) as potentially important sources of shelter for denning and/or refuge from predators. Structurally complex granite outcrops are common in Marengo and Chaelundi State Forests, and throughout much of the tablelands of north-eastern New South Wales. These may further enhance the quality of habitat for *D. maculatus*. A high abundance of hollow trees in the present study site (A. Glen pers. obs.) may also contribute to the quality of the habitat by supporting high densities of hollow-nesting prey, and by providing plentiful den sites for *D. maculatus*.

In addition to habitat quality, spatial extent of habitat is likely to be very important. As discussed in Chapter 6, spotted-tailed quolls occupy large home ranges, and females
appear to have exclusive territories. By definition, such a social system demands very large areas of habitat in order to support a viable population. Based on the sizes of female territories (Belcher and Darrant 2004; Claridge et al. 2005; Chapter 6), areas in the order of hundreds of square kilometres are likely needed to support enough females for a viable population. Populations in smaller fragments would be vulnerable to extinction through inbreeding, genetic drift or stochastic events, unless immigration occurred periodically from other populations (e.g. Soulé 1980).

Marengo and Chaelundi State Forests form part of a very large, continuous expanse of native forest, which encompasses several other state forests, national parks and nature reserves, spanning over 100 km from north to south. Although it is not known whether the density of quolls is consistently high throughout this entire area, it is likely, at the very least, that this large expanse of forested habitat readily allows dispersal of quolls from one area to another. Connectivity of habitat on a large spatial scale is vital to the long-term survival of many species and to the function of ecosystems (Soulé et al. 2004; Hobbs 2005). For example, the apparent dispersal of male quolls following severe wildfire (Chapter 4) was likely aided by the fact that the burnt areas were surrounded by a large expanse of suitable habitat. A similar event in an isolated forest fragment would potentially be much more damaging. Similarly, there would have been no barrier to subsequent migration into the burnt area once vegetation and prey communities began to recover. The relative ease of dispersal in this landscape probably moderates the impacts of localised disturbances such as fire. As well as buffering populations from the impacts of stochastic events, migration is also important in minimising inbreeding and genetic drift (Soulé 1980).

The large expanse of forested habitat in north-eastern New South Wales also means that much of the available habitat is protected from edge effects (e.g. Harris 1988; Dijak and Thompson 2000). In particular, foxes are absent from, or occur at very low densities in many forested areas separated by more than around 2 km from freehold land (Catling and Burt 1995). As discussed in the following section, the low density of competitors such as foxes may be an important factor contributing to the abundance of spotted-tailed quolls in Marengo and Chaelundi State Forests.
8.4. Density of competitors

Although this study has confirmed the presence of eutherian predators (foxes, feral cats and wild dogs) in Marengo and Chaelundi State Forests, quantitative estimates of their abundance were not attempted. However, a concurrent study by Forests New South Wales and the Department of Environment and Conservation (unpublished data) monitored the relative abundance of predators in the study area using an index derived from tracks on sand plots. Foxes were shown to occur at very low density. This is supported by the results of Catling and Burt (1995, 1997), who recorded no evidence of foxes in Chaelundi State Forest, and by my own observations. Foxes were rarely sighted during the present study, and only one individual was captured, despite an extensive trapping effort (Chapter 7). Wild dogs and feral cats, on the other hand, were much more frequently recorded on sand plots (Forests NSW, DEC unpublished data). Population viability analysis (Chapter 7) showed that quoll populations may be sensitive to either exploitation or interference competition, while the combined effects of both are likely to have drastic effects on a population’s probability of survival. Based on their propensity for interspecific killing (Palomares and Caro 1999; Körtner et al. 2004; Chapter 1) and the high degree of dietary overlap between foxes and quolls (Chapter 7), foxes are more likely to compete strongly with *D. maculatus* than are feral cats or wild dogs. Furthermore, the apparently low density of foxes in north-eastern New South Wales contrasts strongly with areas further south where spotted-tailed quolls have declined (Catling and Burt 1995). Thus, the rarity of foxes in Marengo and Chaelundi State Forests may be a major factor contributing to the abundance of quolls. As discussed in Chapter 1, the relatively high abundance of wild dogs in the area may suppress the abundance of foxes, thereby protecting quolls through an indirect commensal relationship. Future research should aim to test this speculation.

8.5. Home range size

In Chapter 6, it was shown that spotted-tailed quolls in Marengo State Forest appear to occupy smaller home ranges than those described in southern New South Wales and Victoria. For example, the estimated mean home range of female quolls in this study was around 30 - 50% of the estimates obtained by Belcher and Darrant (2004) and Claridge *et al.* (2005). Although mean home range size may have been underestimated in the present study, this is unlikely to account for a difference of such magnitude. If female home ranges are indeed smaller in north-eastern New South Wales, this may
allow higher densities of *D. maculatus* to exist. In turn, small home ranges may be a consequence of abundant resources such as prey and den sites.

### 8.6. Management implications

The results of this study have a number of implications for the management of forestry operations in areas where spotted-tailed quolls occur. Firstly, the importance of maintaining (or increasing) densities of hollow-bearing trees must be emphasised. Tree hollows are important to quolls as a source of both shelter and prey. The importance of hollow-bearing trees is recognised by Forests New South Wales (e.g. Williams 2001). In north-eastern New South Wales, a minimum of five hollow-bearing trees (and five mature ‘recruit’ trees) must be retained for every hectare of harvest area, and this figure is increased to eight where high densities of greater gliders occur (IFOA 1999). This additional prescription for greater gliders is primarily intended to maintain the prey base for large forest owls such as the powerful owl, but is also likely to benefit populations of *D. maculatus*. It is possible, however, that powerful owls may compete with and/or prey upon spotted-tailed quolls, which could potentially negate any such benefit.

As mentioned in Chapter 6, the frequent use by quolls of fallen logs as den sites and as a means of travel suggests that these may be an important structural feature of the habitat. Fallen timber is abundant in Marengo and Chaelundi State Forests, largely due to the forestry practice of leaving timber off-cuts *in situ*. This practice should continue, and be introduced in any areas where it is not currently applied.

During the course of the present study, selective logging was conducted within the trapping area, and quolls continued to be trapped in close proximity to these operations. In addition, much of the trapping area had been subject to harvesting less than two years prior to the commencement of this study (Forests NSW unpublished data), and continued to support high densities of quolls. This demonstrates that quoll populations can persist in areas subject to selective logging. However, it is imperative that such operations continue to be managed in a way that seeks to minimise disturbance. The maintenance of prey populations and structural habitat features is likely to be of great importance.
8.7. Future research

This study demonstrates that there is considerable potential for competition to occur between spotted-tailed quolls and foxes. However, conclusive evidence may be gained only from fox removal experiments. As discussed in Chapter 7, there are two possible approaches to such experiments: 1) to monitor the response of quolls to removal of eutherian carnivores at the population level, and 2) to monitor the short-term response of individual quolls to the removal of other carnivores. Theoretically, the first approach is preferable because it is populations, rather than individuals, that are of most concern in conservation (Mcllroy 1982; Soulé 1985; Caughley and Sinclair 1994). However, such an approach may be logistically difficult (Chapter 7). The second approach would focus on individual quolls whose home ranges were known to overlap with those of eutherian predators. By collecting detailed information on such individuals, responses to predator management may be detected. For example, individuals may expand or shift their home range, or make more frequent use of certain microhabitats or resource patches following removal of eutherian predators. Detection of such responses would require very accurate monitoring with fine spatial and temporal resolution. Emerging technologies such as satellite telemetry (e.g. Ballard et al. 1998) and contact telemetry (e.g. Sirtrack 2005) may provide useful insights, particularly as new equipment approaches a size and weight that may be fitted to quolls. Dietary shifts may be detected by analysis of scats, while changes in body condition may be detected by repeated trapping. Individual responses such as these may be more readily detectable than population-level responses, and would provide a strong indication that populations are likely to respond to ongoing predator management. Confirmation that behavioural responses at the level of the individual may translate to population-level shifts have been obtained for several species, such as snowshoe hares (*Lepus americanus*) (Hik 1995) and house mice (Dickman 1992c; Arthur et al. 2004, 2005).

A host of interactions is also likely to occur among other mammalian predators and prey communities in Australia. Maintaining or restoring ecosystem function will require an improved understanding of these relationships. As stated in Chapter 1, future research should focus on testing putative interactions with controlled, replicated experiments that manipulate the densities of predators. Here, I make some more specific suggestions. Firstly, because interactions among predators appear to be moderated by structurally complex habitat, initial experiments should be conducted in open areas such as the
Australian arid zone, where effects are likely to be more easily detectable. For example, a dingo removal experiment might be conducted in open spinifex areas of central Australia. Alternatively, an introduction experiment might be conducted by re-routing sections of the dingo barrier fence or by releasing dingoes into large, purpose-built predator enclosures. Such experiments would need to monitor the abundances of foxes, feral cats, rabbits and native prey before and after manipulation of dingo density. Similarly, the impacts of foxes on cats and quolls should be clarified by controlled, replicated fox removal experiments. The knowledge gained from experiments in open habitats could then be used to design experiments capable of detecting more subtle interactions in forested habitats, such as the eastern coastal ranges of Australia. Experiments might also investigate systems where, for example, foxes are initially abundant and cats scarce, and vice versa, in order to tease out the intricacies of three-way interactions and non-linear effects.

In all of the above experiments, the likely subordinate predators should be monitored using radio collars fitted with mortality sensors. This will help to clarify the mechanism of any observed impact. If interspecific killing is responsible, freshly-killed carcasses can be located, whereas spatial or temporal avoidance between predators can be detected by changes in movement patterns. Prey availability and the diets of all predatory species should also be monitored before and after manipulations are conducted, thereby allowing detection of exploitative effects.

8.8. Conclusions
The spotted-tailed quoll remains abundant in areas of north-eastern New South Wales, despite having declined dramatically across much of its geographical range. The principal factors that are believed to have caused the species' decline either do not apply to these areas of abundance, or their effects have been more moderate. These factors include clearing and alteration of habitat, habitat fragmentation, and the effects of eutherian predators and their control.

The area in which this study was conducted forms part of a very large expanse of forested habitat, and is therefore relatively unaffected by the first two of these factors. However, eutherian predators are present in the area and, in the case of feral cats and wild dogs, are relatively abundant. Foxes, on the other hand are scarce. Foxes, wild
dogs and feral cats are all likely to compete with *D. maculatus*, both through exploitation and interference. However, by virtue of their smaller home ranges (Saunders *et al.* 1995; Meek and Saunders 2000), foxes can exist at much higher densities than wild dogs. Feral cats can also exist at high densities (e.g. Denny *et al.* 2002). However, it is likely that cats do not compete as strongly with quolls as do canids, because cats consume smaller prey on average (e.g. Jones and Coman 1981; Catling 1988; Molsher *et al.* 1999), and may not be dominant over quolls in aggressive encounters (e.g. Le Souef and Burrell 1926). Thus, foxes are likely to be a more significant threat to populations of spotted-tailed quolls than are wild dogs or feral cats. The very low density of foxes in the present study area, along with the large expanse of relatively undisturbed habitat, probably explains the high abundance of *D. maculatus*. 


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