Is the Dingo Top Dog?

The influence of dingo management on the behaviour of introduced carnivores in arid Australia, with implications for native fauna conservation

by

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Candidate's Declaration

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university. To the best of the author's knowledge, it contains no material previously published or written by another person, except where due reference is made in the text. Specific contributions by others are referred to in the acknowledgements and status of papers sections.

Renee Louise Brawata August 2012

Status of Papers

The following is a list of chapters from this thesis that have been published, submitted or in the processes of submission in modified forms. Co-authors and their respective contribution to the work are identified below.

Paper Title	Techniques for Monitoring Carnivore Behaviour using Automatic Thermal Video.
Authors	Renee L. Brawata, Timothy H. Raupach and Teresa Neeman
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Source Chapter	Chapter 3

Co-author Contribution:

1) Timothy Raupach was responsible for software relating to the remote recording of thermal images, including designing the thermal imaging software to meet the authors needs as stated and modifying the software as requested. He assisted in early field trials and provided feedback on the version of the paper submitted for publication.

2) Dr.Teresa Neeman was the statistical supervisor on the student panel for this thesis and it was the author's judgement that she warranted co-authorship based on her input and advice on statistical analysis for any papers published from chapters 3-7.

Paper Title	Does management of a top carnivore influence the response of mesopredators and prey to rainfall in arid ecosystems? Evidence for a Baseline Density theory.
Authors	Renee L. Brawata and Teresa Neeman
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Co-author Contribution

Dr Carmel Pollino was an advisor on the student panel for the Bayesian analysis. Her co-authorship was based on assistance provided to the student when using Bayesian software, advice on statistical analysis and feedback given to the student during the formation of the Bayesian model as well as constructive comments on the written paper.

During completion of the thesis, a further two papers have been published under the authors maiden name (Visser, R.L.) as proceedings from a workshop on trophic regulation by the dingo. While these papers present a review on the general thesis topic, they do not contain information directly obtained from chapters in the thesis, and therefore have been included only in the appendix (Appendix 1).

Renee Louise Brawata

Dedicated to my two sons –

Finnis Aedon, the Sun, the light of my life and

Rhys Ashley, the Moon, my angel among the stars.

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Renee Louise Brawata, August 2012

Abstract

An improved understanding of how ecosystems function is important for effective natural resource management and biodiversity conservation. Recent research suggests that top-order predators have important ecological roles in many ecosystems through controlling populations of smaller predators. This thesis examined how the management of Australia's apex predator, the dingo (*Canis lupus dingo*), influenced the activity and behaviour of two introduced mesopredators, the red fox (*Vulpes vulpes*) and feral cat (*Felis catus*) and select prey species. The aim was to increase our understanding of the role dingoes may play in the conservation of endangered fauna through the trophic regulation of exotic mesopredators.

The study monitored the activity and behaviour of dingoes, foxes, feral cats and select prey species at five sites in arid Australia. Dingo management varied between the study sites. Sites included areas where dingoes remained uncontrolled, where dingoes were controlled through exclusion fencing and where 1080 poison baiting was conducted. At each site the activity of predators and prey, including macropods, rabbits and small vertebrates was monitored over two summers. Sampling times included prior to, three months post and one year post a significant rainfall event. Transects and scent stations were used to measure activity while behaviour was monitored through direct observation and the use of a thermal imaging camera attached to a remote recording system.

Results showed the management of dingoes to be a key determinant of the activity of foxes and select prey, including macropods, rabbits and small mammals. Feral cat activity showed a positive response to both dingo and fox control through poison baiting. Dingo management also affected the activity of mesopredators around shared resources, particularly in proximity to water resources. Both feral cats and foxes showed an avoidance response to the presence of dingoes around water points, and again feral cats displayed an increased response to the removal of both canids. Habitat use by mesopredators did not appear to be affected by dingo management, and while foxes showed a behavioural avoidance response, limited data was collected on the response of feral cats to dingoes at shared food and water resources so results were inconclusive.

The results of this study supported the presence of top-down regulation occurring in the arid ecosystems under some conditions and that behavioural mechanisms, such as avoidance, are important in the ability of dingoes to regulate smaller predator populations. While arid ecosystems are traditionally viewed as "bottom-up" or productivity driven, evidence from this research showed that while the strength of trophic regulation by dingoes may fluctuate, top-down effects occurred both prior to and post significant rainfall events at the study sites. In particular, strong relationships were found between dingo management, fox activity and fox behaviour at the study sites regardless of rainfall.

In conclusion, it may be that dingoes provide a net benefit to prey populations, particularly medium-sized and small mammals, through reducing predatory impacts of foxes and under some conditions, feral cats. Thus retaining dingo populations in some ecosystems may assist in the management of biodiversity over the long term, including the conservation of native fauna populations susceptible to fox and feral cat predation. While further research into the trophic effects of dingoes in other bioregions is recommended, through improving our understanding of such trophic interactions, results from this research could assist managers in making more ecologically informed decisions about control of top-order carnivores in arid areas.

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List of acronyms and abbreviations

DBF	Dingo Barrier Fence
MRH	Mesopredator release hypothesis
RHD	Rabbit Haemorrhagic Disease
SNP	Sturt National Park
BL	Bollards Lagoon
QS	Quinyambie Station
MW	Mundowdna Wilpoorina
FS	Finniss Springs
GPS	Global Positioning System
GPP	Gross primary productivity
FOV	Field-of-view
HFOV	Horizontal field-of-view
VFOV	Vertical field-of-view

Chapter 1: Introduction

1.1 General Introduction

Australia's recent history has seen vast changes to the landscape and mammalian fauna within it. Since European settlement more than 50 native vertebrate species have become extinct, including 27 terrestrial mammal species (Smith and Quin, 1996), and many more have experienced dramatic declines in their distribution and abundance (Short and Smith, 1994; Burbidge *et al.*, 2008). Other species, introduced to the continent with the coming of Europeans, have thrived. Of the later, two exotic predators, the European red fox (*Vulpes vulpes*) and the feral cat (*Felis catus*), are now found in most habitats throughout Australia. Along with habitat loss, predation by the red fox and feral cat are regarded as the primary causal factor behind the disappearance of so many native species from the continent (Johnson, 2006).

On mainland Australia the dingo (*Canis lupus dingo*) has been the apex predator since the extinction of the thylacine (*Thylacinus cynocephalus*) around 4000 years ago. More recently, the introduction of the domestic dog (*Canis familiaris*) into dingo populations has led to hybridisation between these two species (Corbett, 2001). On mainland Australia, the dingo and dingo-hybrids (hereafter referred to as dingoes) now fill the niche of top predator.

There has been much recent speculation into the role the dingo may play in trophic regulation of Australian ecosystems. Recent research in the US has shown that in some communities, large carnivores may exert "top down" regulation forces on ecosystem function through the suppression of smaller carnivores (Crooks and Soule, 1999). The removal of large carnivores from such communities may result in "mesopredator release" (Soulé *et al.*, 1988), where populations of smaller predators increase in response to top predator removal.

Previous studies in Australia have shown an increase in cat and fox abundance, and a decrease in small (under 30gm) to medium-sized (30gm – 5kg) mammals in areas where dingoes are in low numbers or absent (Letnic *et al.*, 2009a; Letnic *et al.*, 2009b; Newsome *et al.*, 2001), and a decrease in fox populations where dingoes persist in significant numbers (Smith and Quin, 1996; Johnson and VanDerWal, 2009). From these findings, it is possible that dingoes, as "top dog", may play a vital role in maintaining ecosystem health by aiding in the control of fox and cat populations and, in turn, minimising the impact of these smaller predators on native prey. However, evidence for this process and an understanding of the mechanisms behind dingo, fox and feral cat interactions remain unclear.

In many regions of Australia dingo populations are currently controlled by methods such as poisoning, trapping or shooting. Such control of dingo populations may have a direct impact on their ability to limit cat and fox numbers, and reduce other benefits of maintaining dingo populations, such as control of other pest species such as rabbits (*Oryctolagus cuniculus*) and feral goats *(Capra hircus)* (Newsome, 2001). If dingoes influence behaviour and suppress abundance of introduced carnivores, native wildlife populations may benefit from maintaining dingo populations in the ecosystem and current management strategies that remove dingoes as a pest species may have the unintended consequence of encouraging fox and cat predation on native fauna.

1.2 A comparative review of the ecology of the dingo, fox and feral cat in the arid zone

1.2.1 The Dingo

The dingo, a medium-sized canid of the genus *Canis,* was introduced to Australia from East Asia around 5000 years ago (Savolainen *et al.*, 2004). Since the demise of the thylacine on the mainland some 4000 years ago, the dingo has been Australia's largest terrestrial predator. The dingo is widespread across the Australian mainland, but extensively controlled in the south-east of the continent due to conflict with sheep grazing (Fleming, 2000) (Figure 1.1). The current status of the dingo in Australia is unique and conflicting. For example, in NSW, the dingo is an indigenous animal under the *Threatened Species Conservation Act 1995* due to its presence on the continent prior to European settlement, however it is regarded as a pest species under the *Rural Lands Protection Act, 1998*, and remains unprotected in many National Parks.

Dingoes live up to 12 years in the wild, and purebred animals may vary in coat colour varies from sandy yellow to red ginger, black and tan, white or black. Females have one oestrus period a year and mating usually occurs in April/May. Gestation is around 63 days, with an average of five pups per litter born in the cooler dry months of June through to September. Pups are independent at 3-4 months but often remain within their maternal packs until the following breeding season. Males disperse more often and further than females, as young females may remain longer and act as "helpers" for the alpha females following litters (Catling *et al.*, 1992). Lack of food due to drought may inhibit reproductive success and infanticide is common (Corbett, 1988).

Dingo packs usually comprise of 3-12 individuals. The dingo social structure is hierarchical, with each pack containing both an alpha male and female in addition to a number of subordinate members (Thomson *et al.*, 1992). Larger packs are more often found in arid areas, and as such pack size may be inversely related to environmental stability (Newsome *et al.*, 1983a). Dingoes communicate by howling and scent marking with pheromones, both of which are used to defend distinct territories. Pack territories may spatially overlap, particularly around shared resources (such as water), but packs do not temporally overlap (Corbett, 1995). In pastoral areas, where dingoes are often heavily controlled, dingo may exist in small amicable groups called 'tribes'. While tribes share a living area, they tend to hunt alone and do not defend a distinct home range. 'Loner' or solitary dingoes may temporarily inhabit areas defended by packs, with minimal association with resident dingoes (Corbett, 1995).

Dingo home range size has been found to be a trade-off between dingo density and both the regularity and reliability of food and water resources, rather than pack size (Thomson, 1992b). Pack territories are usually larger in arid areas, where larger pack sizes form to take advantage of hunting larger prey such as macropods. For example, in the Fortescue River region of northwest WA, the average territory size was 80 km^2, while dingo density ranged from 4-23 individuals per 100 km^2 (Thomson, 1992b). Some parts of home range, termed 'core areas' are used regularly, while others are visited much less often (Harden, 1985).

The dingo is highly adaptable in its hunting techniques, and as such its diet reflects a broad array of prey items. In most regions individuals will hunt solitarily most of the time, and consume smaller staple prey items, such as medium sized mammals, in addition to scavenging for food. Throughout much of Australia the dingoes' primary prey is rabbits (Green and Catling, 1977; Marsack and Campbell, 1990). However, their flexible social structure allows dingo packs to hunt cooperatively in order to hunt larger prey when medium-sized prey declines, or when larger prey items, such as macropods, are more common (Corbett and Newsome, 1987; Marsack and Campbell, 1990; Thomson, 1992a; Whitehouse, 1977; Coman, 1972; Corbett, 1974; Robertshaw *et al.*, 1985; Shepherd, 1981).

In all parts of Australia, the dingoes' diet composes mainly of mammals – around 75% of total consumption on average, and up to 96% in some areas (Marsack and Campbell, 1990). Almost 80% of these mammals can be classed as medium sized and smaller. Nationwide, almost 80% of the dingoes diet comprises of 10 species, which strongly suggests that dingos are specialists, however in terms of hunting strategies, the generalist tag applies although a wide range of hunting tactics are used across its range (Corbett, 1995). Dingoes appear to prefer fresh prey, turning only to carrion when prey abundance declines during drought (Thomson, 1992a). As such, patterns in predation, particularly in the rangelands, may be strongly associated with rainfall, with certain species targeted during flush periods following rains, with other species more important in dingo diet during drier times (Corbett and Newsome, 1987).

Supplementary water and food resources (such as cattle) and high numbers of introduced prey species (namely rabbits) have been thought to have allowed for an increase in dingoes numbers across Australia to densities much higher than found prior to European settlement (Daniels and Corbett, 2003). This in turn increases predation pressure on native species when rabbit numbers decline, either through drought, or disease (Corbett and Newsome, 1987). Rabbit numbers have severely declined in many regions in number since the arrival of Rabbit

Haemorrhagic Disease (RHD), and the effects of this on long term dingo densities and impacts of native prey are yet to be determined.

Dingoes may have contributed to the demise of the thylacine (*Thylacinus cynocephalus*) (Archer, 1974; Fillios *et al.*, 2012; Letnic *et al.*, 2012a) and other native fauna species, such as the native hen (*Gallinula mortierii*) (Baird, 1991). It is recognised that dingoes play a key role in suppressing populations of large introduced herbivores in many ecosystems. Mortality rates of feral pigs (*Sus scofa*) have been closely associated with dingo abundance (Woodall, 1983) suggesting that dingo predation can reduce feral pig densities (Choquenot *et al.*, 1996). Similarly, dingo predation is important in the control of feral goats (Parkes *et al.*, 1996). While large numbers of feral goats and feral pigs are found throughout NSW, these species are found in much lower abundance in South Australia and Queensland where populations of dingoes remain (Newsome *et al.*, 2001). Dingoes also play a key role in regulating large native herbivores (Caughley *et al.*, 1980; Corbett and Newsome, 1987; Newsome *et al.*, 1983a). As such, the removal of dingoes from ecosystems often results in an unregulated increase in these prey species.

The importance the dingo may have in suppressing populations of other, smaller predators, in particular foxes, has been the focus of much recent debate. An inverse relationship has been found between the presence of dingoes and the density of foxes (Letnic *et al.*, 2010; Newsome, 2001) and direct predation on foxes has also been observed (Marsack and Campbell, 1990).

1.2.1.1 Control of dingo populations in Australia

Since the arrival of Europeans, the dingo has been regarded as a threat to livestock enterprises and consequently was controlled as an agricultural pest throughout much of the continent (Rolls, 1969). The current management of dingo populations in Australia is determined by a number of inter-related factors, including government policies and legislation, land tenure and landholder values. In many situations the dingo is a declared pest under legislation, while at the same time recognised as a native species, with an important functional role as a top predator. Adding to the confusion are inconsistencies between commonwealth and state legislation, which contain a conflict of information, identify dingoes as both a pest and protected species. Although 'pure' dingoes, those of genetic purity, are often thought of as separate from hybrid animals or feral dogs in such cases, an inability to identify live pure dingos in the field (Newsome and Corbett, 1982) means that generally all wild dogs are controlled in many landscapes.

As such, there are two major identifiable factors threatening dingo populations In Australia. The first of these is lethal control for the protection of livestock (Fleming and Korn, 1989). Dingo control is carried out by a number of methods, namely exclusion fencing (the major barrier being the Dingo Barrier Fence, hereafter DBF), shooting, trapping and poisoning (strychnine and 1080) (Fleming, 2000). Dingoes, as a wild dog, are a declared pest species on public lands in Western Australia, Queensland, News South Wales, Victoria, and as such, landholders are required to constantly control them. Dingoes remain unprotected in the Northern Territory, but are afforded a measure of protection in the Australian Capital Territory and within National Parks in other states. North and west of the DBF, in cattle grazing regions, dingoes are controlled by landholders individually as seen fit, and while some landholders practice regular control, others view dingoes favourably for their role in controlling populations of other agricultural pests such as feral pigs (Woodall, 1983), feral goats (Parkes *et al.*, 1996), rabbits (Allen and Sparkes, 2001) and over abundant native mammals such as macropods (Newsome *et al.*, 1989). A brief history of dingo control in NSW and SA as it pertains to this study is given in Chapter 2.

Targeted control of dingoes in select areas, seasons or particular prey cycles are strategies often used by government departments to meet legislative requirements and surrounding landholder expectations (Meek and Shields, 2001). The use of baited buffer zones is a common strategy employed to negate the impact of dingoes which move from protected areas, such as National Parks, to surrounding free-hold lands (McIlroy *et al.*, 1986a). However, the effectiveness of 1080 baiting as a control method to reduce livestock losses remains in question (Gentle *et al.*, 2007), as baited areas act as dispersal sinks for local dingo populations (Pulliam, 1988; Woodroffe and Ginsberg, 1998). Although baiting may reduce dingo abundance initially, livestock losses may in fact increase with a high likelihood of recolonisation of the baited areas by individuals from unbaited areas within 6 months of baiting taking place (Allen, 2000). Similarly, aerial baiting across large scale habitat is not effective in the long term, with dingoes increasing to initial numbers within one year (Fleming *et al.*, 2001a; Meek and Shields, 2001) and changes to the age structure and activity of populations increasing predation levels (Allen and Gonzales, 1998). Baiting in sheep production areas is often not effective due to high numbers of alternative prey (Allen and Sparkes, 2001). The loss of baits to non-target species, such as foxes, is common, and more research is needed into the impacts of large scale bating on native fauna populations (Glen and Dickman, 2003; Glen *et al.*, 2007b; Murray and Poore, 2004).

Practices used to reduce dingo densities may also have a direct impact on the maintenance of social structure of dingo populations (Thomson, 1986; Thomson and Marsack, 1992).The impact of 1080 baiting and other control methods, particularly aerial baiting, on the social structure of dingo populations is also unknown, but may include loss of pack cohesiveness, such as fracturing of packs may occur leading to the formation of an increased number of new packs, into which domestic dogs or dingo/dog hybrids may infiltrate more easily.

This leads to the second major factor threatening dingo populations: hybridisation with domestic and free-ranging (feral) dogs (*Canid familiaris*) (Elledge *et al.*, 2006; Wilton *et al.*, 1999). Close proximity to settled and agricultural areas has led to pure dingoes, those that have not been hybridised with domestic dogs, being rare, possibly extinct, in the eastern states. North and west of the DBF, the level of hybridisation decreases as remoteness from human settlements increases (Corbett, 1995). Because of the high levels of hybridisation in dingo populations in many areas, it is thought that protecting animals for their role in ecosystem function, regardless of appearance or genetic purity, would be the best approach for biodiversity conservation (Daniels and Corbett, 2003).

1.2.2 The Fox

The European Red Fox (*Vulpes vulpes*), hereafter referred to as the fox, is a medium-sized canid that was introduced to Australia in the 1870's for the sport of hunting. The fox is highly adaptable; from their original release in southern Victoria, foxes are now in a wide range of habitats across southern Australia (Figure 1.1), absent only from parts of arid Australia, Kangaroo Island, the tropical north and until recently Tasmania, where fox were deliberately released in 2001 (Lapidge and Berry, 2004).

The fox is a recognised agricultural pest in Australia (Saunders *et al.*, 1995; Saunders *et al.*, 2010), and predation by the fox has been shown to be a major cause in the decline and extinction of many native species (see section 1.5 of this chapter). The spread of the fox across mainland Australia appears to be strongly associated with the expanding distribution of the rabbit. Foxes are most common in agricultural areas where sheep are grazed, where there is a high abundance of rabbits and carrion from kangaroo shooting. These areas provide high and reliable food availability, den sites and few predators (Saunders *et al.*, 1995). In contrast, the distribution and density of foxes in arid Australia appears to be somewhat limited in the presence of high dingo densities north of the Dingo Barrier Fence (DBF) (see Chapter 2) (Wilson *et al.*, 1992). Foxes are also common in urban areas.

The behaviour and ecology of the fox varies widely between habitats, and is influenced by a number of factors including resource availability, resource distribution and climatic variability (Voigt and Macdonald, 1984). Foxes are primarily nocturnal, but may increase their diurnal activity when prey is scarce, such as in winter, which also coincides with cooler daytime temperatures in the arid zone (Saunders *et al.*, 1995). The diet of the fox is highly varied and seasonally influenced; although primarily carnivorous, the fox is an opportunistic scavenger and able to take a wide variety of prey. In arid and semi-arid Australia, foxes have been shown to have a preference for mammals, with many diet studies indicating rabbits as the staple prey item (Bayley, 1978; Martensz, 1971; Catling, 1988; Molsher *et al.*, 2000; Risbey *et al.*, 1999; Paltridge, 2002; Read and Bowen, 2001). Other regularly eaten prey items include macropods, small mammals and carrion (Banks *et al.*, 2000; Catling, 1988). Invertebrates, reptiles and birds may be seasonally or locally important in the diet (Holden and Mutze, 2002; Read and Bowen, 2001); particularly in the absence of rabbits (Paltridge, 2002), or after rainfall during "boom" rodent periods (Eldridge *et al.*, 2002). The fox has been found to live independently of free water (Sargeant, 1978), although it is probable that free water increases survival rates during summer in the arid zone, particularly in times of low prey availability.

Foxes usually live in family groups, the composition of which varies between habitats (Saunders *et al.*, 1995). In Australia family groups of foxes predominantly consist of one adult pair along with their current litter of cubs, which disperse upon maturity. Family groups occupy distinct territories, with well-defined borders that do not overlap (Meek and Saunders, 2000; Voigt and Macdonald, 1984). Foxes, as with other species of canids, keep territories intact by aggressive encounters and avoidance behaviours, the latter including scent marking and vocalisations. The extent of which a fox patrols its territory and visits territory boundaries may be determined by the size of the territory, but daily movements rarely exceed 10km (Saunders *et al.*, 1995). It may take up to two weeks for an individual fox to cover their whole territory in rural areas (Sargeant, 1972). Home ranges may also shift seasonally or when other territories become available, usually through the mortality of the resident fox (Voigt and Macdonald, 1984; Kinnear *et al.*, 1998). Home range boundaries are disregarded during juvenile/sub-adult dispersal and when males increase activity when looking for a mate (Saunders *et al.*, 1995).

Foxes pair up and breed once a year in early winter and have high reproductive success. Foxes are sexually mature in their first year, most adults breed, the average litter size is 4 cubs (but can be up to 10) and cub survival is high due to few diseases and natural predators. The main threats to cub survival include predation by birds of prey, dingoes and human induced mortalities (Saunders *et al.*, 1995). Cubs are born in early spring and disperse from their natal territory in late summer. The dispersal of sub-adult foxes begins in summer and goes all the way until the onset of winter breeding period (Figure 1.2).

The density of foxes in an area is determined by the productivity of the environment and the availability of resources, particularly that of food (Saunders *et al.*, 1995). Survival may also depend on foraging success and interspecific and intraspecific competition (Edwards *et al.*, 2002). In one study, the average density of foxes in arid zone over a 10 year period was estimated to be 0.6 km^{-1} (Read and Bowen, 2001). However, fox densities fluctuate dramatically between seasons and periods of climatic variation due to close association with prey abundance, disease and competitive interactions. Immigration is an important factor in maintaining large fox populations, and this is a significant problem with removal management strategies, as the removal of resident foxes has been shown to increase the activity of survivors (Fleming *et al.*, 1996).

1.2.3 The Feral Cat

The feral cat (*Felis catus*) (referred to hereafter as separate from domestic, stray or semi-feral individuals of the same species) is a medium-sized carnivore exotic to Australia. The origins of the first introduction of the species to the continent remained under scrutiny for some time, however an evaluation of historical sources has revealed that domestic cats were brought to Australia by Europeans in the early nineteenth century and introduced from multiple points along the coastline (Abbott, 2002) with further releases outside settled areas to control rodent and rabbit outbreaks (Rolls, 1969). The descendants of these animals became independent from reliance on humans, and 'feral' cats became established across the whole continent.

The feral cat is now found throughout Australia (Figure 1.1). Feral cat densities vary across habitats and appear to be determined by food availability (Molsher *et al.*, 1999), particularly rabbits and possibly the existence of other predators in the ecosystem, such as foxes (Molsher, 1998) or dingoes (Kennedy *et al.*, 2011). The relative densities recorded for feral cats in the arid zone are low overall, but can fluctuate locally with the variability of the arid environment, probably reflecting the boom in prey numbers in response to rains (Pettigrew, 1993).

Feral cats are usually solitary (Page *et al.*, 1992), with individuals meeting only to mate (Leyhausen, 1979). However, feral cats have been found to be communal under some circumstances, such grouping in areas of abundant, localised prey (Pettigrew, 1993). In most situations, male and female individuals defend a distinct territory which forms the core area of their home range. Home ranges of individuals overlap (Leyhausen, 1979; Molsher *et al.*, 2005) and consist of a number of regularly visited localities connected by a network of pathways (Corbett, 1979). Home range size appears to vary with prey distribution and abundance (Fitzgerald and Karl, 1986), with smaller home ranges found where prey populations support higher feral cat densities (Edwards *et al.*, 2001). In general, home range size varies between sex and size, with males occupying larger home ranges than females (Jones and Coman, 1982b) and larger cats occupying larger areas (Molsher *et al.*, 2005). In semi-arid Victoria the mean average home range size for male feral cats was 620 ha, and for females 170 ha (Jones and Coman, 1982b), while mean home ranges recorded in open woodland in NSW were 288 ha for males and 140 ha for females (Molsher *et al.*, 2005). In semi-arid woodlands, male feral cats occupied much larger home-ranges to account for lower prey densities (2210.5 ha) (Edwards *et al.*, 2001).

A number of factors have been shown to influence the circadian activity of feral cats, such as season, sex, social status, activity and density of primary prey species (Konecny, 1987) and avoidance of potential predators (Langham, 1992). This being so, feral cats are primarily nocturnal hunters (Page *et al.*, 1992), with an increase in diurnal activities recorded in habitats with adequate shelter (Molsher *et al.*, 2005). Feral cats display different hunting strategies depending on the prey species targeted; they both stalk and ambush prey or lie in wait for prey to approach (Dickman, 1996b). For these hunting strategies, habitats in the arid zone with adequate cover are more optimal for the cat to avoid detection, while open or unprotected habitats make prey more visible and therefore more vulnerable to predation (Dickman, 1996b). In arid regions, feral cats appear more common in sheltered habitats, such as grasslands (Gibson *et al.*, 1994) and creek lines (Southgate *et al.*, 2007), while studies in semi-arid areas record feral cats' habitat use in proportion with availability, with a preference for wooded areas (Molsher *et al.*, 2005). The predator's small size and flexibility allow it to access rabbit burrows with ease; research has shown that rabbit burrows are commonly used for shelter (Jones and Coman, 1982b; Molsher *et al.*, 2005).

The diet of the feral cat in arid and semi-arid areas is varied; prey items include a wide range of native mammal, birds and reptile species, including species up to about 2000gm (Gibson *et al.*, 1994). Feral cats are known to show a dietary preference for smaller mammals such as young rabbits, rodents or small marsupials when available, particularly species <350gm (Catling, 1988; Dickman, 1996b; Paltridge *et al.*, 1997; Risbey *et al.*, 1999; Molsher *et al.*, 1999) while seasonally birds, reptiles or invertebrates may become more important (Paltridge *et al.*, 1997).

Feral cat densities and diet have been shown to respond to availability of prey (see review in Dickman, (1996b). Feral cats may exhibit prey-switching behaviour to more abundant prey both during times of drought or food shortages (Catling, 1988; Molsher *et al.*, 1999; Risbey *et al.*, 1999) and in response to prey increases after rains. For example, the dramatically fluctuating populations of the long-haired rat (*Rattus villosissimus*) became prominent in the diet of feral cats during the rodent's population "boom" periods (Paltridge *et al.*, 1997). Preferred prey items may be seasonal, with feral cats increasing their reliance on reptiles and small mammals during the summer to early autumn (Bayley, 1976), while rabbits form the majority of the diet during the winter and spring months (Bayley, 1978). Larger individuals have been known to take adult rabbits (Paltridge *et al.*, 1997) and there is some evidence to suggest that feral cats may aid in the regulation of rabbit populations when rabbits occur at low densities (Newsome *et al.*, 1989; Pech *et al.*, 1992). Carcasses are not used as a regular food source as often as dingoes and foxes, but cats have been known to scavenge during times when prey is scarce (Catling, 1988; Paltridge *et al.*, 1997; Jones, 1977) or when carcasses are readily available (Molsher *et al.*, 1999).

Feral cat litters have been recorded from September to March in NSW (Molsher, 2001) and all months of the year except April in Victoria (Jones and Coman, 1982a). Domestic cat females come into oestrus 2-3 times per year. Similarly, two peaks in breeding have been recorded in feral cat populations in semi-arid NSW, with the larger peak occurred during September-

October and a smaller peak in December-January (Molsher, 2001). The young become independent after about 6-8 months (Leyhausen, 1979). Feral cat populations appear to peak in abundance during late summer (Jones and Coman, 1982b), which would coincide with the independence of juveniles from spring litters (Figure 1.2). There appears to be high mortality of kittens (Molsher, 2001), juveniles and sub-adults (Jones and Coman, 1982a) in feral cats populations. Direct predation on feral cats has been recorded by both foxes (Lunney *et al.*, 1990; Paltridge, 2002; Risbey *et al.*, 1999) and dingoes (Paltridge, 2002).

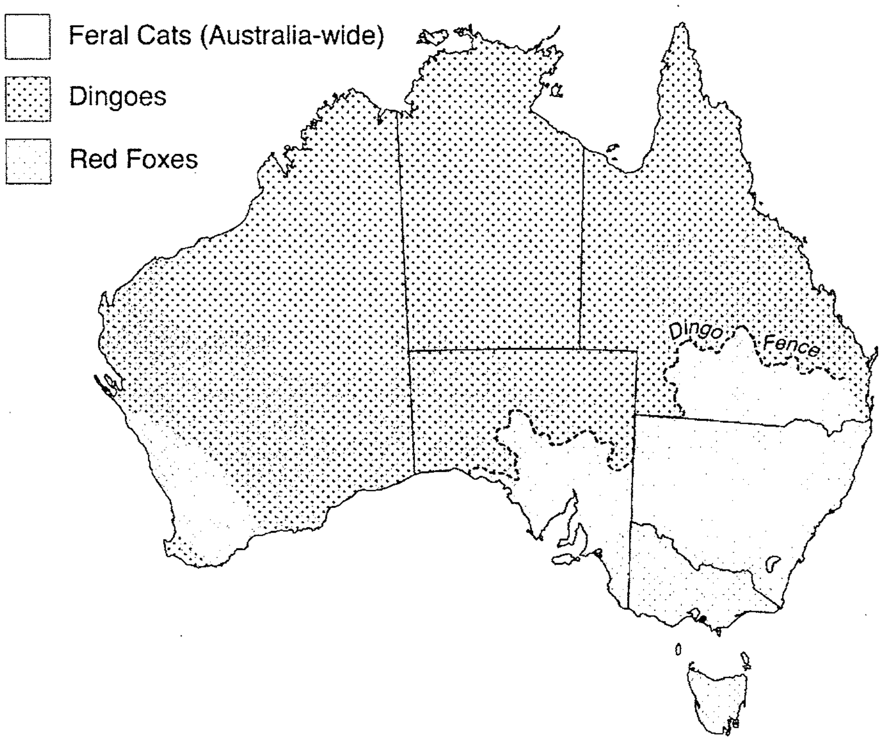


Figure 1.1. Map of current distribution of dingoes, foxes and feral cats in Australia.
Darker areas indicate overlapping distribution of the three predators.

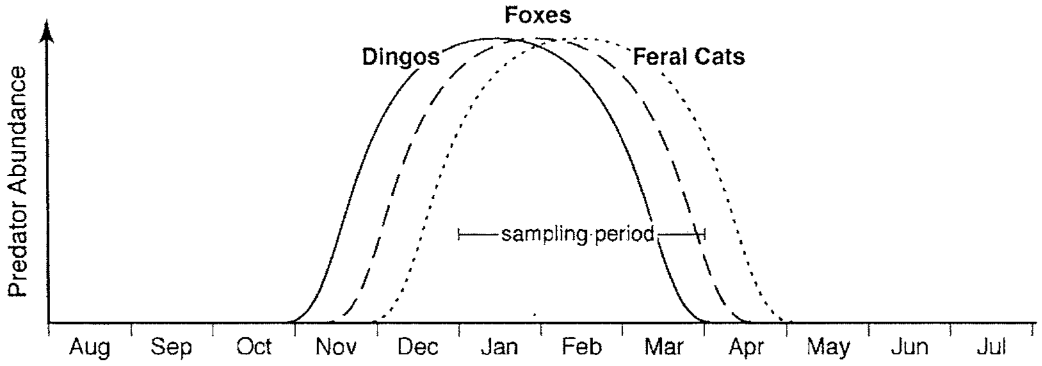


Figure 1.2 A time line of abundance in relation to breeding activity for dingoes, foxes and feral cats in arid Australia.

1.3 The role of predation by foxes and feral cats in the decline of native fauna in arid Australia

The modern decline of native fauna across Australia has been attributed to interactions between predation, reduced vegetation cover, disease, land use changes, introduced herbivores and grazing by domestic stock, changing fire regimes and most recently, climate change (Burbidge and Mckenzie, 1989; McKenzie *et al.*, 2007). However, predation by exotic mesopredators, particularly the red fox (Maxwell *et al.*, 1996; Saunders *et al.*, 2010), is thought to be the most important mechanism facilitating declines (Burbidge and Mckenzie, 1989; Morton, 1990; Dickman *et al.*, 1993; Smith and Quin, 1996; Smith *et al.*, 1994a; McKenzie *et al.*, 2007). Introduced predators have led to the extinction of insular species and a decline in biodiversity in many ecosystems (Courchamp *et al.*, 1999) with endemic prey populations particularly vulnerable to exotic mesopredators (Crooks and Soule, 1999; Soulé *et al.*, 1988; Zavaleta *et al.*, 2001; Sargeant, 1972; Salo *et al.*, 2007).

Increases in fox distribution and abundance following the expansion of agriculture across Australia coincided with the local and regional extinctions of many native fauna species (Southgate, 1990; Short, 1998; Friend, 1990). Loss of mammalian fauna across Australia has been particularly severe in arid areas (Smith and Quin, 1996), with species declines of up to 40% in some regions (Dickman *et al.*, 1993). The effects of fox predation are particularly key for small to medium-sized ground-dwelling mammals (Burbidge and Mckenzie, 1989; Dickman, 1996a; Dickman *et al.*, 1993; Short *et al.*, 1998).

In a review of extinctions of terrestrial vertebrates in Western Australia, Burbidge and McKenzie (1989) found virtually all species that had exhibited severe declines to be non-arboreal species with mean adult body weights between 35gm and 5500gm. These 'critical weight range' species are highly vulnerable to fox predation and many now persist only on islands or areas of the mainland where foxes are rare or absent (Saunders *et al.*, 2010). Predator-removal experiments have demonstrated that fox predation continues to suppress extant populations of several species (Kinnear *et al.*, 1998; Banks *et al.*, 2000) and has led to the failure of reintroduction experiments (Calver *et al.*, 1998; Short *et al.*, 1992).

The impact of feral cats on native wildlife remains less understood (Dickman, 1996b; Dickman, 1996a). Feral cats prey on a wide variety of native fauna species (Dickman, 1996b; Edwards *et al.*, 2001), but the most vulnerable appear to be ground foragers and nesters and communal species <220gm. In particular, small mammals < 35gm appear to be a more important dietary item for cats than for foxes (Risbey *et al.*, 1999; Read and Bowen, 2001; Smith and Quin, 1996). Reptiles and birds may also be more at risk of predation by cats and may sustain feral cat populations when rabbits or small mammals are at low densities (Edwards *et al.*, 2001). Cats are also known to impact on populations of medium sized mammals (Horsup and Evans, 1993; Christensen and Burrows, 1995b; Gibson *et al.*, 1994), with impacts of feral cat predation particularly key on island ecosystems (Burbidge and Manly, 2002). Evidence strongly suggests that predation by feral cats has contributed to the decline and extinction of a number of native species on mainland Australia (Dickman *et al.*, 1993; Gibson *et al.*, 1994; Horsup and Evans, 1993) and offshore islands (Jones, 1977), including species of rodent, bandicoots and ground nesting birds (Abbott, 2002). Of the mainland species, most declines have occurred in arid areas (Dickman, 1996b). The unsuccessful of reintroduction of endangered mammals such as the boodie (*Bettongia lesueur*) and mala (*Largorchestes hirsutus*) into arid areas has also attributed to predation by feral cats (Christensen and Burrows, 1995a; Gibson *et al.*, 1994).

Declines in many native species moved from east to west across the continent following agricultural expansion (Dickman *et al.*, 1993). Reduced habitat lead to increased invasion by introduced species and increased vulnerability of prey, with fox invasion coinciding with the greatest species losses Short (1998). In many cases exotic predators caused severe reductions in the abundance and geographical range of prey species (Burbidge and Mckenzie, 1989). However, impacts of predation vary spatially and temporally depending on other contributing factors (Fisher *et al.*, 2003).

Fisher *et al.* (2003) modelled intrinsic and extrinsic factors implicated in the decline of Australian marsupials and found the most consistent predictor of decline was overlap with the range of sheep. While some authors argue the mechanism by which sheep affect persistence is habitat degradation associated with pastoral expansion (Lunney, 2001), the abundance of sheep is strongly correlated to fox abundance and negatively correlated with dingo abundance (Letnic *et al.*, 2009b). For example, Smith and Quin (1996) presented evidence that fewer species of conilurine rodents have suffered extinction or significant range reductions within the range of the dingo due to negative correlation with foxes, rabbits and sheep.

1.3.1 Control of foxes and feral cats in Australia

Control of fox and feral cat populations is necessary for the successful establishment of reintroduced populations (Short and Turner, 2000; Kinnear *et al.*, 2002; Friend and Thomas, 1995) and for the persistence of many endangered and vulnerable species (Friend, 1990; Friend and Thomas, 1995; Kinnear *et al.*, 2010; Kinnear *et al.*, 1998; Short *et al.*, 2002). Control of foxes in Australia is carried out primarily through baiting, shooting, trapping and for small areas of high conservation exclusion fencing (Saunders *et al.*, 2010; Moseby *et al.*, 2009; Moseby and Read, 2006). Baiting with sodium monofluoroacetate (1080) is the most common control method in many regions, and is effective due to the high tolerance of native species to the toxin (de Tores *et al.*, 2011). This reflects the natural occurrence of sodium monofluoroacetate in the native flora genus *Gastrolobium,* which occurs throughout Western Australia. Lower tolerance is found in native fauna in the eastern states, and the susceptibility of native predators such as the tiger quoll *Dasyurus maculatus,* means the poison must be used with some caution in these areas (Glen *et al.*, 2007b; de Tores *et al.*, 2011; McIlroy, 1986; McIlroy, 1992; McIlroy *et al.*, 1986b; Murray and Poore, 2004). In addition, control of feral cats through poison baiting is limited due to the small uptake of baits (de Tores *et al.*, 2011; Risbey *et al.*, 1997; Short *et al.*, 1997).

While initial declines in foxes occur following control, effects may be limited and short term (Gentle *et al.*, 2007; Harding *et al.*, 2001). Immigration may lead to rapid reinvasion of foxes into treatment areas (Priddel and Wheeler, 1997), therefore fox control programs for the protection of biodiversity are usually conducted regularly for sustained control (Gentle *et al.*, 2007; Saunders *et al.*, 2010). Total eradication is not an option in most areas, so perpetual money, time and labour are spent on no-end-in-sight programs, with costs of fox control greater by far than any other pest species (Reddiex and Forsyth, 2006; Reddiex *et al.*, 2006). A significant reduction in time, labour, money and biodiversity loss may arise from utilising a biological control for both foxes and feral cats - a naturalised apex predator, the dingo.

1.4 Top carnivores and trophic cascades – the mesopredator release hypothesis.

Knowledge on how populations are regulated is important to understand ecosystem function (Murdoch, 1994). Ecologists have recognised the importance of this understanding for successful ecosystem management, and as such processes of population regulation have been the focus of much ecological research over the past decades. Theories such as the niche concept (Hutchinson, 1957), source-sink theory (Pulliam and Danielson, 1991; Dias, 1996; Pulliam,

1988) and traditional food web models (Paine, 1980; Elton, 1927) have emerged in an attempt to explain observed patterns.

However it has recently been recognised that some of the earlier theories that emerged in food web ecology may fail to recognise the importance of intra specific and interspecific interactions (Polis, 1991). For example, food web models commonly identify primary producers, herbivores and carnivores as segregated units, failing to accommodate the importance of individual animal-plant and animal-animal interactions (Hunter and Prices, 1992). Traditionally tiered models of tropic levels assume predators only eat the level below them (Spiller and Schoener, 1994) while in fact in many ecosystems interactions are much more complex. Interaction strength and vulnerability is not equal between all predators and prey (Schmitz and Suttle, 2001; Schmitz *et al.*, 2008) and in addition to density mediated effects, behaviourally (trait) mediated effects may play an important role in ecosystem function (McPeek, 1998; Schmitz *et al.*, 2008; Schmitz and Suttle, 2001; Schmitz *et al.*, 2004).

The stability of populations is affected by food web structure (Macarthur, 1955) and the community interactions this structure generates (Krebs, 2002). Their position at the top of the trophic web means that apex carnivores can have significant influence on community structure through direct and indirect effects (Terborgh, 1988; Schmitz, 2007; Paine *et al.*, 1990) and their presence in an ecosystem can often be an indication of ecological stability, richness and diversity (Estes, 1996; Santiapillai and Jayewardene, 2004; Sergio *et al.*, 2006). In contrast, the removal of top predators from ecosystems can have cascading effects down through the trophic web (Schmitz *et al.*, 2010; Schmitz *et al.*, 2000; Pace *et al.*, 1999; Estes *et al.*, 2011), impacting indirectly the abundance (Crooks and Soule, 1999; Soulé *et al.*, 2005) and diversity (Schmitz, 2006; McPeek, 1998; Terborgh, 1992) of species in lower trophic levels.

The control of top predators in some ecosystems has led to unknown and unintended effects on the abundance and diversity of other organisms (Paine, 1980; Estes *et al.*, 2011). The importance of top predators in structuring such ecosystems is often recognised only after apex predator populations have been reduced or eradicated. For example, the extermination of a once common apex predator, the sea otter (*Enhydra lutris*), from marine ecosystems has led to an over-abundance of sea urchins, the sea otters' main prey, and a decreased algae communities on which the urchins feed (Estes and Palmisan, 1974). The removal of sea otters was also associated with changes in the foraging activities of other marine species, such as gulls (Trapp, 1979), and has been implied as a possible contributing factor in extinction of a marine mammal, Steller's sea cow (*Hydrodamalis gigas*), which was highly dependent on the algae communities for food (Haley, 1978).

Evidence of top predators structuring communities is predominately from marine ecosystems (Estes *et al.*, 2004; Estes *et al.*, 2009; Estes and Palmisan, 1974; Williams *et al.*,

2004) or invertebrate predator interactions (McPeek, 1998; Schmitz, 2007; Schmitz *et al.*, 2000). Evidence for the top-down regulation by mammalian carnivores in terrestrial ecosystems is still emerging (see reviews in Estes *et al.* (2011), Pace *et al.* (1999) and Strong (1992). Large carnivores have been eradicated from many terrestrial ecosystems primarily due to conflict with human interests such as hunting (Crooks, 2002; Weber and Rabinowitz, 1996) and livestock enterprises (Allen and Sparkes, 2001; Treves and Karanth, 2003; Kleiven *et al.*, 2004; Nilsen *et al.*, 2007; Patterson *et al.*, 2004).

In terrestrial ecosystems, large carnivores have been shown to play a vital role in controlling herbivore populations (Nilsen *et al.*, 2007; Ripple and Beschta, 2006; Ripple and Beschta, 2008), and may limit the abundance of smaller predators in some communities (Palomares *et al.*, 1995; Berger *et al.*, 2008; Letnic *et al.*, 2010; Creel and Creel, 1996). The extermination of the North American grey wolf (*Canis lupus*) and its recent reintroduction back into some part of America has shown the effect of wolf removal on large herbivore populations and plant community diversity and structure (Beschta and Ripple, 2007; Ripple and Beschta, 2004; Ripple and Larsen, 2000; Ripple *et al.*, 2001; McLaren and Peterson, 1994). Wolves have also been found to have top-down effects on smaller predators, such as coyotes (Berger and Conner, 2008; Berger and Gese, 2007). Experimental removal of coyotes as the apex predator has led to a decline in the abundance and diversity of prey species, including rodents and birds, and an increase in the relative abundance of mesopredators (Henke and Bryant, 1999; Rogers and Caro, 1998).

In an attempt to understand the role of intraguild interactions in community structure, the predator-mediated coexistence hypothesis recognises that keystone predators (Paine, 1966; Paine, 1995) play a role in mediating the abundance and distribution of other predators, which in turn increases the diversity and abundance of prey species due to competition and differences in predator prey preference (Caswell, 1978). Furthering this, the mesopredator release hypothesis (MRH) (Rogers and Caro, 1998; Soulé *et al.*, 1988) states that large predators have a suppressive effect on smaller predators (hereafter mesopredators) and indirectly a positive net benefit on mesopredator prey. Where top predators have been removed, mesopredators, once limited by larger carnivores, may increase, thus increasing predation pressure on select prey vulnerable to mesopredator predation (Sargeant, 1972; Crooks and Soule, 1999; Henke and Bryant, 1999; Schoener and Spiller, 1999; Wallach *et al.*, 2009a).

Evidence is still emerging in support of the MRH, and some authors remain critical of its relevance to certain ecosystems. Not all authors support a link between top predators and biodiversity (Andelman and Fagan, 2000) and in some ecosystems the effects may be species-specific (Gruner, 2004) (also see review in Sergio *et al.* (2008) or depend on productivity, human induced effects, habitat complexity, prey life-histories and other intrinsic factors (Russell *et al.*, 2009; Ray, 2005; Boyer *et al.*, 2003). It has been suggested that the MRH does not take into account anthropogenic changes to the landscape (Litvaitis and Villafuerte, 1996) and that top down regulation, and thus mesopredator release, may only occur in resource-abundant ecosystems (Russell *et al.*, 2009) Some ecologists argue that "bottom-up" forces, where ecosystems are regulated by movement of energy up the food chain (Power, 1992), have primacy due to the very existence of all fauna including high trophic levels relying on energy generated by primary productivity (Hunter and Prices, 1992; White, 1978). Such arguments are particularly relevant to arid regions, where large variability in resource availability may strongly affect trophic interactions.

A further obstacle for support of the MRH in many ecosystems is that research is often hindered by logistical limitations. Using traditional experimental designs (e.g. BACI), apex predator populations would need to be manipulated over large temporal and spatial scales. As this is often impractical in field situations, research is often conducted on small spatial scales which may be irrelevant to the large-scale processes, such as habitat fragmentation or lethal control, by which top-predators are removed (Schmidt, 2003). In addition, snap-shot studies of communities where top predators were exterminated decades ago often inaccurately link current ecosystem states to past processes and fail to consider the lack of appropriate baselines in the interpretation of research outcomes (Elmhagen and Rushton, 2007). Other studies examining mesopredator release effects in ecosystems have relied on a combination of data sets for correlative analysis (Johnson *et al.*, 2007) leaving room for other interpretations due to random and influencing variables on prey species (Polis *et al.*, 2000). Finally few MRH studies have measured the response of mesopredators to top predator removal (Gehrt and Prange, 2007; Prange and Gehrt, 2007). Instead, the majority of studies have focused on the response of mesopredator prey to the removal of top predators (Berger *et al.*, 2001; Crooks and Soule, 1999; Schmidt, 2003; Letnic *et al.*, 2009a; Wallach *et al.*, 2009a).

While debates remain on the relative importance of "top-down" vs. "bottom-up" (Paine, 1966; Polis and Strong, 1996), most researchers now agree that both top down and bottom up forces act on ecological communities simultaneously (Sinclair and Krebs, 2002; Menge and Sutherland, 1976; Hunter and Prices, 1992; Power, 1992; Menge, 2000). As such, the major challenge to ecologists now is to gain an understanding of the relative strength of top-down and bottom up forces in regulating populations (Borer *et al.*, 2005), and under what ecological states the importance of each changes (Hunter and Prices, 1992; Courtney, 1988). For example, productivity may determine food web structure, while top-down forces may dominate trophic dynamics (Fretwell, 1977). In addition food-webs are dynamic; interactions and strength of bottom-up or top-down forces may vary seasonally, over geographical areas and in response to other environmental change (Paine, 1980).

Finally, while many studies have attempted to determine the relative importance of top-down or bottom-up regulation, rarely have any attempted to examine the role of behaviour in mediating trophic cascades (Spiller and Schoener, 2001; Lima, 1998). The presence of intra-guild interactions in different forms and strengths adds a complex dimension to trophic webs that needs to be considered (Polis and Holt, 1992). For example, apex predators may influence mesopredators abundance through direct predation, or indirectly through intra-guild interactions such as interference competition or instigating avoidance behaviours (see review in Chapter 6). Similarly, top down effects may mediate prey behaviour through stimulating anti-predator defences (Lima, 1992; Williams *et al.*, 2004), leading to differing prey vulnerabilities (Spiller and Schoener, 1994; Schmitz *et al.*, 2004). While knowledge on the importance of trait-mediated interactions as a mechanism in trophic cascades is limited (Turner and Mittelbach, 1990), it is likely both predator and prey behaviour play a key role in the dynamics of most ecosystems (Lima, 2002; Lima and Zollner, 1996).

1.5 Interactions between dingoes, foxes and feral cats - potential for mesopredator release?

In Australia, the dingo fills the niche of top carnivore in many ecosystems, primarily in arid areas and the northern biomes west and north of the DBF. In arid regions, introduced feral cats and foxes, in addition to native reptiles and raptors, occupy the niche of mesopredator. While it is likely that interactions between dingos, foxes and feral cats are important in ecosystems where the three predator species co-occur (see Figure 1.1, this chapter), mechanisms behind such interactions remain poorly understood (Glen and Dickman, 2005).

A negative correlation between dingo and fox abundance has been found in arid ecosystems (Letnic *et al.*, 2010) and other bioregions (Catling and Burt, 1995; Johnson and VanDerWal, 2009; Letnic *et al.*, 2010). Similarly, studies involving apex predator manipulation have demonstrated an increase in fox abundance when dingo populations were reduced through control (Jarman, 1986; Thomson and Marsack, 1992). Feral cat abundance has also been shown to be negatively correlated with dingo and fox abundance (Catling and Burt, 1994), with local declines in dingo populations leading to dramatic increases in feral cats (Kennedy *et al.*, 2011; Pettigrew, 1993). Studies suggest feral cat abundance may increase when foxes and dingoes are controlled (Molsher *et al.*, 1999; Short *et al.*, 1997) which may in turn lead to a decrease in small mammal abundance (Risbey *et al.*, 2000).

Interactions between dingoes and exotic mesopredators may be either through direct effects such as predation (Karki *et al.*, 2007), opportunist killing (Berger and Gese, 2007; Palomares and Caro, 1999) or suppression of reproductive success, including reduced survival of young. Direct killing of foxes by dingoes (Marsack and Campbell, 1990) and local avoidance of dingoes by foxes (Mitchell and Banks, 2005) have been recorded. Cats are eaten consistently but infrequently by dingoes (Corbett, 1989) and occasionally foxes (Coman, 1973).

Alternatively, indirect mechanisms may important in dingo/fox/cat interactions, such as niche overlap in habitat, food or temporal dimensions (Schoener, 1974; Arjo and Pletscher, 1999; Major and Sherburne, 1987; Gosselink *et al.*, 2003). Competition during food shortages and prey declines is likely to occur due to dietary overlap. Mammals predominate in the diet of all three predators with rabbits the primary prey in many areas. However, while dingoes and foxes tend to target medium sized mammals, feral cats focus on small mammals, and only dingoes target large mammals such as macropods (see section 1.2 of this chapter). This segregation of prey sizes may result in fundamental differences in niche dimensions and reduce competition between species (Neale and Sacks, 2001a; Rosenzweig, 1966). High populations of primary prey, such as rabbits, also allow populations of feral cats and foxes to persist in the presence of dingoes as they buffer them from interspecific competition. Competition then increases between the species when staple prey populations are in decline, and dingo packs may then out-compete foxes and feral cats as cooperative hunting increases access to larger prey.

Dingoes may also instigate avoidance behaviour in the smaller carnivores (Sargeant *et al.*, 1987; Vanak *et al.*, 2009; Scheinin *et al.*, 2006; Durant, 1998; Hayward and Slotow, 2009; Voigt and Earle, 1983), particularly when competition for shared resources such as prey, water and shelter, is high, and dingoes may then dominate such resources through interference competition (Johnson and Franklin, 1994; Switalski, 2003; Henke and Bryant, 1999). Dingoes may thus limit access to shared resources (prey, carcasses and water) by facilitating avoidance, or through direct interactions such as predation and aggressive encounters. Environmental conditions may play a key role in determining the presence or strength of interactions between predator species (Linnell and Strand, 2000), which are likely to vary with season, habitat, prey abundance and across bioregions (Visser *et al.*, 2009) (see Appendix 1)

It is important to understand mechanisms behind trophic interactions for optimal management of biodiversity (Schoener, 1974; Tilman, 1987). While dingoes may have negative impacts on larger native prey species, such as macropods, if dingoes can suppress populations of foxes and cats either by direct or indirect mechanisms, retaining dingoes in ecosystems may be beneficial for the survival of smaller native prey species vulnerable to fox and cat predation (Dickman, 1996a; Risbey *et al.*, 1999; Risbey *et al.*, 2000; Short and Smith, 1994).

1.6 Aims and scope of thesis

This thesis aims to investigate the possible role of the dingo, as an apex predator, in structuring ecological communities of arid Australia through top-down effects. By monitoring activity and resource use of dingoes, foxes and feral cats at select study sites, this research examined whether management of dingo populations influences the activity and behaviour of two exotic mesopredators, the red fox and feral cat. In doing so, behavioural change is explored as a possible mechanism through which the dingo may regulate mesopredator populations in arid Australia.

Based on information gained from reviewing the published literature, I constructed a plausible conceptual model of the major plausible interactions between the three predators, prey and key ecosystem variables for a theoretical arid zone ecosystem (Figure 1.3). Based on this conceptual model I proposed the following research questions:

1. Does dingo management influence the activity of mesopredators (foxes and feral cats) and select prey species?
2. Does dingo management influence the use of habitat by mesopredators?
3. Does dingo management influence the effect of proximity to water resources on mesopredator activity?
4. Does dingo management affect the visitation rates and behaviour of mesopredators at shared resources (food and water)?

In arid regions, rainfall has a dramatic effect on prey abundance and distribution, and drought may enhance the effect of interactions between the predators through increasing competition for limited food and water. Therefore I also posed the question:

5. After a prolonged dry period, how does a rainfall event affect the predator interactions examined in the questions above?

From these questions, and consistent with the MRH, I hypothesised that:

- Foxes, feral cats and large prey (macropods) will decrease their activity when dingo populations remain uncontrolled, while medium sized and small prey (including mammals and reptiles) will increase activity.
- Where dingo populations remain uncontrolled, foxes and feral cats will increase their use of more sheltered habitats and avoid habitats frequented by dingoes.
- Foxes and feral cats will decrease activity in close proximity to water resources where dingo populations remain uncontrolled.
- At sites where dingo populations remain uncontrolled dingoes will dominate shared resources such as food and water, and foxes and feral cats will display decreased visitation rates and time spent at resources.

- These interactions will remain consistent even with an increase in productivity following rains.

If feral cats or foxes are found to be avoiding areas of high dingo activity, not exploiting potential food or water sources, or changing activity patterns in areas where dingoes are present, this may indicate evidence of top down effects of dingoes on mesopredators. Dingo management strategies or control measures may influence intraguild interactions and have important implications for biodiversity conservation.

The thesis structure is composed of ten chapters divided into three distinct sections. The first three chapters introduce the subject and outline the methods used. This first chapter introduces the study species, background literature and relevant hypothesis as they pertain to this research. Chapter 2 provides the background of the study sites, study rationale and experimental design, and also outlines general field methods used. Chapter 3 describes the use of innovative technology to develop a new method to monitor behaviour and interactions of predators at shared resources.

Chapters 4, 5, 6 and 7 include analysis of field data to address the research questions outlined above. Chapter 4 examines the effect of dingo management on the activity of dingoes, cats, foxes and select prey species at each study site, both prior to and post a large rainfall event. Chapter 5 examines the effect of dingo management on habitat use by dingoes, foxes and feral cats. Chapter 6 examines the effect of dingo management on predator activity in proximity to water, both prior to and post a large rainfall event, while Chapter 7 examines the effect of dingo management on the behaviour and visitation rates of predators to shared resources such as water and carcasses.

The third and final section of the thesis focuses on synthesis and discussion of research findings. Chapter 8 uses Bayesian analysis to synthesis research outcomes into one model which assesses the relative strength of dingo, mesopredator and prey interactions. The model draws its initial structure from the influence diagram presented in Figure 1.3, and in light of study findings from Chapters 4-7, tests this conceptual model and related hypotheses presented in this thesis. Chapter 9 is the general discussion where the research outcomes are discussed in the context of existing literature, while Chapter 10 is the concluding chapter of the thesis, summarising pertinent study findings and suggesting possible directions for future research to increase our understanding of the role of dingoes in arid ecosystem function.

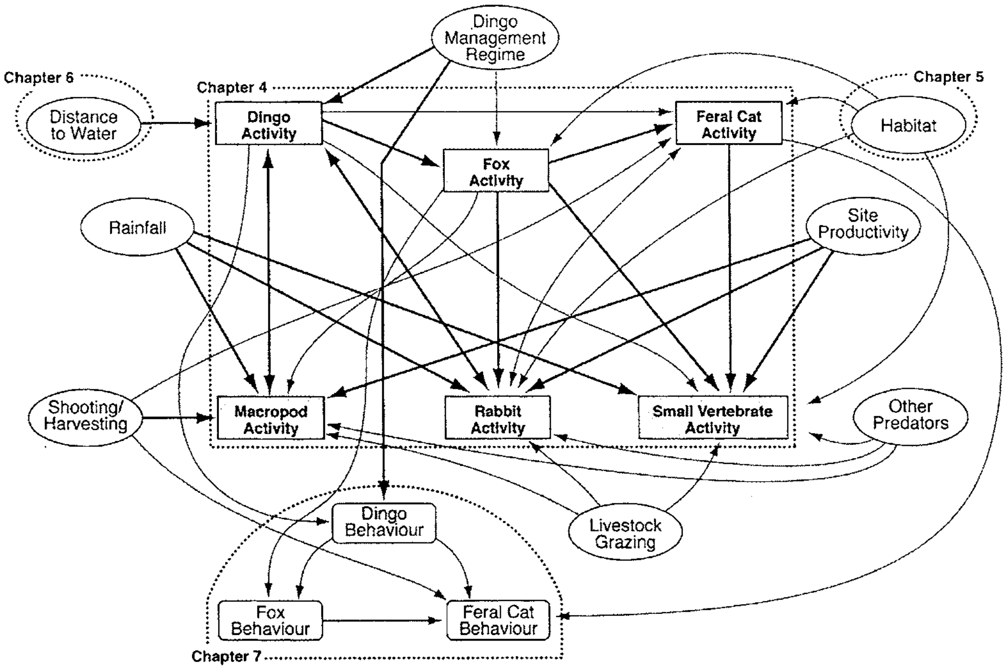


Figure 1.3 Conceptual model of interactions between predators (dingoes, foxes and feral cats), and between predators, prey and regulating factors of an arid environment.

The conceptual model was developed in the form of an influence diagram; arrows indicate possible strength of interactions as sourced from literature and in line with the MRH. Box shape and shading shows links between animal activity, behaviour and environmental variables as investigated in indicated chapters of this thesis.

Chapter 2: Experimental design, study sites and assessment of predator and prey populations

2.1 Experimental Design

2.1.1 Introduction

For the reasons discussed below, this study was conducted as an observational study (Altmann, 1996). It relied on the opportunistic observation of uncontrolled events at five selected study sites, each with predator and prey populations that had been affected by differing management histories.

An ideal experimental design for this study would encompass a large scale, controlled experiment (Englund, 1997) with purposefully manipulated predator populations monitored over a long period of time (Krebs, 1991). Data may also be recorded on predator and prey populations prior to manipulations taking place (Green, 1979). A large scale experiment would cover tracts of land that included a wide variety of landscapes, large experimental areas with a high number of animals at each sample site and data collected over a period of 5-10 years (Heske *et al.*, 1994).

In a PhD situation, sampling large experimental areas over a long time frame is impractical. The design of this study was limited by the fact that a PhD timeframe only allows for 2-3 years of sampling. Another limitation is that most accessible tracts of land across arid Australia have predator and prey populations that have been previously manipulated due to varying land management regimes. On grazing lands, dingoes and foxes are often controlled by baiting or shooting and some prey populations, such as macropods, may be harvested. In addition, the majority of the accessible arid lands are under pastoral lease. Studies conducted on pastoral leases must take into account confounding variables such as increased water availability through artificial water points, and grazing by stock, which may change vegetation patterns and supply alternative food resources for predators (Molsher *et al.*, 2000; Newsome *et al.*, 1983a; Paltridge *et al.*, 1997; Read and Bowen, 2001; Whitehouse, 1977). The difficulties arising from such changes are exacerbated when working with private landowners as differing agendas also may result in a sudden change in management strategies during the period of sampling.

This study took into account the above considerations by incorporating current and previous manipulations of both predator and prey populations in the final experimental design. When designing the study a trade-off had to be made between an experimental design that sampled a small amount of detail from many sites with increased replication. The design which was finally chosen took the latter path where a relatively large number of observations were taken at only a few sites. Logistically it was not feasible to sample a large number of sites at any level of detail. Timeframes, funding and logistical constraints as well as the large distances involved in travelling between study sites meant that only a few sites in a limited area could be sampled.

2.1.2 Experimental Design Rationale - Dingo control in Australia

A major logistical and experimental constraint when studying dingo populations, particularly when attempting to tease out interactions with other species, is that many populations have been or are currently subject to control in some form. The overarching question of the role the dingo may play in trophic regulation of arid ecosystems needs to be placed in the context of different dingo management strategies. As the influence of such population management on the dingo's ecosystem function forms the basis of this study, research questions are based around differing dingo management regimes found within the study location.

This study was conducted in the arid zone of New South Wales and South Australia. Table 2.1 lists historical and current dingo control methods used in these two states. Of particular relevance to the design of this experiment is the control of dingo populations using 1080 poison baiting, shooting and exclusion fencing.

From an experimental point of view, the problem of controlling dingo populations with 1080 is that both dingo and fox populations are manipulated (Allen and Sparkes, 2001; McIlroy *et al.*, 1986a; Thomson *et al.*, 2000). The use of 1080 to manipulate dingo populations was included in the experimental design in order to examine what occurs under current management practices. As a method of dingo control, shooting is more target-specific, and was used as an alternative population manipulation technique in the experimental design.

The dingo barrier fence (DBF) is a physical barrier that separated sites with no dingo populations (or only a few individuals) from sites with relatively stable dingo populations under varying management regimes (Figure 2.1). The DBF was completed to its current length in 1946; it is 5614 km long and stretches from south of Dalby in Queensland along the NSW, Queensland and South Australian borders to the coast at Fowlers Bay in South Australia (Corbett, 1995). It separates areas "outside" the fence (to the north and west of the barrier in NSW and South Australia) where dingoes and cattle grazing coexist, from sheep grazing areas "inside" the fence in NSW where dingoes and wild dogs are strictly controlled. It forms at least one border of all experimental sites used and is the major manipulation method of dingo populations considered in this study.

The Wild Dog Destruction Board, established under the *Wild Dog Destruction (Amendment) Act 1957*, is responsible for the physical maintenance of the DBF in NSW. In

South Australia this responsibility lies with the Dog Fence Board, which consists primarily of landholders. The Dog Fence Board organises and conducts routine baiting along the DBF borders and barrier zones.

In NSW, under the *Rural Lands Protection Act 1998 (Amendment)*, dingoes, wild dogs and their hybrids are declared a noxious species and owners and occupiers of lands are required to continually suppress and destroy them (Fleming *et al.*, 2001b). The exception to this is in national parks, where the dingo is not declared a noxious species and so long as it remains on Service land it is effectively protected. The dingo is recognised as a native species under the *Threatened Species Conservation Act 1995* however remains listed as "unprotected" outside reserve lands under Schedule 11 of the *National Parks and Wildlife Act 1974.*

In South Australia, the *Animal and Plant Control Board (Agricultural Protection and Other Purposes) Act 1986* identifies dingoes, wild dogs and hybrids as pests south of the fence in the sheep zone but recognises dingoes as a wildlife species north of the fence (Fleming *et al.*, 2001b). The exception to this is a 30 km buffer zone in which dingoes are routinely baited along the fence boundary to reduce breaches of the fence. In addition, landholders are obligated to destroy all dingoes seen in the vicinity of the DBF and baiting is only conducted where there is evidence of dingo activity in the vicinity of the fence, and is otherwise dictated by the landholder. As the dingo is a recognised wildlife species north of the fence, restrictions on ground baiting and prohibition of aerial baiting afford it a small amount of protection (Fleming *et al.*, 2001b).

2.1.3 Sampling Design

Experimental sites were chosen firstly, due to their location either side of the DBF, which was the major determinant of whether there were resident dingo populations at the site, and secondly, to ensure a representative variety of current dingo management strategies practised. Three sites were located north of the DBF in the "dingo" area and two sites were located south of the fence in the "no dingo" area (Figure 2.1).

The study sites located north of the DBF were considered as treatment sites, where the treatment was historical and current dingo management regimes (see Table 2.2). The first study site (Finniss Springs) contained a dingo population that had not been controlled by any means for more than five years. The second site (Quinyambie Station) contained a dingo population that was controlled by opportunistic shooting. The third site (Bollards Lagoon) contained a stable dingo population and had no predator control (1080 baiting or shooting) on the property for at least two years. This site was sampled, 1080 baits were laid and the site was re-sampled the following summer, 18 months after baiting took place. The study sites south of the DBF were considered the control sites. At one site, no predator control was conducted (Sturt National

Park) and at the second site predator control was conducted using sporadic baiting and shooting (Mundowdna Wilpoorina). A more detailed description of the five study sites and their management histories is covered in the section 2.2 of this chapter.

Table 2.1 Historical and current dingo control methods used in NSW and South Australia
Adapted from (Fleming *et al.*, 2001b)

Time Period	Control Methods
1788 - 1948	Dingoes and other dogs were included in early colonial legislation to remove threats to the livestock industry. Control measures included shooting (with bounty payments from 1836), trapping, poisoning (strychnine) and exclusion fencing.
1914/1917	The rabbit-proof fence is converted to the DBF. The fence runs along the Queensland - NSW border, and later includes the South Australia - NSW border section in 1947.
1946	In 1946 manufactured strychnine bait formulated and used in NSW. Experimental aerial baiting took place in South Australia.
Mid 1960's	1080 (sodium mono-fluoroacetate) replaces strychnine as the most widely used poison (although strychnine still used) and poisoning is under tighter regulation.
1965 - 1974	Large scale aerial baiting campaigns using 1080 were conducted in most states. More accurate scientific information on dingoes informs control programs which become more efficient and target specific.
1974 - 1992	Aerial baiting reduced, then no longer conducted in NSW.1080 baiting is widespread.
1992 - current	1080 baiting, (monitored under legislation - *Rural Lands Protection Act 1998*), trapping and shooting remain as the most common control methods for dingo and wild dog populations.

Table 2.2 Study sites attributes, including predator and prey management regimes

	Dingoes Bollards Lagoon	**No dingoes** Sturt National Park	**Dingoes** Quinyambie Station	**Dingoes** Finniss Springs	**No dingoes** Mundowdna Wilpoorina
Predator control method	1080 Baiting. No 1080 baiting for at least 3 years, baited then re-sampled 18 months later	No predator control. No 1080 baiting for at least 3 years	Opportunistic shooting only, no 1080 baiting.	No predator control	1080 baiting (in the last 12 months) and opportunistic shooting
Land Tenure	Pastoral lease	National Park	Pastoral lease	Aboriginal Land	Pastoral lease
Grazing regime	Cattle (2000 head)	No livestock for 30 years	Cattle	No livestock for 15 years – history	Sheep and cattle
Prey	Kangaroos (low) Rabbits	Kangaroos (high) Rabbits	Kangaroos (low) Rabbits	Kangaroos (low – hunted) Rabbits	Kangaroos (high – harvested) Rabbits
Mesopredators	Feral cats Foxes (low)	Feral cats Foxes (high)	Feral cats Foxes (low)	Feral cats Foxes (med)	Feral cats (shot) Foxes (high)
Water	Artificial water available (bores), no greater than 10km apart	Only one dam holding water, all bores closed	Artificial water available (bores), no greater than 10km apart	Natural springs and dam, larger distances apart (up to 30km)	Artificial water available (bores) no greater than 10km apart

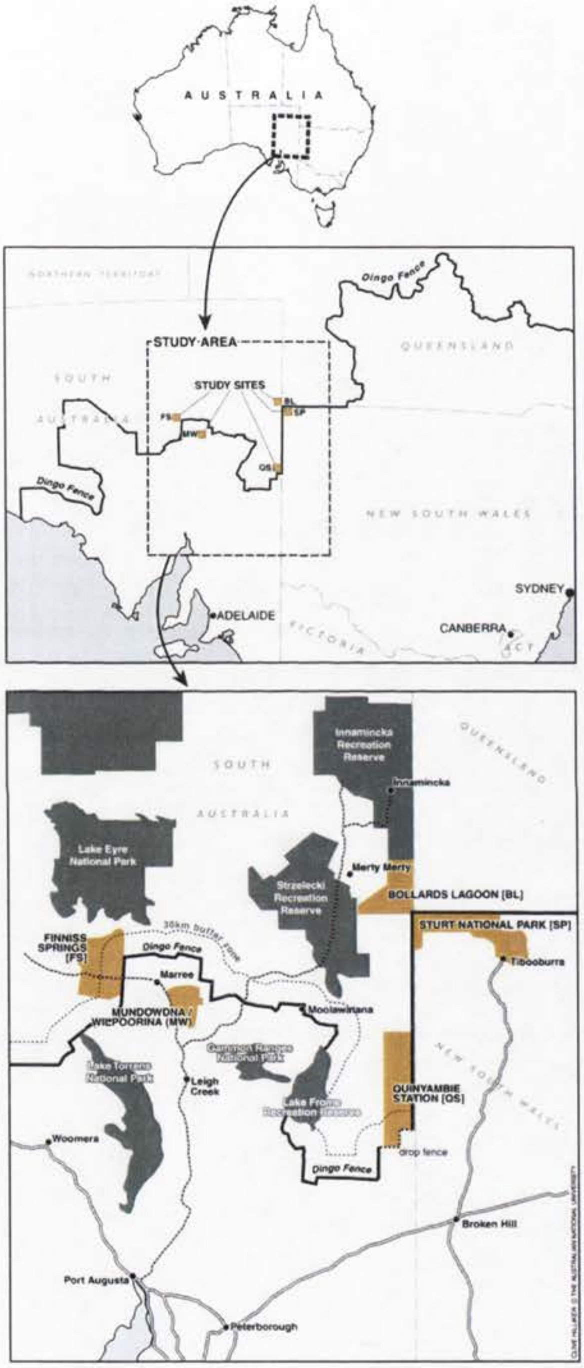


Figure 2.1 Location of study sites in reference to the Dingo Barrier Fence.
The DBF was used to separate study sites with dingo populations from those where dingoes are in very low numbers or absent.

At each of the study sites, population indices for the three target predators and select prey species were estimated. Predator behaviour was also observed. Details of methods used for measuring population indices and behaviour are outlined in section 2.3 and 2.4 of this chapter.

Replication of measurements was conducted on a spatial and temporal scale, with each site containing two separate sampling areas from which data were collected over two years (Figure 2.2). Sampling areas were positioned to contain at least one major watering point, and were constructed around a 20 km long transect of access road. The effective sampling area for predators along each transect measured approximately 100 km^2, calculated using a boundary strip of 2.5 km wide either side of the transect. The boundary strip width was calculated using the approximate movement radius of the feral cat (248 ha) (Molsher *et al.*, 2005), the smallest predator in the study (Krebs, 1999). For prey species, the sampling area was much smaller, as spotlighting and sand transects only measured animal activity within approximately 100m of the road (see section 2.3.2 of this chapter).

The two sampling areas at each study site were separated by at least 10 km for sites north of the fence in "dingo" areas and by at least 3km for sites in the "no dingo" areas south of the DBF (Figure 2.2) to minimise pseudoreplication (Hurlbert, 1984). These distances took into account the radius of the average home range size of a dingo in the arid zone where artificial water is available (95.8 km^2) (Thomson, 1992b; Thomson and Marsack, 1992) in the "dingo" sites and the average home range of a male fox (6.67 km^2) in the arid zone (Marlow, 1992a) at "no dingo" sites, as foxes were the species with the largest home range at these sites. Digital cameras were used in each sample area to identify individual animals and to monitor possible overlap of individuals between study areas (see Chapter 7). The location of sampling areas away from the property boundaries minimised the likelihood of any influence by dingo management activities carried out on surrounding properties or bias arising from artificially high abundances as a result from animals congregating along the DBF.

To limit seasonal variation within data, and to allow for some standardisation of the data, sampling took place during the "summer" period (January-April). Selecting this period of the year for sampling avoids predator movements associated with the winter breeding season (see Chapter 1). It is also the period when resources, in particular water, are most likely to be in short supply for all three carnivores, increasing the chance of recording competitive interactions. It does, however, include the time of maximum dispersal of young for both canid species (see Chapter 1) and thus was aimed to record peak annual populations at each site. In addition, the successful use of some methods adopted in this study, in particular sand transects and scent stations, required that sampling be restricted to one period of the target species' annual cycle as otherwise significant error related to seasonal variation may occur (Fleming, 1996). This also enabled comparisons to be made between indices estimated for different sampling years. Other variables were standardised where possible to allow some general comparisons to be made between sites (see section 2.1.4of this chapter).

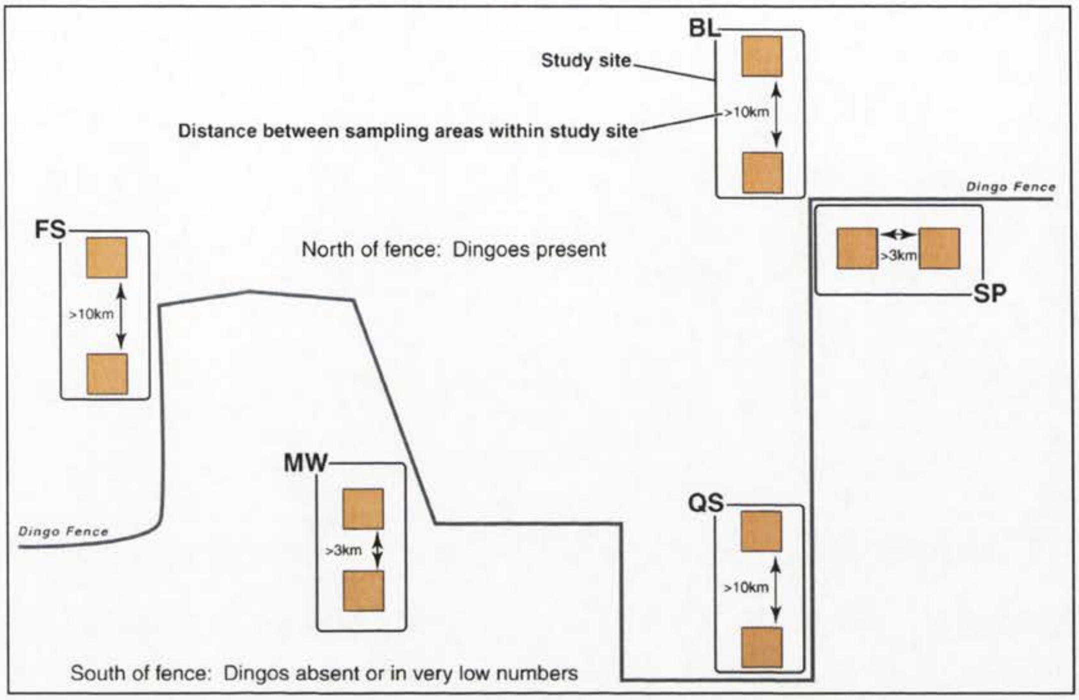


Figure 2.2 Diagram of experimental design, showing separation of sampling areas within each study site.
SP = Sturt National Park, BL = Bollards Lagoon, QS = Quinyambie Station, MW = Mundowdna Wilpoorina, FS = Finniss Springs.

Both natural and anthropogenic influences out of my control occurred during the second year of this research. These influences led to a change in the initial experimental design and restricted the study questions that could be asked. The original experimental design had only four sites, including two sites north and two sites south of the DBF. During the second year of sampling, an unscheduled 1080 baiting campaign was conducted at one site north of the fence where a large dingo population had previously not been baited. This meant that an additional, unbaited site needed to be found and an extra year of sampling conducted. The second sampling season was also restricted due to very high rainfall occurring across the arid zone, including the study sites. Flowing rivers prevented access to some study sites and the abundance of surface water meant that animals whose movements were usually restricted by permanent water sources could disperse across large areas. A positive aspect of this was that environmental variability was recorded in the data. A negative aspect was that some animals were not detected as they dispersed following prey populations away from the study areas. These influences are further discussed in Chapters 4, 6 and 8.

2.1.4 Standardisation Measures and other considerations

To allow general comparisons to be made between study sites, variables beyond the researcher's control were identified and where possible standardised within each of the sampling areas. Methods used to standardise variables included the quantification of site productivity, noting current and historical grazing regimes and the selection of sampled prey species.

2.1.4.1 Site productivity

In addition to habitat type and water resources (see Chapters 5 and 6) each study site was classified using an estimate of its productivity. Productivity of a system is a major determinant of species richness and is also related to animal activity (Bailey *et al.*, 2004). Productivity may affect abundance, home-range size and spatial distribution of each species, and therefore was an important consideration in this study. Each site was assessed for productivity during both years of sampling by estimating the gross primary productivity of each sampling area during the sampling period (GPP, mol CO_2 m^{-2} $month^{-1}$), as well as historical productivity (previous 7 years) (GPP, mol CO_2 m^{-2} $year^{-1}$) to estimate overall annual productivity. GPP was estimated using a continental remotely sensed time series data base (Berry *et al.*, 2007; Mackey *et al.*, 2008).

In summary, the gross primary productivity (GPP (mol CO_2 m^{-2} day^{-1})) for each study site was calculated using monthly estimates of the rate of gross photosynthesis by surface vegetation. This follows the radiation use efficiency model formulated by Roderick *et al.* (2001). The GPP estimates were calculated using MODIS 16-Day L3 Global 250m (MOD13Q1) satellite imagery data (LPDAAC/CSIRO). A time series of 86 months (October 2000 – December 2007) was extracted from the MODUS data for each study site. The area of data extraction for each study site was approximately 1850 km^2 (Table 2.3) and covered both sampling areas. The GPP was then averaged over this area for each month in the time series (Figure 2.3).

Table 2.3 The area for each study site used in GPP calculations.

Site Name	Longitude(decimal)	Latitude(decimal)	Site area (km^2) for GPP calculations
Sturt National Park	141.9667	-29.2	1844.408
Bollards Lagoon	140.85	-28.9667	1868.539
Quinyambie Station	140.9667	-30.2	1826.208
Mundowdna Wilpoorina	138.2167	-29.7167	1852.967
Finniss Springs	137.5	-29.7333	1837.670

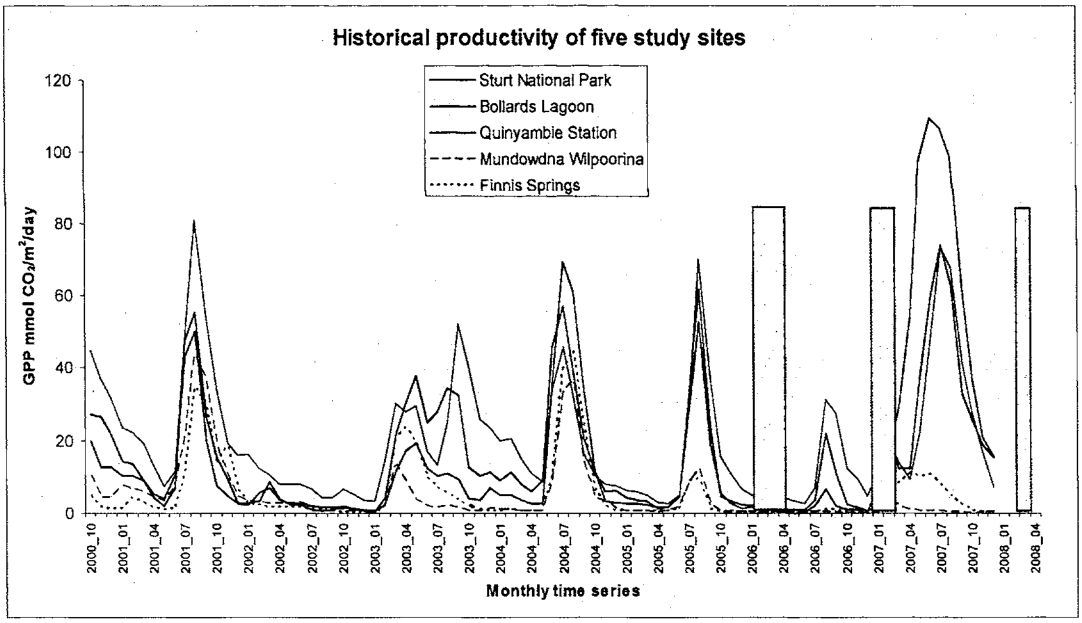


Figure 2.3 Monthly time series analysis for the five study sites.

(October 2000 – December 2007), ☐ Indicates sampling periods (2006-2008).

Figure 2.3 shows distinct productivity peaks which coincide for most of the five sites, with variations in the amount of productivity between sites. As is evident from the graph, sites located in the sand dune country (Sturt National Park, Bollards Lagoon and Quinyambie Station) have higher productivity peaks and overall productivity than the two sites located in the salt lakes bioregion (Mundowdna Wilpoorina and Finniss Springs).

The first sampling period (2006) took place after a number of years of lower productivity, with few peaks, at all sites. A large amount of rainfall occurred across all sites just prior to the 2007 sampling session (see section 2.2.2 of this chapter), leading to a dramatic increase in productivity as vegetation responded to the rains. A larger increase in productivity was evident at sites located within the sand dune country.

The final sampling session occurred in 2008, when only two of the five sites were sampled (Quinyambie Station and Bollards Lagoon), coincided with a decrease in site productivity at all sites. The time lag between predator and prey response to increasing productivity was taken into account when analysing population estimates in Chapter 4.

2.1.4.2 Grazing regime

Grazing pressure and type were important factors as these may change patterns in habitat and food resources for prey species by changing species composition in vegetation communities (Fensham *et al.*, 1999). Temporally, historical grazing regimes are important as many vegetation communities form as plant species respond to grazing regimes that are maintained over long periods of time (Cingolani *et al.*, 2005). Spatially important factors, such as proximity to water, are major determinants for vegetative cover (Pickup and Chewings, 1994) and therefore shelter and food resources for the prey species measured in this study.

Each of the five study sites was under different grazing pressures and types (Table 2.2). Two sites had no stock for 15 years (Finniss Springs and Sturt National Park), although one of these sites (Sturt National Park) had very large macropod populations. Sheep and cattle were grazed at one site (Mundowdna Wilpoorina) and only cattle were grazed at two (Bollards Lagoon and Quinyambie Station). The actual stocking rate and therefore grazing pressure depended strongly on management style and goals, as well as rainfall and seasonal conditions.

Studies indicate that although grazing does affect vegetation, other natural occurrences, such as flooding, have been shown to have more influence on species diversity (Westbrooke *et al.*, 2005). In particular, a combination of factors (such as fire, rainfall and grazing pressure) were found to be more important to small mammal abundance than just grazing pressure alone (Yarnell *et al.*, 2007). Under some circumstances grazing may actually promote conservation outcomes where it is used as a tool to control undesirable, grazing-sensitive plant species and maintain fauna habitat structure (Lunt *et al.*, 2007). The possible effects of grazing on prey abundance and distribution at study sites were not measured but are discussed in Chapter 4.

2.1.4.3 The choice of prey species

Prey species targeted in this study included macropods, rabbits and other small vertebrate prey (small mammals and reptiles). These species were chosen as they have been previously identified as a significant component of predator diets (Molsher *et al.*, 2000; Newsome *et al.*, 1983a; Paltridge *et al.*, 1997; Read and Bowen, 2001; Whitehouse, 1977), were measurable using standard techniques (see section 2.3.2 of this chapter) and were common at all five study sites.

It was an assumption of this study that prey behaviour and habits of measured prey species would be similar at each site. Alternative prey available to predators included introduced herbivores (such as horses, donkeys, goats and livestock), birds, invertebrates and carcasses. These alternative prey sources were recognised as contributing resources that sustained predator populations, but due to logistical and time restrictions, were not measured. Other factors, such as seasonal, perturbation and life cycle changes in prey that may also influence numerical and functional response of predator populations (Hanski *et al.*, 1991; Krebs *et al.*, 1995; Pech *et al.*, 1992), and the lag response of predator populations to increasing and decreasing prey availability (Stenseth *et al.*, 1998) were not measured but were considered in discussions (see Chapter 4).

2.2 Study Sites

The study was conducted at five locations in the arid zone of New South Wales and South Australia. The study sites were not chosen at random, but selected based on availability (management approval), proximity of their locations to each other, logistical considerations (such as access) and similarity in habitat, as well as meeting the dingo management requirements outlined in section 2.1.3.

The five sites used in this study were: Sturt National Park (-29° 12″, 141° 58″), Bollards Lagoon (-28° 58″, 140° 51″), Quinyambie Station (-30° 12″, 140° 58″), Mundowdna Wilpoorina (-29° 43″, 138° 13″) and Finniss Springs (-29° 44″, 137° 30″) (Figure 2.1). The attributes of these study sites are summarised in Table 2.2.

2.2.1 Study Site location and climate

Four of the study sites are located in South Australia and one (Sturt National Park) is located in NSW (Figure 2.1). All study sites lie within the desert climatic zone. This area is characterised by hot, dry summers and cold winters. Average daily temperatures across the region range from 21°C – 39°C during summer (January statistics) and from 6°C – 21°C during winter (July statistics) (Bureau of Meteorology, 2008c). The mean temperature range for Sturt National Park area is 21.9°C – 36.1°C during January (average over 97 years) and 5.4 °C – 17.8°C during July (average over 88 years). Bollards Lagoon is adjacent to Sturt National Park while Quinyambie Station is 300km to the south, therefore the mean summer and winter temperatures of the sites are similar. The mean temperature range for the Marree (SA) area is 21.3°C – 37.7°C during January and 4.8 °C – 19.1°C during July (averages over 68 years)

(Bureau of Meteorology, 2008b). Due to the proximity of Finniss Springs and Mundowdna Wilpoorina to Marree, the mean temperature range would be similar between the sites.

2.2.2 Recent and historical rainfall

Water is the most critical resource in arid ecosystems and changes in its availability are responsible for a high variability in vegetative productivity, animal abundance and spatial distribution (James *et al.*, 1999). Sites are located in the arid zone with a mean annual rainfall of less than 350ml. Droughts are frequent and rainfall is highly variable. All sites used in this study are located within or on the edge of the Great Artesian Basin structural unit. Much of the water provided to both native and domestic animals is from artificial and natural watering points provided by subterranean aquifers.

Mean annual rainfall for Sturt National Park is 226.3ml (average over 120 years) for Bollards Lagoon is 180mm (average over 36 years: 1962-1998) and for Quinyambie Station is approximately 169.6mm annually (average over 116 years) (Bureau of Meteorology, 2008d). Mean annual rainfall for Mundowdna Wilpoorina is 164ml (Jay, 1999) and mean annual rainfall for Finniss Springs is 150ml (Department of Water, 2008).

Figure 2.4 shows recent and historical rainfall for the five study sites. Some gaps were found in rainfall statistics, so data were taken from neighbouring properties. For Quinyambie Station data were taken from Mulyungarie (to the south), and for Mundowdna Wilpoorina data were taken from Wilpoorina only, Bollards Lagoon statistics taken from neighbouring property Lindon (to the east) and rainfall statistics for Finniss Springs were taken from neighbouring pastoral lease Callanna (to the east). The weather station for Sturt National Park was located at the sampling site (Fort Grey). Data for rainfall statistics were obtained from the Bureau of Meteorology website (http://www.bom.gov.au/climate/data; access date 4th April 2009).

During the first sampling period, all study sites had experienced at least 6 years of low annual rainfall (Figure 2.4). In contrast, during the second sampling session all of the study sites had experienced good rains during summer (late January 2007) with some sites inaccessible due to standing water or flooded rivers (Figure 2.4). For all five study sites, the annual rainfall during 2006 was in the driest 10% of years (for years on record since 1975), and 2007 was ranked in the wettest 25%. The response of vegetation to these rainfall events is mirrored by a peak in productivity during the following months (Figure 2.3). The effects of recent rainfall on both predators and prey, including the spatial distribution and activity of each species, are discussed in Chapters 4-6.

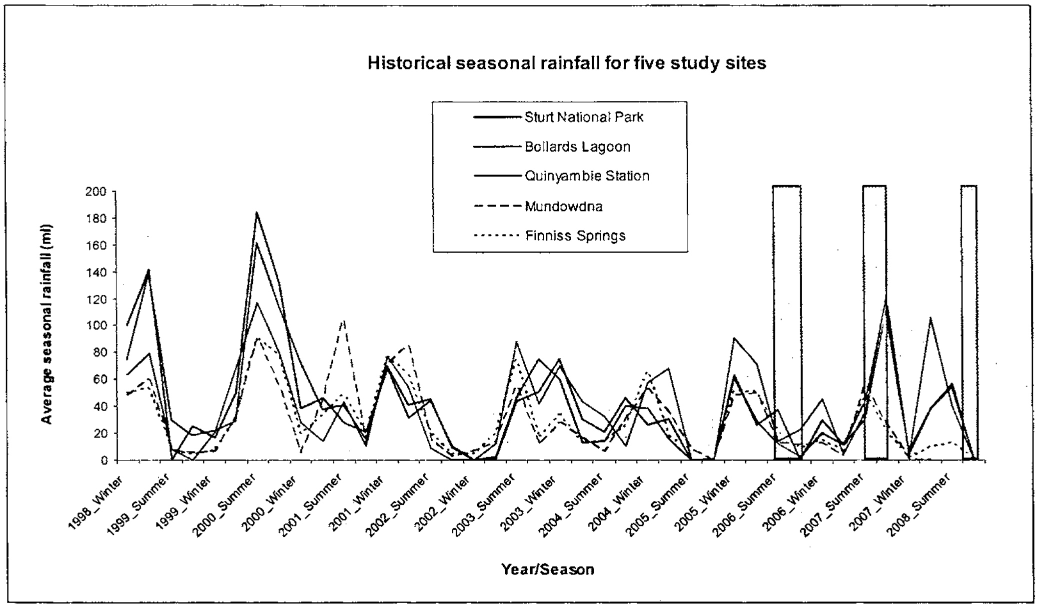


Figure 2.4 Historical seasonal rainfall for the five study sites.

(June 1998 – February 2008). □ Indicates sampling periods (2006-2008).

2.2.3 Topography, landforms and soils

Three sites are located within the Simpson/Strezelcki dune fields IBRA region (Sturt National Park, Bollards Lagoon and Quinyambie Station), with one further site bordering this area that was partially located in both the dune fields and the Stony Plains IBRA region (Finniss Springs). The section of Finniss Springs sampled in this study was the southern area which lies in the Stony Plains IBRA region. The final study site (Mundowdna Wilpoorina) also lies in the Stony Plains IBRA region (Figure 2.5).

The five sites can be broadly associated with two topographical systems. Area 1, containing Bollards Lagoon, Quinyambie Station and the western section of Sturt National Park, is dominated by the North-West Sands land system (McDonald, 1999). The North-West Sands land system is the eastern section of the Strezlecki Desert, and is characterised by immobile, vegetated low red sand dunes (10-15m in height). The inter dune areas contain playas (small salt lakes), clay pans, swamps and lake basins with internal drainage.

The majority of the land at the remaining two sites, Finniss Springs and Mundowdna Wilpoorina, lies on low stony hills with undulating gibber tableland and plains that are interspersed with drainage lines (Mumpie land system). At Mundowdna Wilpoorina, the central regions, particularly the western portion, comprises of red sand plains and dunes and stony country overlain with sands (Wirrigina land system). Salt lakes and kopi lunettes are also common at this site. Both sites are intersected by larger creeks and contain some sand plain country. At Mundowdna Wilpoorina outwash plains, channels and floodplains of the Frome River form the Paradise land system.

2.2.4 Vegetation

Vegetation communities found at the study sites are typical of arid ecosystems and strongly reflect geology and landforms. Vegetation also varies seasonally and in response to rainfall and fire.

Throughout topographical Area 1 (Bollards Lagoon, Quinyambie Station and Sturt National Park study sites) vegetated sand dunes are found across the whole area and are generally uniform in species composition. Vegetation in inter-dune areas is more variable, classified as either claypan or wooded floristic communities. The area is typical of sand hill country in that good growth of herbage and grass usually appears quickly in response to rainfall (McDonald, 1999).

Sand dunes are dominated by low open perennial woodlands, with a tall scrubland understory and scattered hummock grasslands. Dominant woodland species include sandhill wattle (*Acacia ligulata)*, mulga (*A. aneura*), needlewood (*Hakea leucoptera*), whitewood (*Atalaya hemiglauca*) and beefwood (*Grevillea striata*), with a shrub layer of *Cassia*, *Senna*, *Eremophila* and *Dodonaea* species (NSW National Parks and Wildlife Service, 1996). Lobed spinifex (*Triodia lobata*) is found on dunes in the northern areas and narrow-leaf hopbush (*Dodonaea viscosa*) dominates dunes in patches in the western sections (McDonald, 1999).

Inter-dunal vegetation varies depending on soil type. Claypans and lake basins in interdune areas contained temporary swamps of canegrass (*Glyceria ramigera*) and lignum (*Muehlenbeckia cunninghamii*) communities (NSW National Parks and Wildlife Service, 1996). Perennial woodland is supported in more sandy deposits throughout inter-dune areas while further west, canegrass becomes more common. Sandy inter-dunes support similar vegetation communities to dunes, while on heavier sub-soils low shrubland with starbush (*Gunniopsis quadrifida*), blackbush (*Maireana pyramidata*) or cottonbush (*M. aphylla*) is dominant. Groundcovers include buckbush (*Salsola kali*) and common bottlewashers (*Enneapogon avenaceus*). Heavy soils are dominated by Mitchell grass (*Astrebla sp.*). Areas of temporary standing water, such as flats and swamps, are dominated by cottonbush, neverfail (*Eragrostis setifolia*), swamp canegrass (*E. australasica*), scattered coolibah trees (*Eucalyptus coolabah*), spotted emu bush (*Eremophila maculata*) and lignum (McDonald, 1999).

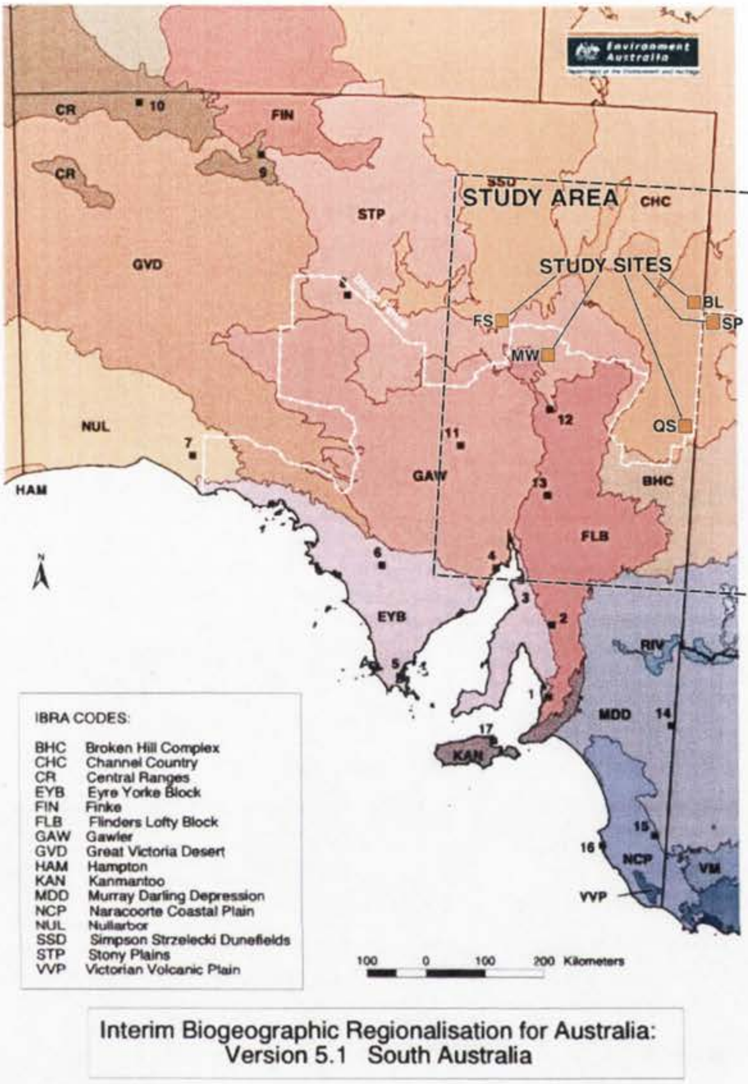


Figure 2.5 Location of study sites in relation to IBRA classifications.
IBRA classifications include the Simpson Strzelecki Dunefields (SSD) and the Stony Plains (STP) bioregions. Adapted from Environment Australia (2007).

Vegetation in topographical Area 2 (Mundowdna Wilpoorina and Finniss Springs) is associated with three main land systems found at these sites: the gibber tablelands (Mumpie system), low sand plains (Wirringina system) and watercourses (Paradise system) (Pastoral Board of South Australia classification).

Depressions (gilgais) in the gibber tablelands support barley mitchell grass (*Astrebla pectinata*) and neverfail with scattered mulga and low bluebush (*Maireana astrotricha*). Perennial species of salt bush, predominantly *Atriplex vesicaria and A. nummalaria* are found in drainage lines. Species found on low sand dunes and sandplains include needlewood, silver needle-bush (*Hakea leucoptera*), marpoo (*Acacia ligulata*), sandhill canegrass (*Zygochloa paradoxa*) and starbush (*Gunniopsis quadrifid*a).

The edges of salt lakes and salty natural springs are dominated by samphire bush, tangle poverty bush (*Sclerolaena intricata*) and water weed (*Osteocarpum acropterum*). The channels of the Frome River (Paradise land system) are dominated by river cooba (*Acacia stenophylla*) while other large watercourses are lined with river red gum (*Eucalyptus camaldulensis*), coolibah, broughton willow (*Acacia salicina*), prickly wattle (*Acacia victoriae*), dead finish (*Acacia tetragonophylla*) and plumbush (*Santalum lanceolatum*). Species such as old man salt bush (*Atriplex nummularia*), cottonbush and prickly wattle are found on the floodplains, swamps and flats of the Frome River.

Vegetation communities on Bollards Lagoon, Quinyambie Station and Mundowdna Wilpoorina are subject to continuous grazing from stock. Grazing pressure on vegetation is higher within 5km of watering points, leading to spatial variations in dominant species, habitat and vegetation growth (see section 2.1.4.2 of this chapter).

2.2.5 Sturt National Park

Sturt National Park (3,104 km^2) is situated in the far north-western corner of NSW. It is bounded to the north by the Queensland border and by the South Australian border to the west. The DBF runs along these state lines, placing Sturt National Park to the south of the DBF in the "no-dingo" area. Only the western section of Sturt National Park was sampled in this study as it contained similar habitat to the neighbouring study sites of Bollards Lagoon and Quinyambie Station.

2.2.5.1 Site management and history

Sturt National Park was initially established in 1972 and was formed from three large pastoral leases (Mt Wood, Olive Downs and Fort Grey).The area had been used for grazing for over 100 years prior to its establishment as a reserve. Sturt National Park is managed by the NSW National Parks and Wildlife Service (NPWS). Main management objectives include the conservation of wildlife, protection of natural features and maintenance of natural ecological processes (NSW National Parks and Wildlife Service, 1996). In contrast, the majority of lands surrounding Sturt National Park are privately owned grazing lands. Bordering properties remain pastoral leases used for both sheep grazing (south of the DBF) and cattle grazing (north of the DBF).

Foxes are controlled in the eastern section of Sturt National Park using 1080 baiting and dingoes are trapped along the boundary fence to the north. The NPWS wishes to maintain existing dingo populations where practicable, and recognises them as a native species. However, dingoes and wild dogs sometimes prey on domestic stock. This means the NPWS District Office must liaise with neighbouring landholders, the Wild Dog Destruction Board for NSW and the

Milparinka Rural Lands Protection Board, and when required assist in strategic wild dog control programs along the national park boundaries (I.Witte, pers.comm. February 2006).

Although the control of introduced species is a management priority, no predator or rabbit control (including 1080 baiting) had been conducted in the western section of Sturt National Park for more than 3 years prior to the commencement of this study. This allowed data on populations of target species that had not been previously manipulated by control to be collected.

2.2.5.2 Water resources

In Sturt National Park, a number of bores tapping into the Artesian Basin were established when the lands were under pastoral leases but now the majority are non- operational. Most artificial watering points have been closed to reduce grazing pressure by the high numbers of rabbits and kangaroos, and only surface water runoff caught in open tanks remains available to wildlife (NSW National Parks and Wildlife Service, 1996).

In the first sampling session of this study only one tank contained water (Quartpot) and the study area was entering its seventh consecutive year of drought. A second tank had recently run dry (Ox tank), and this area was also sampled because it was most likely to contain water in following sample periods. A rainfall event (32 ml) occurred during the middle of the first sampling session (February 2006) across a 5 km strip in Sturt National Park. During the second sampling session (January 2007) a large amount of rain fell across the study site both before and after sampling took place. Total rainfall recorded at Tibooburra for the period of December 2006 – February 2007 inclusive was 84.2 ml (Bureau of Meteorology, 2008d)

2.2.5.3 Predator and prey species

Due to its remnant native vegetation, Sturt National Park provides a variety of habitats for many native species of birds, mammals, reptiles and amphibians. In particular, the site contains sizeable populations of macropods. This is possibly due to the fact that large populations of medium-sized predators, such as dingoes, are not found in the area. Dingoes and wild dogs do occasionally occur throughout the park but in extremely low numbers. There are four species of macropods that inhabit the Park: red kangaroos (*Macropus rufus*) which are common throughout the park: eastern grey kangaroos (*M. giganteus*), euros (*M. robustus*), and western grey kangaroos (*M. fuliginosus*). Emus (*Dromaius novaehollandiae)* are also common.

Introduced fauna species found in the park include two carnivore species, the red fox (*Vulpes vulpes*) and the feral cat (*Felis catus*) as well as feral pigs (*Sus scrofa*), rabbits (*Oryctolagus cuniculus*) and feral goats (*Capra hircus*). At the time of the first sampling (January 2006) rabbit numbers were relatively low, although the species experiences strong seasonal fluctuations in numbers. Rabbits breed in the park during winter and spring and their numbers rise dramatically during this period. They are also patchily distributed across the park: numbers are highest in the sandy western region where the study site took place. Fox numbers are also relatively high in this area. The provision of water via bores and tanks within the park and lack of dingoes due to exclusion by the dog fence may have resulted in the increase in rabbit, kangaroo and even fox numbers.

2.2.6 Bollards Lagoon

Bollards Lagoon (4,047 km^2) is a large pastoral lease situated in the far north-east corner of South Australia, approximately 140km south of Innamincka. The homestead lies 16 km directly west from Sturt National Park. Bollards Lagoon is bounded by the South Australia - New South Wales state border (and the DBF) to the east and the South Australia - Queensland state border to the north. Bollards Lagoon is thus situated on the "northern" side of the DBF and contains populations of dingoes.

2.2.6.1 Site management and history

Bollards Lagoon pastoral lease is primarily orientated to raising cattle for meat supply, however is also involved in the supply of natural gas and in the tourism industry. It was first developed in 1959 when artesian bores were sunk on the property (McDonald, 1999). At the time of sampling approximately 500 head of Hereford cattle were run on the property. In the past, during periods of high rainfall, this has been increased to almost 4000 head. The current carrying capacity of the station is 2864 cattle.

Originally, Bollards Lagoon was the site of the unbaited dingo population for this study. Then, in November 2006, prior to the second sampling session, unscheduled 1080 baiting was conducted around the water points in the study area. Bollards Lagoon was then used as a before and after baiting comparison, and was re-sampled approximately 18 months after baiting took place.

2.2.6.2 Water resources

Water for the property is mostly obtained by bores sunk to tap aquifers of the Great Artesian Basin. Surface water is also used by catchment tanks (dams) particularly in areas of natural swamp catchments as an additional but irregular supply of water (McDonald, 1999).

Bollards Lagoon, as a managed pastoral station, has a number of water access points distributed across the property. This allows fairly uniform access to water for both domestic stock and wildlife (McDonald, 1999). Twenty four water points are distributed throughout the sampling areas, with most sections inside paddocks within 10-15km of a water point, though some areas are further out therefore are less used by stock.

2.2.6.3 Predator and prey species

In addition to livestock, the two most prominent mammalian species found on this pastoral lease are rabbits and dingoes. Both of these species fluctuate in numbers and spatial distribution although dingo populations tend to be particularity dense around water points (see Chapter 6). Recently, the arrival of Rabbit Haemorrhagic Disease (RHD) in the area has dramatically decreased rabbit populations. Macropod numbers are generally low which is probably attributable to the presence of dingoes. Feral cats, and rarely foxes, are also seen on the property, in addition to a number of bird, reptile and small mammal species. Feral camels (*Camelus dromedaries*) have been sighted in the eastern section of the property.

2.2.7 Quinyambie Station

Quinyambie Station (12,119 km^2), one of the largest pastoral leases in South Australia, is located approximately 140 km north-west of Broken Hill and approximately 200 km south of Bollards Lagoon. Its eastern and southern boundaries run along the DBF. The eastern boundary is the NSW state border, while the southern boundary forms part of the South Australian section of the DBF. Quinyambie Station was not sampled until the second sampling session, and was used as a replacement when Bollards Lagoon became a baited site. It contains relatively large and stable populations of dingoes.

2.2.7.1 Site management and history

Quinyambie Station is primarily for raising cattle and has a carrying capacity of 9000 head. The property is also used for various short training courses in station work. No large scale 1080 baiting is conducted but dingoes are controlled opportunistically by shooting (P. Jonas pers. comm. April 2007). As Quinyambie is bordered by the South Australian DBF to the south, it is subject to the 30 km buffer zone baiting in this area. The southern end of Quinyambie Station was baited during October prior to the first sampling. The study sites are located towards the centre of the property, which borders the NSW DBF and therefore were not subject to buffer zone baiting.

2.2.7.2 Water resources

As with other pastoral leases, watering points are distributed throughout Quinyambie Station for livestock access. Both artesian bores and surface water stored in catchment tanks (dams) are used. Watering points are scattered strategically through paddocks with most areas being within 15 km of a watering point, the exception being the western section of the property dominated by the Strezlecki Desert. The paddocks including those in sampling areas contain a total of 14 watering points, distributed fairly uniformly throughout the sampling area. When taking into consideration an area within a 15km radius of sampling transects, water point availability increased to 22 watering points. In total, there are almost 100 watering points scattered throughout the entire property.

During the first sampling session heavy rainfalls brought an increase in surface water availability in the area. Nearby Broken Hill received a total of 139.8 ml of rainfall during the period of December 2006 – February 2007 inclusive (Bureau of Meteorology, 2008a).

2.2.7.3 Predator and prey species

Quinyambie supports a broad diversity of both native and introduced species. Cattle, feral camels and horses are all found on the property, with large herds of domestic horses bred for station use. Dingoes and rabbits are abundant, while cats and foxes are found in lower numbers. Dingoes in particular congregate around water points and are shot opportunistically. Macropods are present but numbers are generally low. Small mammals appear to be more numerous than at other sites, frequent sightings were probably due to an increase in numbers after rains during the first sampling session (see Chapter 4).

2.2.8 Mundowdna Wilpoorina

Mundowdna (1,647 km^2) and Wilpoorinna (904 km^2) stations are managed as one unit with a total land area of 2,551 km^2 (Jay, 1999). The properties are located approximately 20 km east of the township of Marree, South Australia. Like most of the other study sites, Mundowdna Wilpoorina is bordered by other pastoral leases. The DBF runs along the far north-eastern border of Mundowdna Wilpoorina, placing the property in the "no-dingo" area.

2.2.8.1 Site management and history

The pastoral leases of Mundowdna and Wilpoorina were originally used for sheep grazing between 1859 and 1906, and were run as cattle stations from 1906 to 1958. Since 1959 both sheep and cattle have been grazed (Jay, 1999). Stocking rates are dependent on rainfall. At the time of this study, Mundowdna was running 2500 merino sheep and 2500-3000 head of cattle. The property is strategically divided into sheep and cattle grazing areas. Cattle are grazed in areas close to the DBF, and cattle paddocks form a "buffer zone" to the sheep grazing areas. No widespread 1080 baiting had been conducted on the property for 2 years prior to the commencement of this study, but opportunistic baiting was conducted where there were signs of dingoes in the property, particularly in the sheep zone. During the time of the first summer sampling, baits were laid in one of the study areas. Baiting is also regularly conducted in neighbouring pastoral leases (The Clayton and Munpeowrie) (P. Litchfield pers. comm., February 2007).

2.2.8.2 Water resources

At the time of the first sampling period (March 2006) the site was in the ninth consecutive year of drought (P. Litchfield pers. comm., February 2007). Mundowdna lies on the edge of the Great Artesian Basin and is intersected by the drainage line of Frome River (Frome/Paradise land system). Mundowdna has a total of 60 watering points, 20 of which are dams and the remainder artesian bores (Jay, 1999). At the time of the first sampling there were a number of dry tanks and the river beds were also dry, so sampling areas incorporated mainly artesian bores. During the second period of sampling (February 2007) the Frome River was flowing and provided the main water source to stock, so a number of the bores included in the first sampling period were no longer in use. Most of this surface water was off-flow running down from the Diamantina and Cooper's creek in south Queensland, which had received very substantial rainfalls in late 2006. Marree received a total of 42.8 ml of rainfall during the period of December 2006 – February 2007 inclusive (Bureau of Meteorology, 2008b).

2.2.8.3 Predator and prey species

Apart from domestic stock, a number of native and feral fauna species are found at Mundowdna. Foxes and feral cats are both found in substantial numbers across the area. Large feral prey species found at the site at the time of sampling include feral horses (*Equus caballus*) (population estimation 80-200, S.Litchfield pers. comm., February 2007) and donkeys (*Equus asinus*) (population estimation 20-30, S.Litchfield pers. comm.., February 2007). Horses, which were largely uncontrolled prior to 1970, are mainly concentrated around water points. There are no feral goats on the property and rabbits are found mainly in the sandy Wirringina land system. Rabbit numbers had been high on the property during the 1980's, but in 1995 the calicivirus spread through the district resulting in a severe decline in numbers, which remain low. A variety of native bird, reptile and small mammal species are found in the region (Jay, 1999).

A professional shooter works on the property, with a harvest quota of 1200 macropods per season (approximately 2400 annually). Kangaroo numbers have been kept in check by shooters since 1973, predominantly to reduce grazing pressure. Feral cats are also shot opportunistically, with approximately 400 feral cats culled from the property annually (S.Litchfield pers. comm., February 2007). Foxes are generally not controlled except as non-targets when 1080 baiting is conducted to remove the occasional dingo that comes though the DBF.

2.2.9 Finniss Springs

Finniss Springs (1,496 km^2), an old pastoral lease that is now Commonwealth Land, is located along the Oodnadatta Track. It is currently under review for a Native Title Claim, under the *Native Title Act 1985*. It lies approximately 50 km west of Marree, South Australia and directly south of the Lake Eyre National Park, which forms its northern border. Finniss Springs is approximately 70 km from Mundowdna. At Finniss Springs, the DBF swings south, and forms the eastern border of the property, placing it "north" of the fence. It contains small but stable populations of dingoes.

2.2.9.1 Site management and history

Originally used as a collection point for the Old Ghan railway, Finniss Springs was subsequently managed as a pastoral lease from 1955 until 1984. It was minimally stocked for the last ten years of this period, but very heavily stocked prior to this. It was used for grazing both cattle and sheep until 1973, when sheep grazing was discontinued. In 1992 the pastoral lease was resumed and the land came under the control of the Commonwealth Department of Lands. At the request of 19 Arabunna traditional owners, the area remains protected as an Aboriginal Site. It was initially proposed as National Park Reserve lands, to be managed under joint management between the traditional owners and National Parks. This did not eventuate and to date Finniss Springs remains as un-allotted Crown Land where members of the Aboriginal Arabunna community, who were shareholders in the property, continue to practise traditional hunting and access rights. An easement passing through the property, initially established by Western Mining Corporation Ltd and now managed by BHP Billiton, provides access to a major water pipeline that provides water to mining leases at Roxby Downs. The property is of significant conservation value with quality habitat, mound springs and important geomorphological and fossil assemblages. (Department of Water, 2008).

Even though the property has a history of over-grazing, Finniss Springs has recovered well over the past 15 years. Due to its unique management regime, very little 1080 baiting has been carried out on Finniss Springs South in the last 10 years, although the north section is subject to buffer zone baiting annually. Only once in the last 10 years has buffer baiting been carried out at Finniss Springs South, where both study sites were located (P. Bird, pers. comm.., April 2007). Minimal baiting is carried out elsewhere on the property – only one waterhole in the south has been subject to baiting during the last 10 years. Due to such minimal control it is likely that baiting has had very little impact on dingo populations in these study sites, and therefore the populations were considered uncontrolled and structurally intact.

2.2.9.2 Water resources

The landscape of Finniss Springs is dotted with natural basin springs which provide a permanent water source at various locations across the site. Seven natural springs are found on the property. In addition, eight flowing artesian bores are scattered across the property. A few large creeks cut through the property and empty into Lake Eyre South. These were dry at the time of the first sampling period (March 2006) but were in full flow during the second sampling period (February 2007).

2.2.9.3 Predator and prey species

Finniss Springs supports a small number of macropods; populations are most likely suppressed by indigenous hunting and predation by dingoes. In the past, large populations of feral horses have caused extensive damage to natural springs and bores, but at the time of sampling only several individuals remained on the property. Finniss Springs also supports a fluctuating population of dingoes and rabbits, in addition to emus and other bird species, small mammals and reptiles. Feral cats and foxes are also common.

2.3 Methods used for estimation of population indices for predators and prey

Field methods used in this study were selected by taking into consideration logistical limitations including labour effort, time and budget restrictions, the ecology of the study species (for example large home ranges of predator species, see Chapter 1) and the suitability of each method for data collection in the arid zone (determined by previous effective use in other studies). To successfully address the aims of this thesis, field methods were used to collect data on three areas of study: to obtain population indices for predator and prey populations, and assessment of predator behaviour. Predator and prey population indices gained from methods discussed in this section were used to provide baseline data for predator behavioural observations. As data were collected from only two sampling areas at each study site, at least two field methods were used to estimate population indices. The locations of sample plots were as randomly located as logistically possible. A major logistical constraint was the need to have vehicular access to the areas.

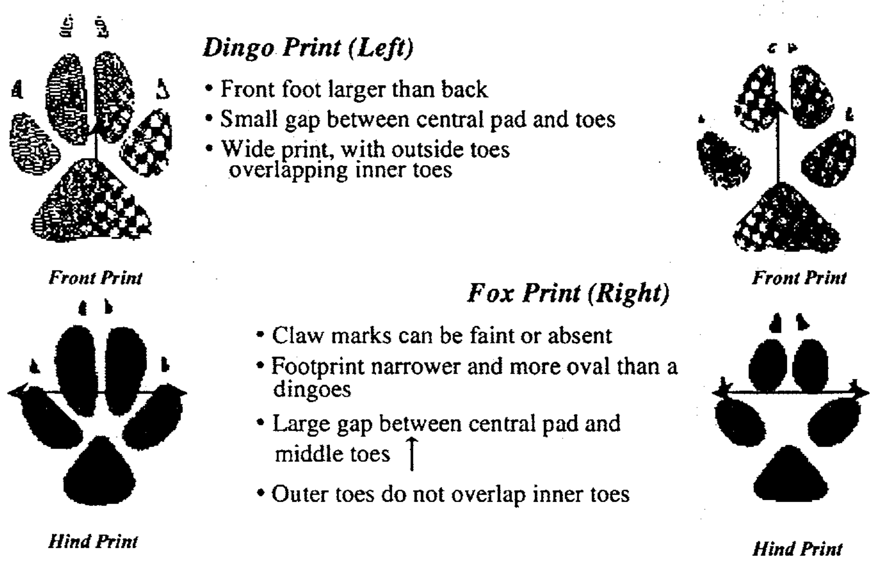
2.3.1 Predator population estimates

As predators are typically cryptic, usually occur at low densities (particularly in arid environments) and are often difficult to observe and capture (Pelton and Marcum, 1977), most studies rely on visual signs of their presence, rather than counting individuals, to determine population density (Edwards *et al.*, 2000; Fleming *et al.*, 1996). Data gained from observation of signs such as footprints or scats can then be used to determine the activity of a species relative to a point in time or space (Caughley, 1977). The raw frequencies recorded are then used to calculate an activity index, which is assumed to be linearly proportional to the true density of the population (Forsyth *et al.*, 2005).

The use of population indices for the collection of field data has some inherent bias. For example, the method assumes equal probability of detection across both time and space (Ellingson and Lukacs, 2003). While the approach of using activity indices to estimate populations has limitations (Engeman *et al.*, 2000), indices may still yield useful information (Johnson, 2008), and it is generally accepted that estimations of populations using activity indices enable researchers to compare temporal and spatial relative activity at the same site between years, or between sites.

Predator populations in this study were assessed using activity indices calculated from two methods of track counts: sand transects (passive track counts) and scent stations (active track counts). Active track counts use a lure to attract target species, passive counts do not. Both of these methods are particularly suited to estimating population indices of wide ranging species, such as carnivores, as less labour is required in comparison to other methods (such as live trapping), no direct interaction with the animals is necessary and the methods can be used successfully to sample large areas. These methods also overcame difficulties associated with sampling three predator species that differed in behavioural ecology such as temporal activity, spatial movement patterns, hunting types and habitat preference (see Chapter 1).

Both these methods rely on accurate observations and interpretations of footprints for quality data. To avoid inaccuracies from inter-observer observations (Wilson and Delahay, 2001), all observations and interpretations of tracks were made by one observer. Difficulties were still encountered when attempting to distinguish between a small dingo footprint and that of a fox. Figure 2.6 shows the standard method employed in this study to distinguish prints of these two species.



Dingo Print (Left)

- Front foot larger than back
- Small gap between central pad and toes
- Wide print, with outside toes overlapping inner toes

Fox Print (Right)

- Claw marks can be faint or absent
- Footprint narrower and more oval than a dingoes
- Large gap between central pad and middle toes ↑
- Outer toes do not overlap inner toes

Figure 2.6 Identification points of fox (left) and dingo (right) paw prints. Adapted from Triggs (1996), prints not to scale.

2.3.1.1 Sand transects

Sand transects (alternatively known as sand pads or track stations, and referred to as transects hereafter) are used as a method to estimate population indices using a passive activity index (Paine, 1980) of both predator and prey species at each study site (Allen et al., 1996).

They were also used for determining use of habitat by all species, including the identification of "hot spots" of animal activity and the spatial movements of predators in relation to habitat and the proximity of water (see Chapters 5 and 6).

The design and sampling method used in this study were based on findings by Mahon *et al.* (1998). Each transect measured 0.5m wide and 50m long. Transects were measured out and then raked using a plastic garden rake to "fluff up" the sand and make it suitable for reading tracks (Figure 2.7). Transects were checked once a day in the morning, determined as the optimum time for reading animal prints in the sand, and any prints found were recorded. All prints found were identified and placed into a category except for bird tracks, which were discarded. Categories included cat, fox, dingo, rabbit, kangaroo, small mammal, reptile and unknown. Unknown tracks were discarded. Each time an animal came onto and then moved off a transect (that is, one crossing) it was counted as one animal. Transects were then raked over to give a track-free transect for recording prints over the next 24hr period.

Transects were checked on three consecutive mornings, the length of time previously determined as the optimal time for data collection using this method (Allen *et al.*, 1996; Forsyth *et al.*, 2005). Wherever logistically possible, transects were sampled prior to scent station sampling so that scent lures did not influence predator presence.

Transects were located off the roads, with the angle of each transect line varying between 60 – 120 degrees to the road. In this study, the method was used to sample a wide variety of species in relation to spatial location. Therefore the sampling design is in contrast to previous studies that have concentrated sampling in areas where the target species would most likely be detected, such as sampling for dingoes or foxes along roads (Allen *et al.*, 1996; Fleming *et al.*, 1996). The use of the road is a popular method for maximising detection of canids, but often overestimates their abundance while underestimating the abundance of cats (Mahon *et al.*, 1998; Edwards *et al.*, 2000; Forsyth *et al.*, 2005) and in this study would also create a bias against detecting many smaller prey species whose movement may be inhibited by roadways.

Transect sites were spaced randomly, being a minimum distance of 400m and a maximum of 3km apart. The location of each transect was selected at random but the exact location of each transect was dependent on suitable habitat. One problem with this design was the need to ensure spatial independence of transects to ensure statistical validity (Engeman *et al.*, 1998). This is generally done by using the radius of a species' average territory size as a minimum distance for sample separation (Roughton and Sweeny, 1982), so that the probability of an individual animal visiting more than one station is reduced (Edwards *et al.*, 2000). In previous studies 500m separation has been considered adequate for foxes and feral cats (Mahon *et al.*, 1998; Edwards *et al.*, 2000), but not for dingoes. A sample spacing of 1 km or more is recommended for dingoes in arid environments (Allen *et al.*, 1996). Due to the limited amount of area accessible to vehicles, habitat restrictions and proximity of water influencing transect placement, the 1 km spacing required in dingo areas was not possible at some sites. Statistical analysis to assess clustering effects is discussed in Chapter 4.

During the first sampling session only 10 transects were sampled for each site. This was increased to 15 transects per sample site in the second sampling session to increase the amount of data gathered. It also allowed for unfavourable weather conditions (such as rain or wind) which sometimes rendered some, or all, transects unreadable. This has been noted as a major limitation of the method in other studies (Glen and Dickman, 2003; McIlroy *et al.*, 1986a). By increasing the number of transects, an adequate amount of data was collected even when some transects were unreadable.

As recognised in previous studies, a second limitation for the use of this method is substrate quality and type (Edwards *et al.*, 2000; Wilson and Delahay, 2001). Variation in habitats between the study sites meant that in some areas, such as on gibber tablelands, the method could not be used. To overcome the problem of reading hard, compact soils, only the drainage lines which flowed through the gibbered areas were sampled. These contained soft, fine soils which did not compact overnight. One disadvantage to using the drainage lines in the gibber was that gibber habitat was classified in the study by the shelter and prey availability found in drainage lines only, rather than including species found on the gibber itself. To avoid bias this limitation may cause, the habitat classification used in the study was “drainage line”. This was deemed to be a more suitable and representative option than omitting the sampling of gibber areas altogether, as they composed a large amount of area at some of the study sites.

The raw frequencies of tracks recorded (that is, the number of crossings per transect per day) were averaged over the number of days on which the transect was readable, and then standardised as the mean number of tracks / transect (50m) per day (Allen *et al.*, 1996). By summing up the counts over the total sampling days, problems associated with non-temporal independence of the samples were circumvented (Edwards *et al.*, 2000; Engeman *et al.*, 1998) Variance for the PAI was then calculated using the method outlined in Engeman *et al.* (1998).

2.3.1.2 Scent Stations

Scent stations were used to monitor the spatial activity of predators and to provide a second, complementary estimation of predator activity in addition to transects. Scent stations are designed to lure predators to a site using olfactory attractants (Allen *et al.*, 1996; Linhart and Knowlton, 1975; Roughton and Sweeny, 1982; Sargeant *et al.*, 2003; Smith *et al.*, 1994b).

In the pilot study, scent stations were constructed using wooden stakes partially buried in the ground. Sand surrounding the stake was smoothed using a rake in a 1m circumference to enable predator visitations to be monitored by recording prints left in the sand (Figure 2.8). The stations were then "scented" with fox/dog and cat attractants including a mixture of prefabricated dog/fox scent (Feralmone®) and a food lure mixture (fish oil). Although catnip (Clapperton *et al.*, 1994) has been found to increase visitation by cats, fish oil was chosen as it is readily available and acted as an attractant for all three carnivores, whereas it was not known as to whether catnip would have a repellant effect on canids. Similarly, carrion, although highly effective for attracting canids (Hein and Andelt, 1994) was not used at scent stations as it may be less attractive to cats.

For data collection, the stakes were removed and scent was applied to naturally occurring objects, such as bushes, rocks and sticks. This was done because of problems experienced with the destruction and removal of the scent posts by young dingoes during the pilot study. It also avoided the problems associated with the wariness of individuals and initial avoidance of new objects in their territory (Sequin *et al.*, 2003).

. Initially, 12 scent stations were established at the first site sampled, however this was subsequently increased to 20 scent stations per site to improve predator detection. Scent stations were checked for visitations on three consecutive mornings. They were initially checked both morning and evening for temporal activity data, but so little daytime activity was recorded using this method that only the morning checks were continued. As with the transects, scent stations were randomly placed a minimum of 400m and a maximum of 3km apart, depending on the required habitat. Again, difficulties were encountered in ensuring spatial separation for statistical analysis and this is discussed further in Chapter 4.

Scent station surveys were limited to binary (presence/absence) data. Although this reduces sensitivity in detecting differences in activity (Engeman *et al.*, 2000), it was deemed more accurate than attempting to decipher prints of individual animals. Visitations to scent stations were calculated as the total number of visitations for each species per total scent station exposures (total number of scent stations x number of sampling nights). Total counts were then averaged and standardised as the mean number of visitations/scent station/day. Sampling error variance was calculated from the ratio of visitations per scent station exposures (see Chapter 4).

2.3.2 Prey population estimates

One method used for population estimates of target prey species was sand transects (see section 2.3.1.1of this chapter for details of this method). Simultaneous sampling for predator and prey populations using transects is an advantage of this method (Allen *et al.*, 1996). Spotlighting was used as the second method of prey assessment.

Figure 2.7 Transect construction in an inter-dune area

Figure 2.8 Scent station design

2.3.2.1 Spotlighting

Spotlighting is a technique by which animals are observed and counted at night using a hand-held high powered light. In this study, spotlighting was used to provide a population index for of two select prey species: large macropods (Arnold *et al.*, 1994) and rabbits (Ballinger and Morgan, 2002; Banks *et al.*, 1999; Poole *et al.*, 2003; Twigg *et al.*, 1998). Spotlighting was also used to record opportunistic predator observations in different habitat types. Spotlighting was not used to estimate predator populations as it has been found to be a less reliable method for measuring mammalian carnivore populations (Edwards *et al.*, 2000; Mahon *et al.*, 1998; Sharp *et al.*, 2001).

Spotlighting was conducted at night along vehicle tracks and commenced around one hour after sunset with an approximate duration of 2-3 hours. Two 20km spotlighting transects were monitored over 3 nights at each sampling site. On a few occasions, weather permitted only two nights of spotlighting. A Nissan Patrol 4WD was driven at a speed of between 10-15km/hr along the transect while an observer recorded animals seen from the roof of the vehicle using a hand-held high powered (200-W) spotlight (Lightforce®). The spotlight was fixed on a standard distance setting so that a maximum observational strip of 100m was seen either side of the road. The observer sat on the roof of the vehicle and slowly swept the spotlight from side to side in a 180° arc and recorded the number of each species detected. When an animal was spotted, the species, time of spotting and distance travelled were recorded. Prey species were usually clearly seen but otherwise identified by eye shine, size and movement. In the case of predator species, the vehicle was stopped and binoculars used to confirm identification when needed. When predators were spotted, the habitat in which they were found was recorded. Data were voice recorded by the observer using a hand-held microcassette recorder and transcribed at the end of the session. Often when predators were detected by eye-shine they could not be clearly seen, so when possible, predator identification was confirmed by checking tracks the morning after.

Limitations of this method were predominantly logistical constraints. Spotlighting is restricted to areas which have adequate vehicle access tracks. Its success is also typically determined by the suitability of the environment (Focardi *et al.*, 2001), with obstruction by vegetation a major influence on target species detection (Edwards *et al.*, 2000; Forsyth *et al.*, 2005). In this study there was some variation in that visibility of species across different habitats both within and between sites. For instance, thicker vegetation on sand dunes often made sampling to 100m difficult at the crest of a dune, leading to some bias and perhaps underestimation of prey species densities in these areas. The detection probability of prey was not estimated, as could have been possible using distance sampling methods (Bart *et al.*, 1998), however in an attempt to minimise this bias, dunes were also sampled from each side prior to and after cresting the dune with the vehicle. In contrast, open gibber plains at grazed sites had high visibility and a high success rate was achieved using this method. In addition, all spotlighting transects passed at least one watering point, in attempt to minimise the potential bias of increasing animal densities close to water.

Other considerations when sampling with this method included weather conditions such as rain and wind (Ballinger and Morgan, 2002; Twigg *et al.*, 1998; Wilson and Delahay, 2001) and moonlight (Twigg *et al.*, 1998). Prevailing wind direction, even for slight winds, influenced visibility due to dust disturbance by the vehicle. In some circumstances sampling nights were not consecutive, as sampling was not conducted on very windy or rainy nights.

Observer bias must also be considered. The use of only one observer to collect data is one method of overcoming the problem of varying skill levels and observational abilities between people. This was logistically difficult in this study. Instead, in order to minimise observer bias, two observers rotated between different sections of transect so that there was an even sampling effort by both people.

When possible, spotlighting was conducted prior to scent station sampling so as not to be influenced by or affect predator movements to and from lures. Even though predator populations were not assessed by spotlighting, an increase in predator activity may have changed prey behaviour and densities in the sample area.

Raw frequencies of prey species detected were standardised as the mean number of animals for each prey category (macropod and rabbit) per spotlight km, averaged over the three nights per transect. These means were then used to calculate the coefficients of variation between sampling areas. In the case of macropods at two study sites (Finniss Springs and Mundowdna/Wilpoorina), harvesting of individuals had to be taken into account (Krebs, 1999).The impact of harvesting on macropod activity is discussed further in Chapter 4.

2.3.3 Additional Methods

In addition to the methods described above, other methods were initially considered for data collection in this study. These additional methods were either not used due to logistical reasons, trialled as part of the original sampling design, but subsequently abandoned when found to be ineffective, or initially used for one purpose (such as population estimation), but found to be more useful for collecting different data.

Pitfall trapping was originally used to determine the availability of small prey species (small mammals and reptiles). Pitfall traps were established and trialled at two sites in Sturt National Park and Bollards Lagoon during the first sampling session. At each site twenty pitfall traps were set: ten within sand dune habitat and ten within inter-dune habitat, using a drift fence design (Braithwaite, 1983; Friend *et al.*, 1989). The traps were kept open for three days and checked each morning and evening to assess the temporal availability of small prey. After two weeks of sampling, capture rates of all species remained very low. Previous studies have shown that pitfall traps, in general, can be an ineffective means for sampling a wide variety of fauna (Laurance, 1992). For the small amount of data collected and the time, labour and resources required to both setup and check pitfalls, the method was judged to be inefficient and the data of least relevance to the study. The method was subsequently removed from the study.

Howling was initially used to determine the minimum number alive for dingo populations. This method has been used previously for coyotes with some success (Gaines *et al.*, 1995). In this study, howling was conducted at the beginning and end of each spotlight transect. The observer howled, waited 2 minutes, and then repeated this procedure 5 times. The number, time and direction of replies were recorded. This method was found to work well at some sites, but not at others and was discontinued as a population estimate. It was, however, used as an indication of resident dingo packs at each of the study sites (Corbett, 1995).

Scat counts were considered, but not used in this study. Scat counts is a commonly used method to estimate predator population indices (Henke and Knowlton, 1995; Sharp *et al.*, 2001). This method has logistical problems associated with sampling over large areas, in that the initial locating of scats can be difficult. This method often favours canids, whose scats are more likely to be found closer to roads. It is therefore generally unsuitable for felids, as their faecal matter is often buried, rendering the method inapplicable to this study.

2.4 Methods used for monitoring predator behaviour

Predator behaviour was assessed using a combination of activity estimates from scent stations and transects (see section 2.3.1, this chapter), in additional to observational methods. Data collected from transects and scent stations provided data on spatial distribution of predator activity and were used to assess distribution of predator activity around resources and habitat use. However, transects and scent station data did not provide detailed information on predator interactions around shared resources.

Most modern studies that examine predator behaviour, particularly those that monitor habitat use and movement, use GPS collars to collect behavioural data (Mech and Barber, 2002). GPS tracking was not used in this study as the method requires large amounts of time and funding and is generally restricted to only a few individuals. While GPS collars are able to collect accurate information on home range size, some spatial interaction between individuals (Merrill and Mech, 2003), and whether individuals are active or resting (Mech and Barber, 2002) they are unable to record detailed behaviour at a particular point in time and space (for example defensive behaviours between species or individuals at food resources) (Anderson and Lindzey, 2003). It was judged that more efficient methods were available for collecting the type of data required to address the aims of this thesis, including methods suitable for recording fine, detailed behaviours at a specific site.

Predator behaviour was recorded using three observational methods: direct observation, digital cameras (see Chapter 7) and thermal imaging (see Chapters 3 and 7). These methods were used to monitor temporal visits and interactions between predators at shared resources. The amount of data collected by direct observation was restricted simply due to observer limitations, including circadian rhythms and the amount of nights of observation needed to collect adequate data. The use of digital cameras was also restricted, as due to limited funds only three were able to be purchased, restricting the number of sites that could be sampled at one time. Sampling methodology and a detailed discussion on the limitations of these methods is included in Chapter 7.

In order to collect enough data on predator interactions, it was necessary to develop a new observational method which could operate remotely, collect large amounts of data and for which the required hardware was readily available. This new method used thermal imaging to observe and record nocturnal behaviour of predators at shared resources. Details on the development of this method and its use in this study are given in Chapters 3 and 7.

Chapter 3: The use of thermal infrared imaging for monitoring the behaviour of three terrestrial carnivores.

3.1 Introduction

Field biologists are continually faced with logistical difficulties when studying species whose natural life histories are not amenable to traditional data gathering techniques. In particular, the study of cryptic or nocturnal species may require the use of modern technologies to enhance human vision and collect sufficiently detailed behavioural data (Hristov *et al.*, 2008). Technologies most commonly used in studies of cryptic or nocturnal fauna include night vision equipment or image intensifiers (Hill and Clayton, 1985), remote photography (Cutler and Swann, 1999), video surveillance methods (Reif and Tornberg, 2006) and thermal imaging (Hristov *et al.*, 2010; Ammerman *et al.*, 2009).

Although each of these technologies has increased data collection abilities in many studies, they are not without limitations. Image intensifiers are restricted in their ability to collect data by both observer skill and the need for an external light source. A further concern is that study species may be disturbed by both visible light and/or human presence (Bart *et al.*, 1998). The use of automated digital cameras, equipped with near infrared lighting, may overcome human observer limitations and disturbance to study species by visible light and/or human presence. Digital technology also provides visual records that can be stored and reviewed. Remote photography has been used extensively in wildlife research for collecting distribution data on cryptic species (see review in Cutler and Swann (1999), although some behavioural studies have been conducted using this technology (Claridge *et al.*, 2004). However the static nature of the images means that remote photography remains restricted in its ability to collect detailed data on interspecific or intraspecific interactions. Cameras can be fiddley and unreliable, have low target detection rates and are restricted in operational range to around 20 m (Swann *et al.*, 2004).

Another option for studying cryptic species behaviour is the use of remote video systems, including closed and open circuit systems. Remote video systems are able to record more detailed behavioural data for most species, but have similar limitations to that of camera traps (see review in Reif and Tornberg (2006). Detection probability using standard video surveillance methods can be low (Kleist *et al.*, 2007) and many systems remain limited in detection range (Scheibe *et al.*, 2008). Whereas studies using video systems to monitor nesting behaviour of birds rarely require cameras to be at greater distances than 10 m from the point of interest (Gula *et al.*, 2010; Kross and Nelson, 2011), monitoring free-ranging mammalian behaviour requires greater detection distances (Huckschlag, 2008). The addition of audio function is a distinct advantage for capturing activity beyond the camera's field-of-view (FOV) (Huckschlag, 2008), however video surveillance systems can be unwieldy and non-target specific, requiring continuous recording with hours of footage to be reviewed for data collection (Sykes *et al.*, 1995). The use of motion or light sensors to trigger event recording may reduce excessive data storage and footage review time, but for many systems false positive recordings remain a significant problem (Scheibe *et al.*, 2008).

Among the most recent remote technology available for the study of wild fauna is thermal imaging (Kirkwood and Cartwright, 1993). Thermal imaging devices detect heat, not light, so are suitable for monitoring animals in the complete absence of visible light (Garner *et al.*, 1995), when the animal is camouflaged against its background, or when other environmental influence such as smoke, fog or haze affect vision (Blackwell *et al.*, 2006). A background to thermal imaging principles is provided in Appendix 2. Thermal technology has been used for monitoring the distribution wide ranging (Brooks, 1970; Focardi *et al.*, 2001; Garner *et al.*, 1995), nocturnally active (Ammerman *et al.*, 2009; Dymond *et al.*, 2000; Kirkwood and Cartwright, 1993) and burrowing (Hubbs *et al.*, 2000) species. Thermal imaging has had limited use in behavioural studies of both bird (Sidle *et al.*, 1993; Benshemesh and Emison, 1996) and bat (Ammerman *et al.*, 2009; Betke *et al.*, 2008; Horn *et al.*, 2008; Hristov *et al.*, 2008) species, but has not been used for the specific purpose of studying cryptic predators.

In this chapter the potential of thermal imaging for studying the behaviour of and interactions between dingoes, foxes and feral cats is explored by developing a fully-automatic thermal video recording system. The recording system was then used to capture behavioural data on the three predators in a range of situations and environments.

In particular, the aims of this chapter were to:

1. Develop a target specific, fully automatic remote recording system that used thermal video to record predator behaviour;
2. Use thermal videos in a human survey to access the interpretability of the method;
3. Compare thermal videos to the traditional behavioural monitoring method of human observation to access the accuracy of the method;
4. Identify the most important aspects of sampling design that influence the capture of accurate and interpretable video, and;
5. Determine best sampling procedures for the use of thermal infrared imaging to monitor the behaviour of three terrestrial carnivores.

The results of this study were then utilised to develop a standardised method for the collection of behavioural data in Chapter 7 of this thesis.

3.2 Method - Designing the technology

The process of developing the thermal infrared method applied in this research involved two major stages. The first stage was the initial setup and design of the hardware and software systems that would supply power and enable the thermal infrared video camera to collect and store data in remote locations.

3.2.1 Technical Hardware

The components and design of the technical hardware used in this study needed to satisfy a number of conditions. It was essential that the hardware was:

- Easily transportable;
- Adaptable enough to meet logistical attributes of different field sites;
- Resilient to the elements;
- Able to operate remotely and;
- Capable of storing large amounts of data.

The thermal infrared video camera used in this study was the FLIR ThermaCAM S45 (FLIR Systems Australia, Notting Hill, VIC). It is light-weight (1.4 kg), portable, (measuring 234 x 124 x 144 mm) and is designed for hand-held or tripod use. The spectral range is 7.5 – 13 µm. The standard 35mm lens has a horizontal FOV of 24°, vertical FOV of 18° and an instantaneous FOV of 1.3 mrad. It contains a germanium lens and has a thermal sensitivity of 0.08°K and a detectable temperature range from -40°C to 2000°C with a maximum of ±2°K, (2%) accuracy. The operating temperature range is -15 to 50°C(FLIRsystems, 2005). The camera is a quantitative system, meaning that it can determine (within the given detectable temperature accuracy) the surface temperature of each pixel in the capture images. The FLIR ThermaCAM S45 has a maximum video frame rate of 50 frames per sec. In this study, recording was conducted at 25 frames per sec. This reduced the amount of data storage required while maintaining the ability to capture reasonably fast motion.

A circuit diagram of the system setup is shown in Figure 3.1. The thermal imaging camera was connected to a Dell D610 laptop computer (Dell Australia Pty Limited., Sydney, NSW) by a firewire connection and powered it externally during remote recording. The power supply was a 12 volt, 80 amp hours deep cycle battery connected to a pure sine wave inverter, simulating normal mains power. This power supply gave the camera and laptop a maximum of 36 recording hours. During recording the camera, laptop, battery, inverter and cabling were enclosed in specially designed water resistant plywood casing, with the deep cycle battery, inverter, cabling and laptop stored separately from the camera in a large waterproof plastic tub.

The camera screwed onto a tripod attachment to enable accurate aiming of the lens. A viewfinder displayed the image seen through the camera on the laptop screen while settings were adjusted. This helped ensure that the camera was aimed accurately and that the FOV encompassed the entire area of interest.

The setup of the camera and supporting hardware used in field trials is shown in Figure 3.2. Figure 3.3 shows a photograph of the camera and laptop *in-situ*.

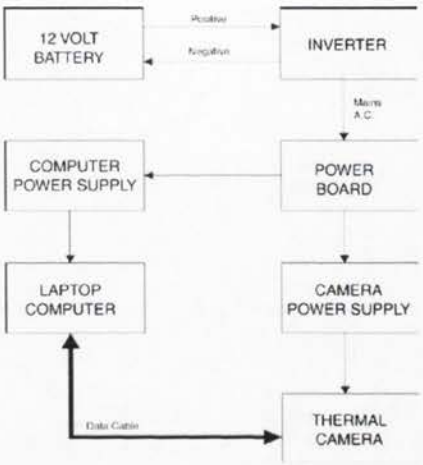


Figure 3.1 A circuit diagram of thermal imaging camera and supporting hardware, showing power flows

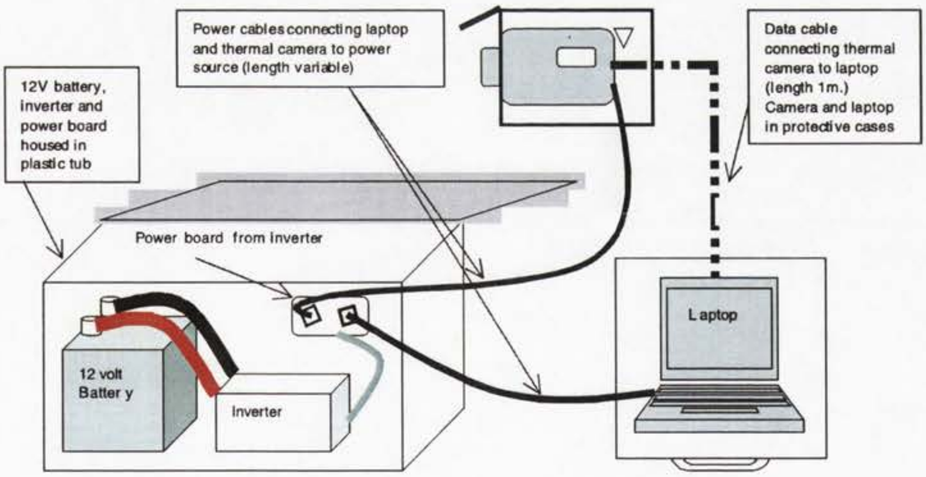


Figure 3.2 Schematic diagram of thermal imaging camera and supporting hardware showing cabling and protective housing of components for use in the field

Figure 3.3 Photograph showing placement of thermal imaging camera and laptop in a field situation (Bago State Forest, NSW)

3.2.2 Software Design

The automatic thermal video capture system was developed to monitor wild carnivores. As such, the system needed to be left unattended for the maximum amount of time possible in order to minimise the impact of human presence. The hardware did not allow for automatic power control; the system remained on at all times while recording in the field. To avoid a prohibitive amount of data storage, the system was programmed to intelligently start and stop recording when target animals entered and left the recording area.

The development of the software can be summarised in three major stages (Table 3.1). The software was written on a trial-and-error basis and was constantly being updated during the process of refining the method. Initial versions of the software (Stage 1) used absolute temperature as a trigger to activate recording. When an object entered the camera field-of-view and was 5°C warmer than the estimated background temperature (lowered to a 3°C difference in later versions), the software would record footage. The success of this method relied on three major assumptions: first that the background temperature would remain low (constant), second that the animals of interest would have a high temperature and third that any object above a certain temperature would be of interest. These three assumptions were shown to be false when a number of difficulties arose using this method. In response to these problems, the detection component of the software was then modified to include both motion sensitivity and background subtraction (Stage 2). Instead of triggering recording based upon absolute temperature values, background subtraction detects the difference in temperature between the object and an average background temperature, which is calculated by comparing each frame to the previous frame as it is received by the camera. Thus it accommodates slow changes in temperature, such as those that occur as dawn approaches, and recording is triggered by sudden movement and temperature change in a continuously adjusted average image.

In the final version of the software (Stage 3), pixel detection size was pre-selected before each field trial. Pixel detection size was calculated by estimating the minimum number of pixels in the edge contour (outline) of the target object at a given distance and was set to accommodate the relative sizes of the three target species (dingoes, foxes and cats). Pixel detection size decreased as sampling distance increased, as similar sized objects appeared smaller in the field-of-view. Typically, a contour detection size between 40 and 60 pixels was used. Temporal buffers were established to reduce the number of false positive recordings. A moving object needed to be within the camera frame for at least 1 sec before recording would commence. This 1 sec buffer was also added to the end of recording, so that there was a 1 sec delay after the object left the FOV before recording ceased. A viewfinder displayed the image seen through the camera on the laptop screen while settings were adjusted. This helped ensure that the cameras' aim was accurate, and that the field-of-view encompassed the entire area of interest.

In summary, a difference between the image received by the camera and the background model was considered large enough to trigger recording if the image included pixels that differed in detected temperature from the same pixel in the average background scene by more than 2°C, and the area of this difference had an outside contour size larger than the selected contour detection size (40 – 60 pixels), and (3) the detected change lasted for more than 1 sec. The final version of software employed a graphical user interface that allowed for configuration of the software to adapt to site specific conditions. Videos captured by the camera were stored in the encoded digital video format of Huffyuv version 2.1.1 (Rudiak-Gould, 2000) directly onto the computer hard drive with both recording time and date saved as metadata with each video file. The software that enabled remote recording of thermal infrared video is hereafter referred to as the *capture software*, and entire setup of hardware and software as the *remote recording system.*

Table 3.1 A summary of the three major stages in software development, showing software features trialled and technical difficulties encountered at each stage.

Stage of Software	Software features trialled	Technical difficulties encountered
Stage One	• Temperature only used as remote trigger. • The maximum ambient temperature during recording was estimated by the operator, and the trigger temperature was set 5°C above the maximum expected background temperature.	• No detection of animals due to lack of contrast between animals and background (caused by increased thermal insulation of winter fur). • If animals were detected due to “hot spots” (face and head) filming often ceased when they turned on an angle to the camera. • False recordings were made due to the heating up of the background in the morning.
Stage Two	• Motion sensitivity added. • Recording was triggered by a combination of motion in the camera field-of-view and temperature change of 3 - 5°C above background temperature. • Introduction of the “running average image”, replaces the set temperature difference trigger with temperature detection range. The camera takes the temperature of the environment approximately every 1/40 second and creates an average image over time. Slow changes are not recorded (eg sunrise) but sudden changes in temperature and movement are.	• The camera was too sensitive to small movements in the field-of-view, resulting in a large amount of false recordings (e.g. trees blowing in the wind, birds and bats flying past). • Problems with temperature changes and false recordings remain.
Stage Three	• Pixel detection size added as a requirement to trigger recording. (calculated by estimating the minimum number of pixels in the edge contour (outline) of the target object) • Pixel size of area of each target species estimated at different distances trialled at captive sites. • 10 second delay changed to 1 second delay at the end of recording. • 1 second delay added to beginning of recording eg triggers have to continue for more than one second before recording will start.	• Manual or automatic pixel adjustment needed, as animals change in size depending on distance from and angle to camera. • Temperature range must be accurate for quality recording. • If animal remains stationary for too long recording ceases until the animal moves again, but camera will begin recording when animal removes again.

3.3 Method -Trialling the technology

The second stage of developing this method involved trialling the system design and collection of footage. The thermal infrared videos collected were then used to construct a survey for experienced ecologists (see section 3.5.1 of this chapter) in order to address the aims outlined in the beginning of this chapter.

Trials were conducted using three target species: the dingo, the fox and the feral cat, in both captive and field situations. Physical attributes and ecology of these species are described in detail in Chapter 2 of this thesis. Of particular relevance to this study is a shared nocturnal habit, dictating that field studies be conducted overnight. Recording at night also aided in maximising thermal contrast between animals and the background. Coat colour was fairly uniform within each species recorded during the trial; the majority of feral cats displayed tabby colouration, while foxes and dingo coast were predominately reddish brown and sandy ginger typical of these species. All trialled animals were assumed to have coats of similar emissivity (see Appendix 2).

Six trial sites were used, situated in both temperate and arid climatic zones of Australia (Figure 3.4). They included three captive sites, where individuals of the three target species were housed, and three field sites, which supported wild populations. For logistical reasons, all three captive sites were in temperate areas, whereas only one field site was in the temperate zone, and two in arid areas.

Captive trials enabled both the initial testing of equipment (hardware and software design) and the collection of species-specific thermal images that were later used to aid in interpretation of images collected in field situations. Field trials tested the function of the remote recording system and capture software in a broad range of environments, and were used to collect information on behaviour of the three target species which was used later in this thesis (see Chapter 7). Images from both captive and field trials were used to test the effectiveness of the technology.

In each trial, the sampling site, camera placement and recording times represented a range of three parameters that would influence detection and later image interpretation. These parameters included vegetation, distance to the target animals and temperature. Temperature measurements included both ambient temperatures at the time of sampling and the temperature range selected on capture software. During data analysis, temperature measurements were combined with camera focus to define the clarity level of each recording (see section 3.3.2 of this chapter).

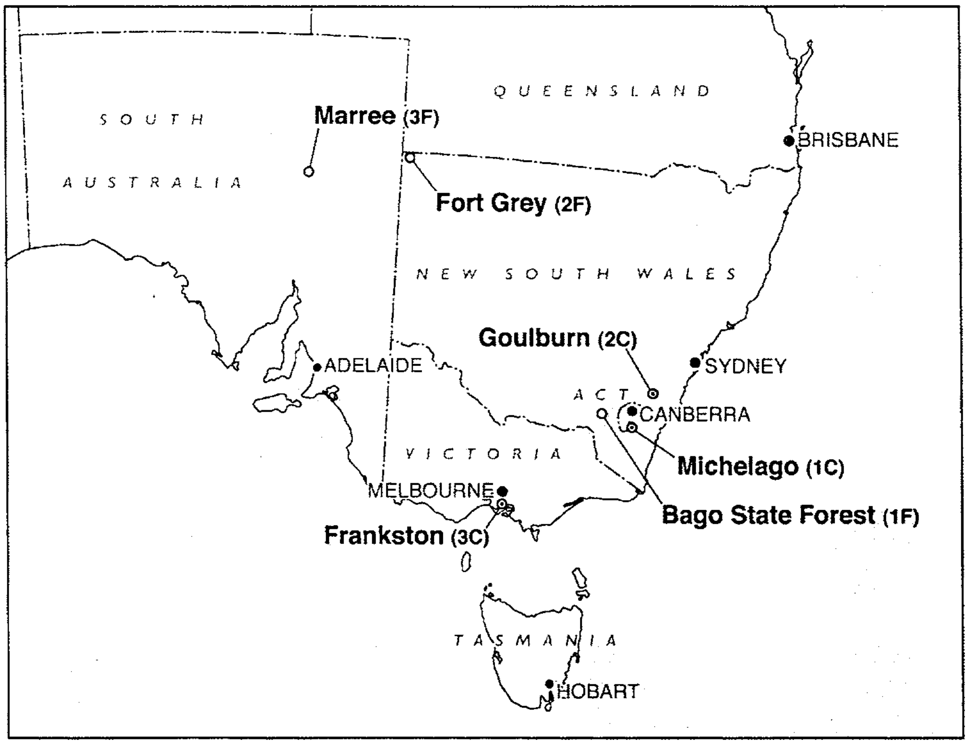


Figure 3.4 Map showing locations of captive and field sites used in thermal imaging trials

At one field site data were collected to compare a standard behavioural observation technique (direct human observation) with thermal imaging to assess the efficiency of the remote recording system (see section 3.4.2 of this chapter).

3.3.1 Collection of footage

3.3.1.1 Captive Trials

Captive trials were conducted at three locations: Michelago, NSW (149° 9' 44"E, 35° 42' 34"S, Elevation 800 m, Map ref. 1C), Goulburn, NSW (149° 43' 4"E, 34° 43' 9"S, Elevation 624 m, Map ref. 2C) and Frankston, VIC (145° 9' 23"E, 38° 9' 26"S, Elevation 6 m, Map ref. 3C) (Figure 3.4).

Where possible, natural environments with freely roaming animals were used, including grassed and vegetated enclosures. This gave captive sites the closest possible resemblance to typical field situations. A summary of captive trial sites, including dates and times of trials, vegetation types present, distances between the thermal imaging camera and target animals and temperature recordings at each site is given in Table 3.2.

Captive trials were used to develop accurate contour detection sizes for recording target species in the field and collect data in grassland environments. We filmed captive dingoes, foxes and cats roaming freely within enclosures, and estimated the distance of individuals from the camera (up to 70 m) by their proximity to objects (e.g. tree stumps, cages, fence line). The camera was attached to a tripod which allowed manual aiming during recording. A wide-angle lens (size 0.3) was trialled at one site, which increased the camera field-of-view to 80° x 60°. However review of the footage revealed the wide angle lens did not aid in improving the ability to monitor behaviour as animals were rendered too small to identify species at very short distances (less than 15m). Subsequently its use was discontinued and no videos taken during trialling the wide-angle lens were used in data analysis.

3.3.1.2 Field Trials

Field trials were carried out at three locations: Bago State Forest, NSW (148° 6' 0" E, 35° 36' 0" S, Elevation 1137 m, Map ref.1F), and two arid zone locations, Fort Grey, in Sturt National Park, NSW (141° 9' 17" E, 29° 7' 20" S Elevation 81 m, Map ref. 2F) and at Finniss Springs and Mundowdna Wilpoorina near Marree, SA (138° 4' E, 29°39' S, Elevation 54 m, Map ref. 3F). Field trials were used to refine the remote recording system and to test the effectiveness of the method in field situations. As with captive trials, three parameters (vegetation type, distance to the target animals and temperature) were noted for each trial. Refer to Table 3.3 for a summary of field trial sites and corresponding environmental parameters.

Food (carcasses) and water were used to lure target species to the sampling sites and provide a focal point for observation. Lures were placed at a predetermined distance of between 10 and 70 m from the camera, with the camera positioned approximately 0.7 m above ground level. Food was used as a lure at all sites in both summer and winter trials while water in dams was only used as a lure in the arid zone summer trials. In all circumstances, the remote recording system was positioned with minimum obstruction between the resource and the camera. Where possible, the camera was placed perpendicular to the most likely approach angle of the animal and never facing directly into the sun's path.

Sampling was conducted at night to maximise thermal contrast between animals and background, and for greater likelihood of capturing images of the target species. The remote recording system was activated in the evening 2 hours before sunset to allow for human scent to leave the area as much as possible before carnivores came to the site. The remote recording system was left to record overnight and checked for video recordings early the next morning. These recordings were reviewed and any necessary changes to the software or positioning of the unit were made before the next night of sampling.

Table 3.2 Summary of captive trials, including details of technical and environmental variables for each survey conducted.

Site and trial no.	Distances used (m)	Ambient air temperature range (°C)	Date, time and season	Remote software stage	Camera temperature ranges (°C)	Habitat and vegetation	Lure used	Day / night images	Species ID/ thermal signatures	Behaviour	Comparison with other techniques
Captive Site 1 (Michelago) Trial 1	3-10, 20, 30, 40	21 Smokey air, no clouds	6/4/05-7/4/05 9am-3pm (Autumn)	Manual filming only	Not Applicable	Grassland (up to 0.5m) and open pasture	NIL	Day images only	Dingoes (alpine type).	Behaviour of captive dingoes.	NIL
Captive Site 1 (Michelago) Trial 2	3-10, 50-70	23 Few high clouds	14/11/05 4pm (Summer)	Manual filming only	Not Applicable	Grassland (up to 0.5m) and open pasture	NIL	Day images only	Dingoes (alpine and desert type).	NIL	NIL
Captive Site 2 (Goulburn) Trial 1	3-35	9-11 Overcast	19/9/05 7am-6pm (Spring)	Stage 2	Temperatures 10°C above background triggered recording.	Open, clear pasture and bare earth	NIL	Day images only	Domestic cats and dogs.	Behaviour of domestic cats and dogs	Wide angle lens used
Captive Site 2 (Goulburn) Trial 2	3-35	17-12 10-6 Clear sky	28/9/05 2pm-7pm 9pm-6am (Spring)	Stage 2	Temperatures 7°C above background triggered recording	Open, clear pasture and bare earth	NIL	Both day and night images taken	Domestic cats and dogs.	Behaviour of domestic cats and dogs	Wide angle lens used
Captive Site 3 (DPI Vic) Trial 1	3-10, 20, 30, 40, 50	13-16 Overcast	15/11/05 1pm-6pm (Summer)	Manual filming and Stage 3	12-21	Captive pens with bare earth and low grass (0.1m)	Some food lures used	Day images only	Captive foxes and feral cats. Cat to 20m only.	Behaviour of captive foxes only.	NIL

Table 3.3 Summary of field trials, including details of technical and environmental variables for each survey conducted.

Site and trial no.	Distances used (m)	Ambient air temperature range (°C)	Date, time and season	Remote software stage	Camera temperature ranges (°C)	Habitat and vegetation	Lure used	Day / night images	Species ID/ thermal signatures	Behaviour	Comparison with other techniques
Field Site 1 (Bago State Forest) 1	30	5-9 Overcast	8/8/05 3pm-9am (Winter)	Stage 1	Temperatures 5°C above background triggered recording	Alpine Forest open clearing, background vegetation	Food	Night images only	NIL target species recorded	NIL target species recorded	Mud around carcass used to confirm species visits
Field Site 1 (Bago State Forest) 2	30	-4-2 Snow on ground	11/8/05 – 13/8/05 3pm-2pm (Winter)	Stage 1	Temperatures 5°C above background triggered recording	Alpine Forest open clearing, background vegetation	Food	Day and night images	NIL target species recorded	NIL target species recorded	Mud around carcass used to confirm species visits
Field Site 1 (Bago State Forest) 3	30	1-12 Scattered cloud	20/9/05-21/9/05 4pm-7am (Spring)	Stage 2	Temperatures 3°C above background triggered recording	Alpine Forest open clearing, background vegetation	Food	Night images only	Foxes and wild dogs	Foxes and wild dogs	Mud around carcass used to confirm species visits
Field 2 (Sturt National Park) 1	25-70	18-29 Clear sky	11/2/06 9pm-7am (Summer)	Stage 3	15-25	Open arid environment with bare earth (sand)	Water	Night images only	Feral cats and foxes	Feral cats and foxes	Human observation monitored species and behaviour
Field 2 (Sturt National Park) 2	15-50	20-33 Clear sky	13/2/06 9pm-7am (Summer)	Stage 3	21-31	Open arid environment with bare earth (sand)	Water	Night images only	Feral cats and foxes	Feral cats and foxes	Human observation monitored species and behaviour
Field 2 (Sturt National Park) 3	15-50	22-32 Clear sky	15/11/06 9pm-7am (Summer)	Stage 3	18-32	Open arid environment with bare earth (sand)	Water	Night images only	Feral cats and foxes	Feral cats and foxes	Human observation monitored species and behaviour

Table 3.3 continued

SITE and Trial	Distances used (m)	Ambient air temperature range (°C)	Date, time and season	Remote software stage	Camera temperature ranges (°C)	Habitat and vegetation	Lure used	Day / night images	Species ID/ thermal signatures	Behaviour	Comparison with other techniques
Field Site 3 (Finniss Springs) 1	30	18-29 Clear sky	22/3/06 8pm-7am (Autumn)	Stage 3	18-25	Open arid environment with bare earth (sand)	Food near Water	Night images only	Dingoes only	Dingoes only	NIL
Field Site 3 (Finniss Springs) 2	15-20	16-27 13-25 Clear sky	31/3/06-2/4/06 7pm-8am (Autumn)	Stage 3	16-26 14-28	Open arid environment with bare earth (sand)	Food near Water	Night images only	Dingoes only	Dingoes only	Prints in sand around carcass and still infrared digital cameras
Field Site 3 (Mundowdna Wilpoorina) 3	10	12-27 13-27 Clear sky	10/4/06-11/4/06 6pm-8am (Autumn)	Stage 3	14-28	Open arid environment with bare earth (sand)	Food near Water	Night images only	Foxes only	Foxes only	Prints in sand around carcass and still infrared digital cameras
Field Site 3 (Finniss Springs) 4	20	11-28 Clear sky	14/4/06 6pm-7am (Autumn)	Stage 3	14-28	Open arid environment with bare earth (sand)	Food near Water	Night images only	Dingoes and foxes	Dingoes and foxes at a shared resource	Prints in sand around carcass and still infrared digital cameras
Field Site 3 (Finniss Springs) 5	25	12-23 Clear sky	16/4/06 7pm-7am (Autumn)	Stage 3	14-28	Open arid environment with bare earth (sand)	Food	Night images only	Feral cats only	Feral cats only	Prints in sand around carcass and still infrared digital cameras

3.3.2 Data collection and categorisation

Videos collected from both captive and field trials were categorised by recording environment (grassland, alpine forest or arid environments), whether vegetation obscured vision of the animal or not, the distance between the camera and the target animal and the clarity of the footage. The animal was considered obscured by vegetation if more than one-third of the animal was hidden from view. Four distance categories were used: 0<15 m; 15<30 m; 30<45 m and ≥45 m. Clarity ratings were subjective and determined by the authors. The video was classed as high clarity if the target species was in focus and it was possible to distinguish a clear outline of the animal. It was classed as low clarity if no clear outline of the animal was visible, whether due to inadequate contrast (through incorrect temperature range settings) or inaccurate focus.

In order to evaluate the accuracy of the remote recording system, the standard human observation technique of direct observation was used concurrently to the remote recording system at one site (Fort Grey in Sturt National Park, NSW).

Direct observation was conducted from the same scene vantage point to that of the remote recording system. Two observers sat in the roof-top tent of a vehicle, which was open at the front to allow an unobtrusive and unobstructed vision of animals throughout the night. Both binoculars and a night vision monocular were used to aid in night vision. Time settings on observer watches were synchronised to those of time settings on the laptop to enable identification of individual animal by time of visit. Time settings on the laptop dictated time and date information on video files collected by the capture software.

When the camera was in position, the horizontal field-of-view (HFOV) was marked out at a distance of up to 70m using natural objects as estimators. This provided human observers with a way of judging when an animal passed across the camera's HFOV. As target animals came into the camera's HFOV, observers recorded the species and relevant behaviours. Behaviour was categorised into six broad categories: Consuming (including drinking and eating), movement (including running and walking), exploring (sniffing around), sitting, sleeping and interacting with other individuals.

3.4 Data Analysis

3.4.1 Sampling Design

To assess the interpretability of thermal videos, a total of 18 experienced ecologists (defined by having a minimum of five years field experience with terrestrial carnivores) participated in a questionnaire of 45 questions, which included 61 videos. Two people were used as a pilot study and their answers were not included in the analysis. An assumption was made that the survey participants were competent in identifying the three target species and recognising typical behaviours. Although all survey participants were skilled mammalogists, none had any previous experience with thermal infrared imaging and none was present at the time of thermal image recording.

Videos used in the questionnaire contained footage of target species taken in the three different environments (forest, grassland and arid), with or without vegetation obscuring the animal, at different distances, and using footage of different clarity. Videos of target species from both captive and field trials were used. Some videos were "placebos" and contained other species (such as herbivores) or no animals at all. To ensure accuracy, only videos with captive animals or those with data also collected via direct observation were included in the questionnaire.

For each question, a thermal video was displayed on a laptop screen, and participants were permitted a maximum of four views before supplying an answer. The questions were asked in a set order rather than being asked randomly as they were ordered to minimise the effect of learning by the participants. Participants were asked to identify the species and to select one or more categories that described the behaviour of the animal that they were viewing. Responses were marked as correct or incorrect. Participants were also asked to identify age and sex of individuals in videos of captive animals but lack of response from participants precluded further analysis.

Data analysis was conducted using the statistical software package Genstat v.13 (VSN International, Hemel Hempstead, UK). Generalised linear mixed models were used to model the probability of a correct response, either towards identifying the species or identifying the behaviour. The presence of vegetation (yes/no), clarity of image (clear/unclear) and distance from animal were considered fixed effects. Distance was modelled as an ordered category, and defined four categories: <15 m, 15<30 m, 30<45 m and $\geq$45 m. The random effects component included the video number and the respondent number. Back-transformed means (modelled probabilities) were calculated based upon the linear predictors. P-values less than 0.05 were considered to be statistically significant, and p-values less than 0.20 to be of interest due to small sample sizes.

3.4.2 Method Comparison

A total of 45 videos were used to compare the effectiveness and accuracy of the automatic video capture system to human observation. Data collected by each method over two sampling nights was combined. Visits and behaviours were placed into one of three categories: either they were recorded by human observation only, by the remote recording system only, or by both methods. Species identification was not used in the analysis as only one target species (the red fox) was recorded at the site. Of the total visits, only those visits that were detected by both the remote recording system and human observation were used to compare the ability of each to detect categorised behaviours. The probability of detection by human observation and the remote recording system was calculated using the proportion of visits and behaviours recorded by human observation, the video capture system, or by both methods.

3.5 Results

A total of 316 thermal videos of the three target species were recorded; most videos were collected at arid field sites (267). Captive predators in grassland environments were also successfully captured on video (46) but only 3 videos of target species were recorded at the alpine forests field site. The camera was placed <15 m of the target species in 37 videos, 15<30 m in 128 videos, 30<45 m in 103 videos and ≥45 m in 48 videos. The average duration of thermal videos was 6.4 minutes, with a median duration of 4 minutes. Selected automated thermal video recordings are included in Appendix 4.

3.5.1 Survey Design

Accuracy of species identification decreased as the distance between the subject(s) and thermal camera increased, with the largest decrease in observer accuracy occurring at distances ≥45 m ($P = 0.03$). In this largest distance category (≥45 m), only 37% of the participants could correctly identify the species. In comparison, in the distance category of 30<45 m, 67% of participants were correct (Table 3.4). Distance did not affect the ability of observers to identify behaviours ($P = 0.56$) (Table 3.5).

There was some weak evidence to suggest that the presence of vegetation may affect observer accuracy of species identification ($P = 0.08$). Only 45% of participants were able to correctly identify the species with vegetation present, compared to 73% without vegetation obstructing part of the animal (Table 3.4). Vegetation appeared to have less effect on the ability of observers to recognise behaviours ($P = 0.13$) (

Table 3.5).

Observer accuracy of species identification increased slightly in videos with higher clarity, but this result was not significant ($P = 0.26$) (Table 3.4). Clarity did not influence the ability of observers to accurately identify behaviours ($P = 0.41$) (

Table 3.5).

3.5.2 Method Comparison

Of the 45 foxes that entered the camera FOV, 60% (95% CI = 46-74%) of visits were recorded by both human observation and the remote recording system. The proportion of visits that were recorded by human observation only (22%, 95% CI = 12-34%) was similar to the proportion of observations recorded by the remote recording system only (18%, 95% CI = 9-31%).

Table 3.4 The effect of vegetation, distance and image clarity on the ability to identify species using thermal videos.
Results shown for 16 survey participants viewing 45 thermal videos collected from captive and field sites during 2007.

Variable	Category	Videos (*n*)	Modelled % of correct responses	Log odds ratio	*SE*	*F*	*d.f.*	*P*
Vegetation	present	11	45	-1.18	0.66	3.17	36.7	0.08
	absent	32	73					
Distance	< 15m	8	84	-0.68	0.29	5.45	36.8	0.03
	15 < 30m	18	70					
	30 < 45m	16	67					
	> 45m	9	37					
Clarity	High	31	74	0.72	0.63	1.29	37.5	0.26
	Low	14	58					

Table 3.5 The effect of vegetation, distance and image clarity on the ability to identify behaviours using thermal videos.
Results shown for 16 survey participants viewing 45 thermal videos collected from captive and field sites during 2007.

Variable	Category	Videos (*n*)	Modelled % of correct responses	Log odds ratio	*SE*	*F*	*d.f.*	*P*
Vegetation	present	6	80	-1.14	0.73	2.42	26.9	0.13
	absent	27	92					
Distance	< 15m	6	96	-0.17	0.28	1.48	32.4	0.56
	15 < 30m	15	87					
	30 < 45m	5	97					
	> 45m	8	87					
Clarity	High	23	93	0.52	0.62	0.71	32.1	0.41
	Low	11	89					

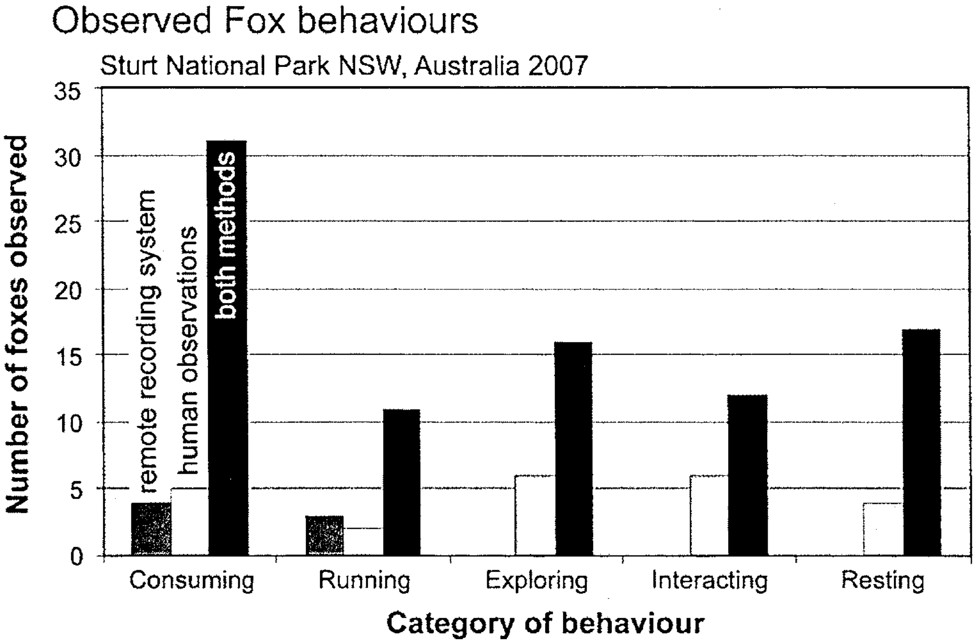


Figure 3.5 The observed categories of fox behaviour using the remote recording system, human observation and both methods.

Of the 88 behaviours recorded, 80% (95% CI = 69-88%) were captured using both methods. A similar number of behaviours were recorded by human observation only (12%, 95% CI = 6-20%) and the remote recording system only (8%, 95% CI = 4-15%). The camera was less likely to detect more stationary behaviours, such as sleeping and sitting, or behaviours that removed them from the field of view (such as exploring), but was better at detecting behaviours that occurred suddenly or on the periphery of vision, such as movement, which were not captured as well by human observation (Figure 3.5). Additional foxes entered areas on the periphery of the lure during sampling, but did not approach the lure closely enough to enter the remote recording systems' HFOV. As such, these foxes were recorded by human observation only and were noted but not included in the analysis.

3.6 Discussion

The main objective of this chapter was to report on the design and trialling of a new method for monitoring carnivore behaviour. In order to collect accurate behavioural data, thermal images needed to contain desired information relevant to the research question, be easily interpretable and accurate. The trialling of different sampling procedures throughout the duration of the study highlighted the most important aspects of survey design influencing the production of quality images. Correct camera temperature range settings (which increased thermal contrast) and the camera placement (which determined the distance from the camera to target animals) were the two most important factors determining image quality. Ground truthing through both prior acquisition of thermal signatures for each species and the use of supplementary methods such as human observation is recommended. Finally, the selection of suitable sampling times and procedures was found to be important in achieving maximum thermal contrast and detection of target species. Each of these factors played a role in obtaining high quality thermal images.

3.6.1 Sampling Design

To collect accurate data using thermal video, images need to be sufficiently clear for accurate interpretation. The video footage recorded by our system was shown to be highly interpretable for the purpose of identifying target species and behaviours. Sampling design influenced an observer's ability to identify species. In our study, the effects of distance to the target species and the presence of vegetation were the two most important factors when determining optimum camera placement, temperature settings and related sampling procedures. Although vegetation was found not to be statistically significant, we deemed it to be of interest and suggest that small sample sizes may have been a confounding factor in our analysis.

The success of thermal imaging in wildlife studies has often been limited by the presence of large amounts of vegetation (Dunn *et al.*, 2002; Haroldson *et al.*, 2003; Hubbs *et al.*, 2000; Naugle *et al.*, 1996; Wiggers and Beckerman, 1993). A decrease in visibility of the target species caused by obstructing vegetation may not only lessen the likelihood of detecting an animal (Galligan *et al.*, 2003) but may also decrease the ability to correctly identify it. The results from this study suggest that obstructing vegetation may limit species identification in some circumstances, but does not affect the ability to interpret behaviour. As species recognition is a major component of both behavioural and abundance studies, the presence of vegetation in the focal area may reduce the effectiveness of the method in some cases.

It is also likely that a decrease in contour size of the target species caused by obstructing vegetation would lower the likelihood of detection by the remote recording system. Similarly, the orientation of the animal to the camera may also influence its detection probability (Best *et al.*, 1982; Croon *et al.*, 1968). A reduction in the thermal contour of an animal occurs when the animal was orientated directly toward or away from the camera. Any further occlusion of the animal (such as from vegetation) could reduce the outline to an amount below the configured threshold, causing recording to cease or not to commence at all. Thus it was important to select a contour size that was small enough to detect such occurrences, whilst minimising recording of smaller non-target objects. A contour size of 40 to 60 pixels was considered optimal as it took into account the relative sizes of the target species at distances between 10 and 70 m.

The presence of vegetation may be a more significant limitation for direct observation than for thermal technology. In heavily vegetated areas an animal's cryptic colouration may camouflage it completely to the human eye, whereas the portions of the animal visible through the vegetation will still appear very brightly on a thermal video. Thus accuracy of target species detection in vegetated areas may actually increase using thermal imaging (Betke *et al.*, 2008; Boonstra *et al.*, 1994; Havens and Sharp, 1998). Difficulties arising from thick vegetation have been overcome in overseas studies by working in areas with primarily deciduous species during winter months when there is less cover (Graves *et al.*, 1972; Kissell *et al.*, 2004). While the use of open canopies or rangelands may overcome the issue of obstructing foliage (Croon *et al.*, 1968; Focardi *et al.*, 2001), it limits surveys to both a season and habitat, which may lead to biased data on both abundance (Adams *et al.*, 1997; Gill *et al.*, 1997) and behaviour. It also restricts the suitability of the method to a limited number of species and conflicts with the findings of this study that the optimal census time is during seasons when animals have shorter summer coats. Finally, in Australia such opportunities would be highly limited, since most native forest and plantation vegetation is composed of non-deciduous species.

Distance between the target species and the camera was the most important variable affecting an observer's ability to correctly identify species (Gill *et al.*, 1997; Sidle *et al.*, 1993; Wyatt *et al.*, 1985). It was important that the target animals appeared sufficiently "large" in the thermal video, and at high enough resolution (Barber *et al.*, 1991; Best *et al.*, 1982; Dymond *et al.*, 2000; Gill *et al.*, 1997; Speakman and Ward, 1998). If distances are too large for the size of the species, detection rates may be lowered (Sidle *et al.*, 1993; Wyatt *et al.*, 1980) and observers may be unable to correctly identify species (Gill *et al.*, 1997). Survey results suggested that observer accuracy was greatly reduced at distances $\geq$45 m.

One limitation of the remote recording system used in this study was that the focus has little depth of field. Focusing the camera to the correct distance was crucial for good image clarity (Boonstra *et al.*, 1995) and depended greatly on accurately estimating the distance that the animal would be from the camera. The automatic nature of the sampling procedure we used meant that the camera was set at a fixed angle and focal point that could only be adjusted prior to recording. This limitation is overcome to some extent by focusing the camera on the point of interest or the area of the scene most likely to be frequented by the target species.

The optimum placement of the camera in relation to the target species was therefore a trade-off between gaining enough detail in the image to correctly identify species, while encompassing enough sampling area (FOV) to capture movements and behaviours (Barber *et al.*, 1991; Graves *et al.*, 1972; Hristov *et al.*, 2005). Using our equipment, focal lures and targeting our three predator species, the optimal sampling distance for detection, identification of species and collection of behavioural data was 30<45 m. One disadvantage of our method is that animals that do not enter the camera's FOV were not recorded. This has been somewhat overcome in other video systems using audio recording in addition to video (Gula *et al.*, 2010; Huckschlag, 2008).

3.6.2 Effects of the Environment

Both physiological adaptations and behavioural mechanisms are used as heat regulation methods by species in arid areas (Barber *et al.*, 1991; Dawson and Brown, 1970; Wolf and Walsberg, 2000) and temporal, spatial and seasonal activity patterns of target species needed to be considered (Cena and Clark, 1973; Dawson and Brown, 1970; Oke, 1987; Porter and Gates, 1969). The optimum time for sampling behaviour in arid environments was during periods of darkness, when residual ground heat had dissipated and the three species increased their activity.

Prior research suggests that colder background environments facilitate species detection (Bernatas and Nelson, 2004; Diefenbach, 2005). Using our system, we were able to effectively monitor nocturnal activities of predators at arid sites during summer. As our software adapted to temperature changes in the background scene during the sampling period, we achieved good thermal contrast through correct software configuration. The use of background subtraction meant that detected objects did not necessarily have to be warmer than the background, but simply that their surface temperatures differed.

The ability of thermal infrared systems to effectively detect target objects is largely influenced by thermometer settings, including the temperature range (Kastberger and Stachl, 2003). Dunn et al. (2002) found high thermal emissions from residual ground heat lead to the effect of 'blown out' thermal images. During our study, we found that such saturated images only occurred when the detectable temperature range on the software was too narrow. Unlike other studies where thermal contrast could be manually adjusted during data collection (Best *et al.*, 1982; Haroldson *et al.*, 2003) the remote recording system used in this study required temperature range settings to be manually set prior to recording. Therefore to achieve good thermal contrast knowledge of the probable temperature changes of the scene over the sample period was required (Best *et al.*, 1982).The preselected temperature range needed to accommodate changes in ambient, background and target object temperatures throughout the sampling period. To facilitate the selection of temperature settings, the software was able to show the user the current minimum and maximum temperatures in the scene during system setup. We found that a good technique was to set the minimum and maximum temperatures to a range slightly larger (around 2°C) than the temperature range at the time of system deployment. This effectively reduced the occurrence of saturated images in arid zone trials (Figure 3.6).

The effect of residual heat is much less pronounced in grasslands compared to arid environments, and we were able to conduct recording during the day (Galligan *et al.*, 2003; Monteith and Szeicz, 1962). In agreement with findings from other studies (Galligan *et al.*, 2003; McCullough *et al.*, 1969), early morning and night gave the highest contrast between target species and background. Sampling in the early afternoon during captive trials showed a significant amount of heat radiated from the grass during this time period, substantially reducing contrast with target species. Animals were distinguishable from the background environment in cooler patches, where grass had been shaded by trees or other objects, and only if they had been exposed to direct solar radiation for a period of time prior to sampling. Since shading decreases surface temperature relatively quickly (Kelly *et al.*, 1954), animals that had been lying in the shade often had a cooler surface temperature than the grass, and were only detected if their temperature substantially differed from the background (Figure 3.7).

At Bago State Forest, we experienced a low detection rate of predators (n = 3). The cause of this result was unclear, but may have been due to use of early stage software developments, low predator densities, increased vegetation, incorrect temperature settings or thermal insulation of target species (Cena and Clark, 1973; Wolf and Walsberg, 2000). In winter, many mammals typically increase thermal insulation, and carry a coat of comparatively thick, dense fur that retards heat loss (Cena and Clark, 1973; Oke, 1987; Walsberg, 1988; Walsberg, 1991; Wolf *et al.*, 2000). This seasonal coat change has been described for two of the three species targeted in this study, dingoes (Shield, 1972) (Figure 3.8) and different species of foxes (Klir and Heath, 1992). Such seasonal alterations to coat structure are highly significant in thermal imaging (Dawson and Brown, 1970; Walsberg, 1991) as heat is trapped within the coat, thermal emissions are lowered and the actual surface temperature of the animal may not substantially differ from the ambient air temperature (Grojean *et al.*, 1981), decreasing detection. Further trials in winter months are therefore needed to assess whether the system will work well under such conditions.

3.6.3 A Comparison of Techniques

When the remote recording system was compared to human observation, it was found to be as effective at recording both visits and behaviour of foxes within the camera FOV. In previous studies using thermal imaging for counting bats, thermal imaging was found equal to or even more reliable than numerical estimates gained from human observation (Betke *et al.*, 2008; Sabol and Hudson, 1995). The remote recording system was better able to detect behaviours that occurred quickly, such as movement, that were more easily missed by human observers. Human observation was better at detecting more stationary behaviours, such as sleeping and sitting. Use of both human observation and the remote recording system increased detection rate dramatically of visits (60%) and behaviours (80%) of target species.

Although appearing equally effective, both methods have inherent advantages and disadvantages that may limit their use in some circumstances. One limitation of human observation is that natural circadian rhythms can cause difficulties when monitoring nocturnal or crepuscular species (Boonstra *et al.*, 1994). In contrast, the remote recording system is limited only by battery life. A further limitation of human observation is that it is subjective and limited to a focal point of interest (Bart *et al.*, 1998). Although the remote recording system FOV is much more limited than human vision, it always records the entire field of view. Digitally stored footage also has a distinct advantage in that can be viewed repeatedly. Data that may be easily missed by an observer in the field is stored, allowing repeated viewings to ensure all recorded information is accurately interpreted.

The remote operation of our system reduces human presence at the sampling site, lessening the bias associated with human disturbance (Galligan *et al.*, 2003). The behaviour of the target species was slightly altered by their reaction to the remote recording system. During recording the camera made a small clicking noise every few minutes as it calibrated the image. The reaction of animals to this noise varied; some individuals ignored it while others inquisitively investigated the camera. The most common reaction was for the animal to look up briefly in response and then continue its previous behaviour. To combat such difficulties, a period of acclimation may be advisable (Speakman and Ward, 1998).

One of the major limitations to the use of thermal imaging technology is the significant cost. The initial outlay for equipment is expensive, however automatic thermal video capture allows cost benefits in terms of saving time and effort both in the field and when reviewing footage (Adams *et al.*, 1997; Benshemesh and Emison, 1996). Our system is highly target specific and enables accurate monitoring of carnivore behaviours at a focal point, with potential for behaviour recognition software to be incorporated in the future.

3.7 Conclusion

The suitability of thermal infrared imaging as a technique to monitor behaviour would be largely dependent on the aims and objectives of the research being undertaken. Thermal imaging would be most suitable for studies that monitor species distribution or behaviour at a focus point. This may include studies on social groups, feeding interactions, hatching behaviours in birds or reptiles and breeding behaviours in burrowing or denning mammals. As thermal imaging records surface temperature, it also has the advantage of being able to combine animal distribution or behaviour studies with physiological research (Lavers *et al.*, 2005). Data on physiological adaptations, states or responses could be collected simultaneously and may bring useful insights when interpreting behavioural data (Tattersall and Cadena, 2010). Thermal imaging has been successfully used for the detection of stress and injury in animals (Cook and Schaefer, 2002; Schaefer *et al.*, 2004), to examine mechanisms of energy utilization

(Kastberger and Stachl, 2003) and to study other thermoregulatory behaviours and adaptations important in life histories of species (Blumberg *et al.*, 2002). The presence of infectious diseases in wildlife populations has also been successfully detected using thermal imaging (Arenas *et al.*, 2002; Dunbar *et al.*, 2009; Dunbar and MacCarthy, 2006), making it a useful, non-invasive tool for the study of wildlife population health. Some authors argue for the need of a standardised method using thermal imaging (Havens and Sharp, 1998; Kissell *et al.*, 2004), however we believe this is not viable in practice because of the high variability of species, behaviours and environments.

Until recently, technology using thermal infrared imaging had limited application in ecological or behavioural studies (Naugle *et al.*, 1996), but this study has shown that, with careful site selection and adaptable software, thermal imaging can be a useful tool for monitoring otherwise difficult to observe species, such as the dingo, fox and feral cat. The remote recording system, as developed through these trials, is used to collect data on behaviour and visitation rates of dingoes, foxes and feral cats at shared resources in Chapter 7 of this thesis.

Figure 3.6 Image showing excellent thermal contrast between a feral cat and the background.
(Image by R. Visser and T. Rauphach, 2007)

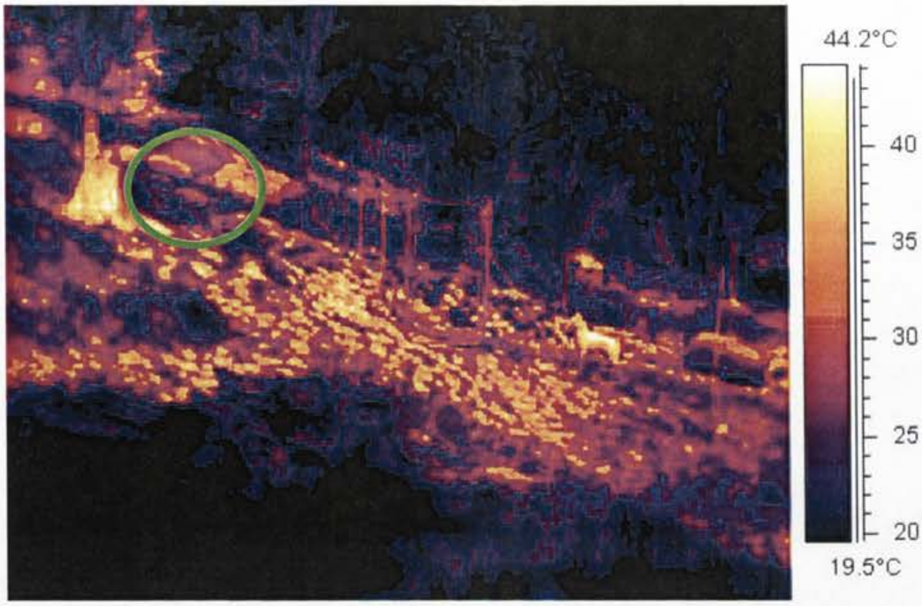


Figure 3.7 A thermal image illustrating the effect of shading on contrast between target species and background objects. Note the difference in visibility of a dingo that has been lying in the shade (within green circle) to the dingo in the sun (visible animal by the cage).
(Image by R. Visser and T. Rauphach, 2006)

Figure 3.8 A thermal image showing the uneven surface temperature in a captive alpine dingo due to insulative coat changes
(Image by R. Brawata and T. Raupach, 2006)

Chapter 4: The influence of management of the dingo on the response of mesopredators and prey to rainfall in arid ecosystems

4.1 Introduction

There are two main theories that attempt to identify the primary driver of ecosystems in arid Australia. First, arid regions are traditionally viewed as "bottom-up" ecosystems, where trophic interactions are regulated primarily by productivity (Jaksic *et al.*, 1997). Many species fluctuate dramatically in response to environmental variability and perturbations, of which the most significant is rainfall (Fensham *et al.*, 2005). Related vegetative productivity is then a key determinant of the abundance and distribution of many herbivorous species and predators that prey on them (Grant and Scholes, 2006; Fensham *et al.*, 2005; Haythornthwaite and Dickman, 2006; Letnic *et al.*, 2005; Previtali *et al.*, 2009; Dickman *et al.*, 1999; Letnic and Dickman, 2006).

Alternatively, "top-down" regulation identifies that apex predators exert regulatory forces on smaller predators, limiting their density and range (Terborgh and Estes, 2010). Regulatory forces may either be through direct predation or by indirect mechanisms such as competition for limited resources or initiating avoidance behaviours (Gehrt and Prange, 2007; Palomares and Caro, 1999). The removal or reduction of large carnivores from ecosystems may lead to 'mesopredator release' (Soulé *et al.*, 1988), where smaller predators are able to increase to higher densities in the absence of top down control (Crooks and Soule, 1999). Under such circumstances, the abundance and diversity of prey species susceptible to mesopredator predation may be greatly reduced (Bruno and Cardinale, 2008). Therefore the reduction or extinction of apex predators may significantly alter ecosystem function and have cascading effects through the entire trophic web (Soulé *et al.*, 2005).

It is likely that both top-down and bottom-up forces play a part in the regulation of arid ecosystems in Australia (Pianka, 1978). One limitation of previous studies on top-down regulation is that they are correlative or employ only short-term, "snap-shot" approaches that are unable to encompass sufficient environmental variability to gain a meaningful understanding of trophic dynamics. For example, while productivity may act as a primary driver in ecosystems, top-down forces may be important under explicit environmental conditions (Holmgren *et al.*, 2006), with interactions varying temporally and spatially in strength (Letnic *et al.*, 2005).

Current research indicates dingoes may be a keystone species in some Australian ecosystems due to their ability to limit populations of two exotic mesopredators, the red fox

(*Vulpes vulpes*) and feral cat (*Felis catus*) (Johnson and VanDerWal, 2009; Kennedy *et al.*, 2011; Letnic *et al.*, 2009a; Letnic *et al.*, 2010; Letnic and Koch, 2010; Letnic *et al.*, 2009b). Studies have shown where dingoes persist, fox activity is reduced and small native mammal species persist in higher abundance (Smith and Quin, 1996; Johnson *et al.*, 2007; Letnic and Koch, 2010; Wallach *et al.*, 2009a). As the decline of many native fauna species, particularly small to medium-sized mammals, has been primarily attributed to predation by foxes and feral cats (Burbidge and Mckenzie, 1989; Short and Smith, 1994) retaining dingoes in ecosystems may assist in the conservation of native species highly vulnerable to fox and cat predation (Burbidge and Manly, 2002; Risbey *et al.*, 2000).

It remains unknown as to whether: dingoes are able to maintain lower densities of foxes with increases in prey abundance, if interactions between predators change in response to rainfall, and what the implications of these factors are for native prey populations in the long-term.

To increase our understanding of the role top-down forces may play in the function of arid ecosystems in Australia, I examine how dingo management influences population indices of dingoes, foxes, feral cats and select prey both prior to and post a significant rainfall event. Using population indices estimated from each of the study sites, I then address the following question:

- How does a rainfall event affect activity of predators and prey under different dingo management regimes?

Consistent with the theory of top-down regulation, I hypothesis that where dingoes remain uncontrolled, mesopredators will be less active overall, large prey will display lower activity while small to medium sized prey maintain higher activity prior to rains and increase more rapidly in response to rainfall events where dingoes are present.

4.2 Methods and Data Analysis

Field methods for collecting the data used to obtain population indices for both predator and prey populations are covered in detail in Chapter 2 (section 2.3). Here I discuss the methods used to analyse data collected from spotlighting, transects and scent station methodologies.

4.2.1 Transect data

Data analysis was conducted using the statistical software package Genstat (VSN International, 2008). A linear mixed model was used to calculate the mean PAI (Passive Activity Index, see Chapter 2, section 2.3.1.1) (Allen *et al.*, 1996)for each species at all study sites, using both site and year as fixed effects and night and sampling area as random effects (Engeman *et al.*, 1998). In order to account for possible temporal and spatial dependence in measurements between the three nights sampling (design effect) the effective sample size was estimated by using the variance calculations from both within and between sampling areas (Table 4.1). A variance inflation factor was calculated from the intraclass correlation where the ICC is the proportion of variance due to sampling area; and was used to estimate the design effect (*DE*) as follows:

Equation 1 Estimation of design effect

$$DE = 1 + (k-1)ICC$$

where k is the number of units within a sampling area (i.e. 3). The effective sample size e = actual sample size (n=6))/ *DE*. Estimates for *ICC*, *DE* and e for each predator species and prey category are shown in Table 4.1. Transect data for each species (derived from the 20 transect plots per sampling area) were pooled for each night (nights 1, 2 and 3). The effective sample size was then used to estimate the standard error for each species at each site using the formula:

Equation 2 Estimation of standard error

$$SE = \frac{SD}{\sqrt{e}}$$

4.2.2 Scent station data

Using binomially distributed data sets (presence/absence of a species at an individual scent station each sampling night) a generalised linear mixed model, with site and year ,as fixed effects and sampling area and night as random effects, was used to calculate a linear predictor (η) for each species at each site per sampling year, so that:

Equation 3 Modelled proportion of visitations per study site per year

$$pr(i,j) = \frac{1}{e^{-n_{ij}} + 1}$$

where *pr* is the modelled proportion of scent stations visited by a particular species at study site i for year j. A 95% confidence interval for each linear predictor was estimated (η ± $t_{.975}$(d.f =24)SE).

Table 4.1 The estimated effective sample size by species (from transect data, all sites / years).

Note: * indicates variance component was estimated to be < 0. Due to large between sampling area variation at Quinyambie Station, small mammals were modelled separately for this site.

Predator Species / Prey Category	Variance (between sampling areas)	Variance (within sampling areas)	*ICC*	*DE*	n - *e*
Dingo	0*	0.11	0	1.00	6.00
Fox	0*	0.07	0	1.00	6.00
Cat	0.01	0.01	0.28	1.56	3.84
Macropod	0.02	0.04	0.35	1.71	3.50
Rabbit	2.10	5.14	0.29	1.58	3.80
Small mammals (not including Quinyambie Station)	0.16	0.32	0.33	1.66	3.61
Small mammals (Quinyambie Station only)	142.54	35.81	0.80	2.60	2.31
Reptiles	14.12	32.89	0.30	1.60	3.65

Observed visitation rates were used to calculate the mean activity index for each predator species at a given study site per sampling night. As the relationship between the mean activity index and proportion of animal visitations is non-linear (Fleming, 1996; Caughley, 1977), the mean activity index ($\bar{x}$) for each species was calculated using a log transformation as follows:

Equation 4 Mean population index of predator species from observed visitation rates

$$\bar{x} = -\log(1-f)$$

where f is the observed visitation rate. The overall mean activity index was then assessed for each predator species at each site per sampling year. A linear mixed model using study site and year as fixed effects, and sampling area and day as random effects, was used to examine the effects of study site and year on mean densities of dingoes, foxes and feral cats.

The residual variation from this model was used to determine whether or not any clustering effects were present for each species per sampling night; clustering may arise from heterogeneity within predator populations.

4.2.3 Spotlighting data

The total number of macropods and rabbits counted each night was divided by the number of kilometres driven, to provide an activity index for each species. The index was expressed as number of animals seen per spotlit kilometre each sampling night. These indices (n = 6) were then totalled over three nights sampling at two sampling areas to estimate an average density index, standard error and coefficient of variation for each species per study site per year.

4.3 Results

4.3.1 Predator activity

No dingoes were detected on transect plots or scent stations at either Sturt National Park or Mundowdna-Wilpoorina during both sampling years. Foxes and feral cats were detected at all of the study sites. Transect data showed between-site and between-year variation in activity indices for dingoes and foxes, but not for feral cats (Table 4.2). When mean daily visitation rates for each predator species were compared, the proportion of scent stations visited was similar across sampling nights, indicating minimal variation in animal activity. The variation in visitation rates for dingoes was around 1%, for foxes 3% and for feral cats 2% over the three nights sampling. Residual deviance for all predator species was < 1, indicating no evidence of over dispersion after taking into account the random effects of the model.

Activity of dingoes on transects varied between sites ($p < 0.001$) and sampling years ($p = 0.02$) (Table 4.2). Dingoes activity increased at sites sampled one year post rains but decrease activity at the site sampled 3 months post rains (Figure 4.1a-e). The highest mean PAI for dingoes were found at Quinyambie Station one year post rains (PAI = 0.85) (Figure 4.1c). Similarly, the highest proportion of scent station visitations by dingoes was recorded at Quinyambie Station during both sampling periods (*pr* = 26.3% and 24.8%), followed by Finniss Springs (*pr* = 19.2% and 16.8%) and then Bollards Lagoon (*pr* =9.9% and 14.9%) (Table 4.3). Mean activity indices from scent stations also showed a differences in dingo activity between sites ($p < 0.001$) and across years for all sites ($p = 0.01$), but no interaction effect was detected (Table 4.2).

Table 4.2 p values shown for the effects of site and year on estimated passive activity index (PAI) and mean activity indices (MAI)
Corresponding residuals (R) and standard error (pooled) values for predator species and prey categories are given. * denotes significant ($p < 0.05$) and ** highly significant ($p < 0.005$) result; n.d. indicates statistic not available.

Species/Category	Site	Year	Site × Year	R	±s.e
***PAI* (transects)**					
Dingo	<0.001**	0.016*	0.778	0.113	0.026
Fox	0.002 *	0.158	0.036*	0.077	0.017
Feral Cat	0.488	0.496	0.993	0.013	0.003
Macropod	0.005*	0.032*	0.046*	0.044	0.009
Rabbit	<0.001**	0.127	0.133	5.142	1.163
Small mammal (all sites)	<0.001**	<0.002*	<0.004**	9.196	2.299
Small mammal (excluding QS)	<0.001**	0.212	n.d.	0.324	0.094
Reptile	0.051	0.197	0.891	32.89	8.22
***MAI* (Scent stations)**					
Dingo	<0.001**	0.011*	0.787	0.009	0.002
Fox	0.033*	0.097	0.158	0.018	0.004
Feral Cat	0.320	0.856	0.332	0.002	0.001

As with dingoes, activity of foxes on transects varied between sites ($p = 0.002$) and between years ($p = 0.04$) (Table 4.2). Sites sampled one year post rains saw an increase in fox activity on both transects and scent stations between sampling periods, however differences between years in fox activity on scent stations was not significant ($p = 0.10$) (Table 4.2). The highest activity estimates for foxes were recorded at Sturt National Park (dingoes controlled through exclusion fencing) 3 months post rains (PAI = 0.74), while fox activity was lowest at Quinyambie Station (dingoes uncontrolled) 3 months post rainfall (PAI = 0.04) (Figure 4.1a, c respectively). Similarly, fox visitation rates recorded on scent stations were highest at Sturt National Park (pr =17.8% and 34.7%) and Mundowdna-Wilpoorina (dingoes controlled) (pr = 24.9% and 13.1%), while the lowest recorded visitation rates for foxes at scent stations were found at Quinyambie Station (dingoes uncontrolled) during both years of sampling (pr = 1.5% and 4.5%) (Table 4.3). Mean activity indices calculated from fox visitations to scent stations at sites sampled 3 months post rainfall showed an increase in fox activity between sampling years at Sturt National Park (dingoes uncontrolled), but a decrease in fox activity at Mundowdna-Wilpoorina and Finniss Springs (Table 4.3).

Table 4.3 The modelled proportion of scent stations visited by dingoes, foxes and feral cats at each study site by sampling year, including 95% confidence intervals.

Site	Rainfall	Dingoes *pr* % (95% C.I.)	Foxes *pr* % (95% C.I.)	Feral Cats *pr* % (95% C.I.)
Sturt National Park	prior to rains	0.0	17.8 (6.1 - 42.1)	1.3 (0.1 - 11.0)
	post rainfall - 3 months	0.8 (0.1 - 4.5)	34.7 (15.1 - 61.5)	1.5 (0.3 - 8.4)
Bollards Lagoon	prior to rains	9.9 (3.7 - 23.9)	0.0	5 (0.8 - 26.3)
	post rainfall - 1 year	14.9 (7.6 - 27.2)	4.7 (1.2 - 17.1)	3.3 (0.7 - 14.1)
Quinyambie Station	post rainfall - 3 months	26.3 (15.7 - 40.5)	1.5 (0.2 - 8.0)	0.8 (0.1 - 6.8)
	post rainfall - 1 year	24.8 (14.7 - 38.7)	4.5 (1.2 - 15.2)	4.8 (1.3 - 16.7)
Mundowdna-Wilpoorina	prior to rains	0.0	24.9 (9.8 - 50.2)	1.5 (0.3 - 8.4)
	post rainfall - 3 months	0.0	13.1 (4.5 - 32.3)	8.2 (2.5 - 24.2)
Finniss Springs	prior to rains	19.2 (10.2 - 33.3)	17.8 (6.2 - 41.6)	4.9 (1.1 - 18.4)
	post rainfall - 3 months	16.8 (9.2 - 28.8)	7.9 (2.4 - 22.8)	6.1 (1.7 - 19.8)

Feral cat activity on transects was fairly uniform across all sites regardless of dingo management strategy ($p = 0.49$) and sampling years ($p = 0.50$) (Table 4.2). The highest PAI for feral cats was recorded at Finniss Springs (dingoes uncontrolled) prior to rains (PAI = 0.18), while the lowest feral cat activity was recorded at Sturt National Park (dingoes controlled through exclusive fencing) three months post rainfall (PAI = 0.04) (Figure 4.1e, a respectively). Mean activity indices for feral cats calculated from scent station visitations did not differ across sites ($p = 0.32$) or years ($p = 0.86$) (Table 4.2). Feral cats were detected on scent stations at all study sites during both sampling years, but visitation rates were low and showed no clear pattern. Visitation rates for feral cats were consistently low at Sturt National Park (dingoes controlled) (pr = 1.3% and 1.5% respectively), but varied between sampling years within the other four study sites (Table 4.3). The highest visitation rates for feral cats was detected at Mundowdna-Wilpoorina (dingoes controlled) 3 months post-rains (pr = 8.2%), but low visitation rates were recorded prior to rains at the same site (pr = 1.5%). Similarly, a very low visitation rate for feral cats was recorded 3 months post rains at Quinyambie Springs (dingoes uncontrolled) (pr = 0.8%) but this increased to 4.8% one year post rains (Table 4.3).

4.3.2 Activity of Prey

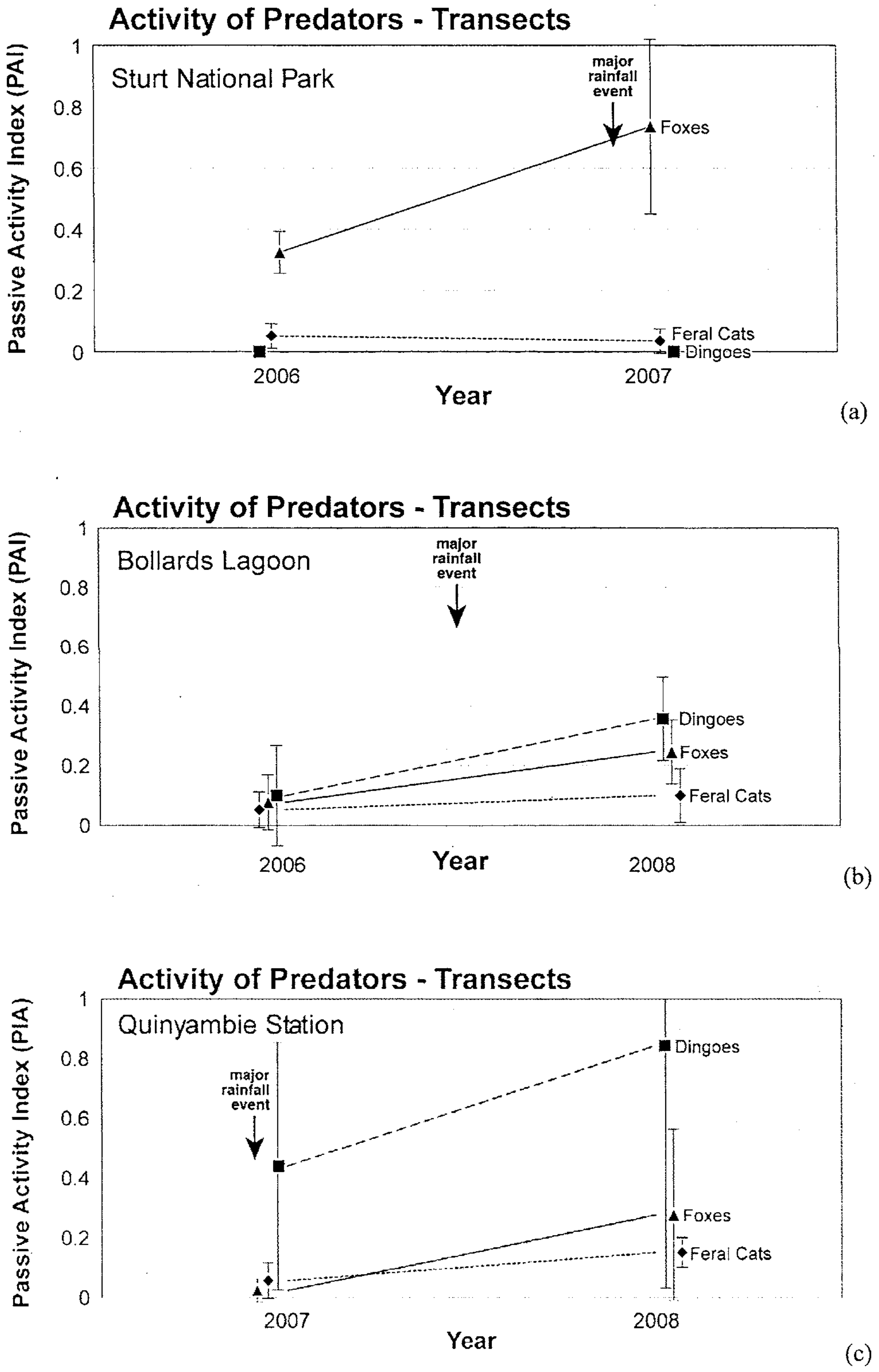
Activity on transects of all prey, including macropods ($p = 0.01$), rabbits ($p < 0.001$), small mammals ($p < 0.001$) and reptiles ($p = 0.05$) differed between the study sites, although reptiles not as markedly as other prey (Table 4.2). Small mammal activity significantly varied between sites even when Quinyambie Station was removed from the analysis ($p < 0.001$) (Table 4.2)

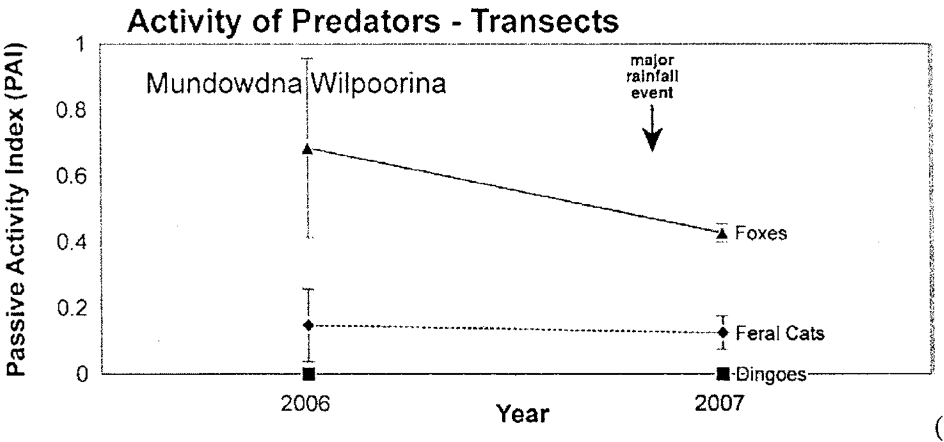
Prior to rains, the activity on transects of small to medium sized prey were lower at Sturt National Park (dingoes controlled through exclusion fencing) than found at other sites (Figure 4.2a-e). The highest activity estimates for small mammals (PAI = 52.71) and rabbits (PAI = 18.90) were found at Quinyambie Station (dingoes uncontrolled) one year post rains (Figure 4.2c). In contrast, the highest activity estimate for macropods recorded on transects was at Sturt National Park (dingoes controlled) prior to rains (PAI = 0.88) (Figure 4.2a). The lowest macropod activity estimates were found at Quinyambie Station (dingoes uncontrolled) during both sampling years (Figure 4.2c). There was some significant variation of activity estimates between sampling years for macropods at all sites ($p = 0.03$) and small mammals at Quinyambie station ($p<0.002$), but not for rabbits or reptiles (Table 4.2). Macropod activity estimates from transects decreased at most sites (Figure 4.2a-e).

Spotlighting results for macropods showed trends similar to transect data for all sites and years with the exception of Sturt National Park (dingoes controlled) during the second year of sampling, where spotlighting found an increase in macropod activity. Activity of macropods determined by spotlighting was lowest at Finniss Springs (0 km^{-1}) and Quinyambie Station (dingoes uncontrolled) prior to rains (0.05 km^{-1}) and highest at Sturt National Park both prior to and 3 months post rains (1.267 km^{-1}; 1.358 km^{-1} respectively) (Table 4.4)

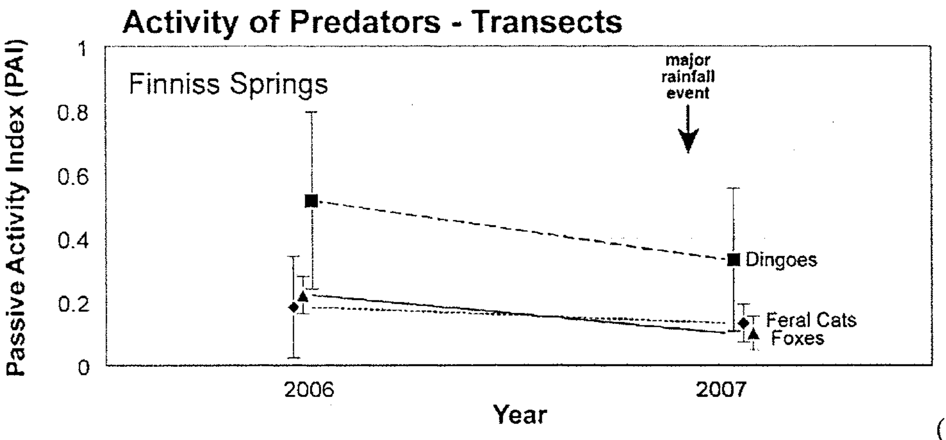
Spotlighting results for rabbits also showed similar trends to transect data for all sites and years. Activity for rabbits detected by spotlighting was lowest at Mundowdna Wilpoorina (dingoes controlled) prior to rains (0.343 km^{-1}) and was also low both prior to rain and 3 months post rainfall at Sturt National Park (dingoes controlled) (0.475 km^{-1} ; 0.458 km^{-1}). Rabbit activity was highest at Quinyambie Station (dingoes uncontrolled), being high at 3 months post rains (2.503 km^{-1}) and increasing substantially one year post rains (7. 85 km^{-1}) (Table 4.4).

Figure 4.1 (a-e) Estimated mean PAI values and standard errors from transect data for predator species by site.



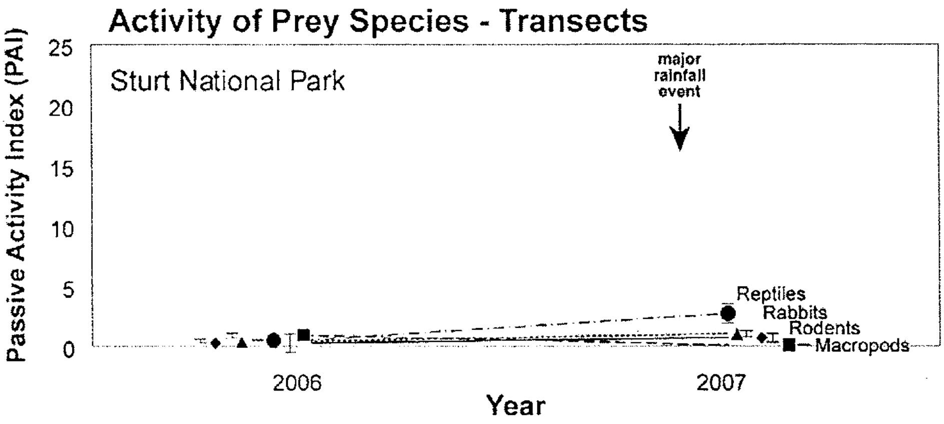

Activity of Predators - Transects
Mundowdna Wilpoorina
major rainfall event
Passive Activity Index (PAI)
1
0.8
0.6
0.4
0.2
0
Foxes
Feral Cats
Dingoes
2006
2007
Year

(d)

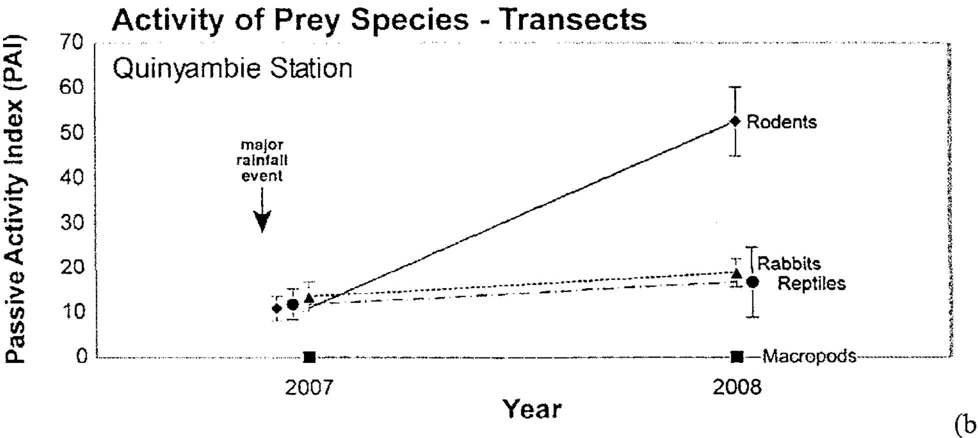

Activity of Predators - Transects
Finniss Springs
major rainfall event
Passive Activity Index (PAI)
1
0.8
0.6
0.4
0.2
0
Dingoes
Feral Cats
Foxes
2006
2007
Year

(e)

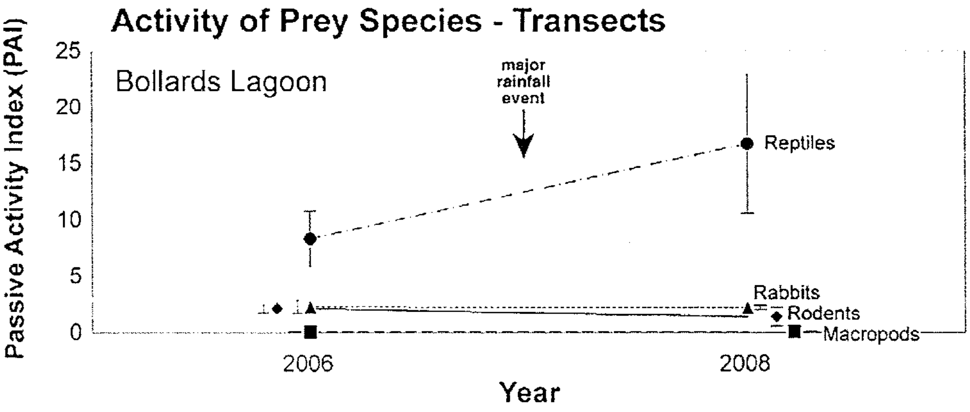
Figure 4.2 (a-e) Estimated mean PAI values and standard errors from transect data for prey categories by site.



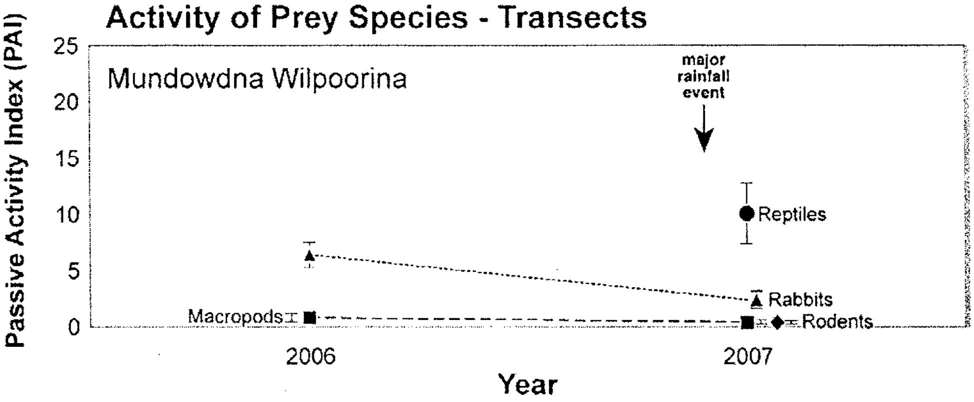
(a)



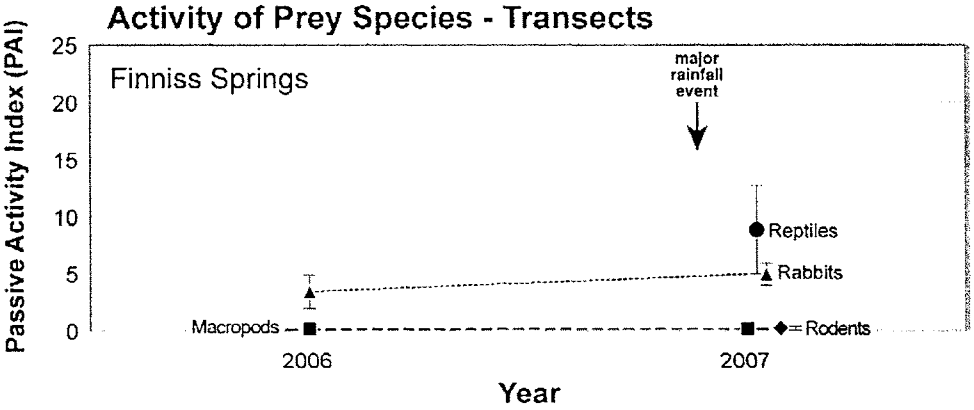
(b)



(c)


Activity of Prey Species - Transects
Mundowdna Wilpoorina
Passive Activity Index (PAI)
25
20
15
10
5
0
major rainfall event
Reptiles
Rabbits
Macropods
Rodents
2006
2007
Year

(d)


Activity of Prey Species - Transects
Finniss Springs
Passive Activity Index (PAI)
25
20
15
10
5
0
major rainfall event
Reptiles
Rabbits
Macropods
Rodents
2006
2007
Year

(e)

Table 4.4 Mean activity index (MAI) from spotlight counts (animals seen per transect kilometre for each spotlight transect (*n* = 6)). Standard errors and coefficients of variation for macropods and rabbits are given for the five study sites for each sampling year.

		Macropods			Rabbits		
Site	**Rainfall**	Mean DI	± s.e.	c.v	Mean DI	± s.e.	c.v
Sturt National Park	prior to rains	1.27	0.46	0.68	0.48	0.08	0.31
	post rains - 3 months	1.36	0.80	1.11	0.46	0.07	0.30
Bollards Lagoon	prior to rains	0.01	0.01	2.45	0.77	0.19	0.49
	post rains - 1 year	0.04	0.04	2	0.73	0.15	0.41
Quinyambie Station	post rains - 3 months	0.05	0.04	1.55	2.50	0.18	0.14
	post rains - 1 year	0.13	0.05	0.69	7.85	1.68	0.42
Mundowdna-Wilpoorina	prior to rains	0.39	0.20	0.93	0.67	0.18	0.52
	post rains - 3 months	0.19	0.07	0.64	0.34	0.05	0.30
Finniss Springs	post rains - 1 year	0	0	0	0.69	0.15	0.41
	post rains - 3 months	0.16	0.02	0.29	0.89	0.11	0.24

4.4 Discussion

Where top predators are retained in an ecosystem, they are often associated with ecological richness and diversity in lower trophic levels (Estes, 1996; Santiapillai and Jayewardene, 2004). Top predators have been shown to control herbivore populations (Berger *et al.*, 2008; Beschta and Ripple, 2009; Elmhagen and Rushton, 2007; Ripple and Beschta, 2008), and moderate the impacts of other predator species on prey resources (Salo *et al.*, 2010). Management of top predators may therefore play a key role in the maintenance of long term biodiversity in some ecosystems.

4.4.1 The effect of dingo management and site attributes on predator activity

Results from this chapter suggest that management of the dingo as top predator is an important determinant of both dingo activity and the activity of a sympatric canid mesopredator, the red fox. The highest activity estimates for foxes were found at sites where dingoes were controlled through exclusion fencing (Sturt National Park and Mundowdna Wilpoorina). Similar to findings by Newsome *et al.* (2001), fox activity was up to 22 times higher in the absence of dingoes. An inverse relationship between the abundance of dingoes and foxes has been reported in many arid zone studies (Short and Smith, 1994; Johnson *et al.*, 2007; Letnic *et al.*, 2009a; Letnic *et al.*, 2009b; Letnic and Koch, 2010).

Dingo control through 1080 baiting has been shown to lower dingo activity in the short term (Allen, 2000). In addition to reducing dingo activity, 1080 baiting may also reduce fox activity (Allen and Sparkes, 2001; McIlroy *et al.*, 1986a; Thomson *et al.*, 2000; McIlroy, 1992). Dingo activity at the baited site (Bollards Lagoon) was lower overall than at sites with no dingo control, while fox activity was lower at the baited site than at sites where dingoes were controlled by exclusion fencing, but was higher overall than at sites where dingoes were not controlled (Finniss Springs and Quinyambie Station). One important consideration when interpreting these findings is the influence of bait placement on predator susceptibility (Bird, 1995). In our study, baiting was conducted around permanent water resources prior to rains when surface water availability was low. Resident dingo packs may exclude foxes from areas surrounding water resources (Brawata and Neeman, 2011), making dingoes more likely to be exposed to baits. In comparison, one year post baiting all three predators increased their activity almost three-fold one. Such an increase in predator activity post-baiting may reflect an increase in abundance (Fleming *et al.*, 1996), changes in activity patterns of the remaining populations individuals (Ables, 1969; Corbett, 1995; Phillips and Catling, 1991) or individual dispersal into vacant territories (Algar and Kinnear, 1992).

While dingo management appeared to have a strong effect on dingo and fox activity, it did not appear to be an important determinant of feral cat activity. Activity estimates for feral cats at all sites were low, as is typical in arid environments (Edwards *et al.*, 2000; Read and Bowen, 2001; Sharp *et al.*, 2001) and were fairly uniform between sites and years (Letnic *et al.*, 2009b; Newsome *et al.*, 2001). Feral cat activity was not strongly correlated with either dingo or fox activity, feral cats appeared less active overall in the presence of high fox activity. This is consistent with other studies that found feral cats increased in density when foxes were controlled (Christensen and Burrows, 1994; Molsher, 1998; Risbey *et al.*, 1999; Risbey *et al.*, 2000; Burrows *et al.*, 2003; Read and Bowen, 2001; Holden and Mutze, 2002).

Some authors have suggested that the presence of dingoes may benefit feral cats, either by providing food that can be scavenged during drought, (Smith and Quin, 1996; Paltridge *et al.*, 1997) or by reducing the suppressive effects of foxes (Letnic *et al.*, 2009b). On a local scale, feral cats were observed to spatially avoided both canid species; an increase in feral cat visits to scent stations corresponded to reduced fox and dingo visitations and a decrease in fox activity during the same sampling period (Mitchell and Banks, 2005). While there is growing evidence that dingoes may impact on feral cat populations (Pettigrew, 1993; Kennedy *et al.*, 2011), results from this chapter were not conclusive and indicate that feral cat activity may be associated with habitat or other site attributes (Mahon *et al.*, 1998). There was a slight increase in feral cat activity at sites dominated by Mumpie land systems, which are associated with a higher proportion of creek lines, a preferred habitat of feral cats (Letnic *et al.*, 2009b). The effect of habitat on feral cat activity is examined in Chapter 5.

4.4.2 The effect of dingo management and site attributes on activity of prey

Dingoes, foxes and feral cats are all opportunistic, generalist predators and as such have an impact on a wide variety of prey (Dickman, 1996a). Macropods have been found to be the most common prey item for dingoes in many studies (Coman, 1972; Corbett, 1974; Newsome *et al.*, 1983b; Shepherd, 1981; Whitehouse, 1977; Robertshaw and Harden, 1985; Thomson, 1992a; Newsome *et al.*, 1983a) and are of particular importance when rabbits occur in low densities or decline during drought (Newsome *et al.*, 1983a; Thomson, 1992a). Previous research has found that dingoes can limit macropod populations (Corbett and Newsome, 1987; Marsack and Campbell, 1990; Caughley *et al.*, 1980; Pople *et al.*, 2000), with dingoes targeting juvenile macropods thus directly affecting recruitment (Shepherd, 1981). Consistent with this, an inverse relationship between dingo and macropod activity was found at the study sites. Macropod activity was highest in the absence of dingoes, even when surface water was limited (Sturt National Park) or where macropods were regularly harvested and productivity was low (Mundowdna Wilpoorina). High macropod activity at low productivity sites in the absence of dingoes may be a reflection of reliable water resources (at sites with stock), or alternatively, the result of an artificially high density of animals unable to disperse due to the DBF. Where dingoes are present, predation on macropods may increase at sites that carry stock as dispersed water resources allow dingoes to occupy more areas on a continual basis (Corbett, 1995). In addition, macropods may be more vulnerable to dingo predation around artificial waters (Newsome, 1965; Shepherd, 1981).

Predation is also an important limiting factor for rabbit populations (Pech *et al.*, 1995; Pech *et al.*, 1992; Risbey *et al.*, 2000). Where rabbits are abundant in arid regions, all three predators targeted them as primary prey (Parer, 1977; Bayley, 1978; Catling, 1988; Molsher *et al.*, 1999; Risbey *et al.*, 1999; Corbett and Newsome, 1987). However, while rabbits are found on both sides of the DBF, larger increases in rabbit populations occur in areas where dingo populations remain (Newsome *et al.*, 2001). This pattern in rabbit abundance has been attributed to a lack of competition from sheep grazing (Newsome *et al.*, 2001) but may also be associated with a reduction in fox predation. At the study sites, a strong inverse relationship between fox and rabbit activity was found. There was also a trend for feral cat activity to mirror trends in rabbit activity, although rabbit activity was not indicative of feral cat activity *per se*. Previous studies have shown increases in fox and feral cat densities following increased rabbit abundance (Morton, 1990; Holden and Mutze, 2002; Molsher *et al.*, 1999; Read *et al.*, 2008) and that the combined predation of foxes and feral cats can regulate rabbit populations at low densities (Banks, 2000; Pech *et al.*, 1995; Pech *et al.*, 1992). When foxes are controlled, rabbits have been shown to increase 6-12 times their initial abundance (Banks *et al.*, 1998; Newsome *et al.*, 1989).

One further consideration that may influence rabbit activity in this study is the spread of Rabbit Haemorrhagic Disease (RHD) after rains. The impact of RHD may have a confounding effect on predator and prey activity. RHD may reduce rabbit numbers by up to 85% (Mutze *et al.*, 2002; Newsome *et al.*, 1989; Read and Bowen, 2001) followed by declines in predator survival and recruitment (Newsome *et al.*, 2001; Holden and Mutze, 2002). However, declines in predators do not always occur, suggesting the effects of RHD on predator populations may be site specific and dependant on the availability of alternative food resources at the time of the outbreak of the disease (Davey *et al.*, 2006).

RHD was reported at Bollards Lagoon during summer 2007 (G. Rieck, pers. comm., April 2008) and affected rabbit populations at Mundowdna-Wilpoorina in September 2006 (P. Litchfield, pers comm., January, 2007). The combined pressures of predation and RHD may lead to reduced rabbit numbers and an increase in predation on alternative prey, such as small mammals (Blumstein *et al.*, 2004). In comparison, no RHD was reported at Quinyambie Station during sampling, and high activity estimates for rabbits were recorded in comparison to other high productivity sites. When rabbits are at high densities environmental fluctuations appear to be more important than predation in regulating abundance (Newsome *et al.*, 1989; Cooke, 1982).

Rabbits increase their sensitivity to predation impacts when activity is very low (Pech *et al.*, 1992; Salo *et al.*, 2010). With the exception of Quinyambie Station, rabbit activity was low at all study sites, but was lowest at Sturt National Park, where fox activity was uniformly high. In the absence of dingoes, foxes maintained high activity levels during times of low rabbit activity through utilizing alternative food resources, such as carcasses (Holden and Mutze, 2002; Paltridge, 2002). Such supplementary food resources can sustain artificially high predator populations during times of low prey availability (Pech and Hood, 1998; Pech *et al.*, 1995; Corbett and Newsome, 1987; Courchamp *et al.*, 1999). Unregulated densities of carnivores may suppress prey populations to an extent that prey become trapped in a "predator pit" (Newsome, 1990) and unable to increase, even in response to rains (Smith and Quin, 1996).

At Sturt National Park, it is likely that the drought-induced availability of macropod carcasses as an alternative food resource has led to artificially high densities of foxes prior to rains and the low activity of rabbits post rainfall (Banks *et al.*, 2000; Krebs, 1996; Pech *et al.*, 1992). Furthermore, artificially high densities of foxes and low availability of primary prey (rabbits) may lead to excessive or "hyper" predation on remaining native prey populations, such as small mammals and reptiles (Courchamp *et al.*, 1999; Pech and Hood, 1998). In support of the hyperpredation theory, the lowest activity estimates for small mammal and reptiles both were prior to and post rains at Sturt National Park. In contrast, higher activity was recorded for small vertebrates on the neighbouring property of Bollards Lagoon, where baiting of both canid species occurred. The role of livestock carcasses in increasing predation on native prey may now be even more important since RHD has led to a major decline of rabbit populations in arid and semi-arid areas (Pech and Hood, 1998).

In contrast to fox activity, there appeared to be no clear pattern that would suggest a significant relationship between feral cat activity and the activity of small vertebrates. Even though small vertebrates are an important dietary item for feral cats (Bayley, 1976; Bayley, 1978; Eldridge *et al.*, 2002; Catling, 1988; Risbey *et al.*, 1999) and the hunting style of feral cats is well suited to their capture (Read and Bowen, 2001), evidence for negative impacts of feral cats on small vertebrate populations remains inconsistent (Eldridge *et al.*, 2002; Risbey *et al.*, 2000). With the exception of Sturt National Park, reptile activity was similar among sites, but small mammals were estimated to have the highest activity indices where dingoes were present and productivity was high, and the lowest activity where fox activity was highest and productivity lowest. Small mammal activity was also low at low productivity sites even in the presence of dingoes, thus appeared to be influenced by a combination of predator activity and site productivity (Dickman, 1996a; Dickman *et al.*, 2001; Dickman *et al.*, 1999). We observed that the activity of small vertebrates, particularly mammals, was distributed patchily across sites and there was large disparity between sampling areas. Possible reasons for this inconsistency may be variation in microhabitats, grazing patterns or patchiness of rainfall (Westbrooke *et al.*, 2005; Yarnell *et al.*, 2007).

4.4.3 Responses of predators and prey to a significant rainfall event

In arid environments, the impact of rainfall on animal activity occurs in three key ways. First, mobile species may disperse as surface water becomes available in previously water remote areas (Corbett, 1995; Ealey, 1967). Second, increases in primary productivity lead to increases in prey activity and abundance. Predators may initially respond to such increases in prey with changes in activity, while increased predator densities as a result of high juvenile recruitment and survivorship occur the following breeding season (Pech *et al.*, 1995; Previtali *et al.*, 2009). Third, due to the prey switching tactics of opportunistic, generalist predators, time since rainfall alters predation impacts on different prey species (Corbett and Newsome, 1987; Randa *et al.*, 2009).

The distribution and availability of surface water plays an important role in determining site carrying capacity for predators and prey (James *et al.*, 1999). The first sampling period for this study took place after 5-7 years of lower-than-average annual rainfall across the region, and both predator and prey activity was the lowest recorded for most categories. A major rainfall event occurred at the study sites the following summer. Rainfall is known to initiate breeding in both rabbits (Wood, 1980) and small mammals (Dickman *et al.*, 1999); indeed, a massive eruption of two species of hopping mice (*Notomys fuscus* and *N. alexis*) was found at Quinyambie Station immediately post rainfall. One year after the rainfall event, activity of small mammals at this site continued to increase significantly, while increases in small prey at less productive sites or where dingoes were absent were much more marginal.

Prior to rains at sites with few permanent waters, such as Finniss Springs and Sturt National Park, both predators and prey would have been spatially restricted, placing intense pressure on food resources surrounding remaining surface water. A large rainfall event would lead to surface water became more readily available, enabling mobile prey species to disperse rapidly to areas of new growth. Predators would also disperse, following prey movements (Sinclair, 1983). At Sturt National Park, fox presence on transects increased immediately following rains, suggesting an increase in dispersive movements. At the same site, a large increase in macropod activity detected by spotlighting revealed macropods had also dispersed to areas away from permanent waters to access new vegetative growth. Similarly, a decrease in canid activity on transects following rains at Finniss Springs may have been due to the movement away from sampling sites as creeks and drainage lines provided an abundance of surface water across the site.

Restricted movement and dispersal after rains may not be as evident at pastoral sites, where artificial water resources for stock are distributed evenly across the landscape, enabling predators and prey to be more homogeneously distributed on a continual basis (James *et al.*, 1999). Regular availability of evenly distributed surface water may reduce interference competition between carnivore species (Valeix *et al.*, 2010) and support larger predator and prey populations (Owen-Smith, 1996). A lack of increase in predator activity immediately post rainfall may reflect a lag period before predator populations are able to numerically respond to increased abundance of prey (Stenseth *et al.*, 1998), while increases in predator activity one year post rains are likely due to increase breeding success and higher juvenile recruitment (Read and Bowen, 2001; Saunders *et al.*, 1995).

The existence of, and ease of access to, artificial water points may also play an important role in sustaining prey populations, particularly rabbits (Newsome *et al.*, 1989; Cooke, 1982) and macropods (Bayliss, 1985). Rabbits were regularly seen drinking at dams at pastoral sites (authors observation), but appeared to actively avoid the only permanent water resource at Sturt National Park, most likely due to the continual high activity of foxes in close vicinity to the water (Valeix *et al.*, 2008). At all sites, activity indices for less mobile prey species, such as rabbits and small mammals, were considered more likely to indicate local increases in activity in response to rainfall, rather than a change in their distribution across the landscape.

4.4.4 Prey switching, rainfall and regulation: The baseline density theory

Mammalian carnivores display great flexibility in hunting behaviours, and the practice of prey switching in many predator species allows the exploitation of alternate food resources around fluctuating staple prey (Randa *et al.*, 2009; Curio, 1976). Corbett and Newsome (1987) found that preferred prey items of dingoes were related to the time that had elapsed since a large rainfall event. When preferred prey is scarce, such as during drought, reptiles and carrion play an important role in sustaining predator populations (Whitehouse, 1977; Paltridge, 2002; Bayley, 1978; Jones, 1977). Immediately after rains, small mammals increase and, due to both their availability and 'catchabilty', are targeted by all three predator species (Corbett and Newsome, 1987; Eldridge *et al.*, 2002). At Quinyambie Station, an increase small mammals in response to rains is the most likely explanation for an increase in predator activity one year post rainfall (Pavey *et al.*, 2008). With predators targeting small mammals, a combination of lower predation pressure and higher food availability would have enabled rabbits to increases in activity at Quinyambie Station one year post rains. Now abundant, rabbits then become the preferred prey item (Corbett and Newsome, 1987; Catling, 1988). As found in this study, fox and feral cat activity in particular appeared to be strongly associated with increases and decreases rabbit activity (Christensen and Burrows, 1995b; Davey *et al.*, 2006; Pech *et al.*, 1992; Banks, 2000).

The flexible social structure of dingoes allows them to exploit larger prey such as adult macropods and livestock when rabbits decline (Newsome *et al.*, 1983a; Thomson, 1992a). In contrast, mesopredators switch to targeting smaller prey such as small mammals or reptiles (Molsher *et al.*, 1999; Read and Bowen, 2001). Foxes do prey on juvenile macropods (Banks *et al.*, 2000), however their impact would likely be limited to lowering recruitment during flush periods as they prey only on one life stage of the population (Russell *et al.*, 2009). Consistent with this pattern, results indicate that during times of low rabbit activity, activity indices for small vertebrates were significantly lower where dingoes were absent and foxes activity was high, while activity indices for macropods were significantly lower where dingoes occurred. Similarly, Smith and Quin, (1996) found declines in conilurine rodents correlated to high fox and feral cat abundance, with declines less severe in areas where dingoes were abundant.

Therefore while dingoes may periodically suppress rabbits and small mammals (Corbett and Newsome, 1975), mesopredators, by targeting rabbits and small vertebrates more consistently, would have a larger cumulative impact overall on these prey in the long term (Banks *et al.*, 2004). One interesting observation was that most rabbits seen post rainfall at Quinyambie Station, a site of high productivity and dingo activity, were adults (author's personal observation). Therefore high activity estimates for rabbits at this site could not be attributed solely to juvenile recruitment, but may instead be indicative of a stable adult population. These findings support the premise that where dingoes are retained in the ecosystem, there may exist more stable populations of rabbits and smaller prey that allow a larger and more rapid response to rainfall (Banks, 2000; Pech *et al.*, 1992; Letnic and Koch, 2010; Short and Smith, 1994).

In this study, predator activity fluctuated in response to rainfall; at most sites where dingoes, foxes and feral cats co-existed, all three species increased their activity with increasing prey. However, in the presence of dingoes, fox activity did not increase to levels found at sites where dingoes were absent. For example, estimates for Quinyambie Station indicate fox activity increased one year post rainfall, however, despite high productivity and the highest activity of rabbits and smaller prey at the site, the increase in fox activity was less than occurred in the absence dingoes. While the strength of intraguild interactions may vary with dingo density, site productivity and amount of rainfall (Sieben *et al.*, 2011), results from this study suggest dingo-fox interactions are present even when productivity and prey availability is high.

It is important to consider these results in light of the limitations of this study. First, it is difficult to assess the effect that unmeasured native predators, such as raptors and reptiles, may have on prey populations. For example, large varanids are able to increase in abundance where other predators are controlled, and would likely have a significant impact on prey populations under such circumstances (Lloyd, 2007; Sutherland *et al.*, 2011). Second, not all prey species were measured. Invertebrates can form a major part of mesopredator diets during drought and birds have been found in both fox and cat diets in arid regions (Catling, 1988; Read and Bowen, 2001). However the long term key interactions in arid Australia appear to occur between predators and their primary prey of macropods, rabbits and small mammals (Davey *et al.*, 2006; Newsome, 1990; Newsome *et al.*, 2001; Newsome *et al.*, 1989; Pech and Hood, 1998; Pech *et al.*, 1995; Pech *et al.*, 1992; Corbett and Newsome, 1987) on which this study focused.

In summary, dingoes perform two vital functions in ecosystems. First, consistent with the theory of top-down regulation (Soulé *et al.*, 1988), dingoes may both limit and regulate fox populations. Sinclair (1989) defines population regulation as the process by which a population returns to its equilibrium density, and population limitation as the process that sets the equilibrium density. During poorer conditions, dingoes may limit fox populations, effectively reducing the breeding population of foxes and the ability of foxes to increase with increasing prey. Dingoes may then regulate foxes populations when prey availability increases post rainfall, thus maintaining lower fox activity over the long term (Sinclair *et al.*, 1998).

Second, dingoes may both directly and indirectly decrease predation pressure on smaller prey, due to their ability to both limit fox populations and to utilize a wider range of prey resources. Thus dingoes may be a key determinant of 'baseline densities' of both foxes and prey species in the long term, where the baseline density is the density at which mesopredators or prey are maintained on average across a number of years by top down regulation, from which populations may fluctuate up and down in response to increases or decreases in resources through bottom up forces. The removal or periodic suppression of dingo populations through 1080 baiting may therefore enable mesopredators to maintain higher baseline densities over the long term, and lowers the baseline density of smaller prey. Through their role in determining baseline densities of both mesopredators and some prey, dingoes may play a key role in the regulation in arid ecosystems and the maintenance and conservation of smaller prey populations.

4.5 Conclusion

Consistent with the theory of top-down regulation, the results indicate dingoes are able to suppress fox activity where dingoes are uncontrolled (or opportunistically controlled) and dingo activity is high. At sites where dingoes were absent or in low numbers, fox activity was high, whereas 1080 baiting lowered both fox and dingo activity. In contrast, feral cat activity did not appear to be affected by dingo management strategies, but appeared to respond to increases in prey except in the presence of high fox activity. Activity of feral cats appears to be more associated with productivity and habitats at study sites (see Chapter 5).

These results were consistent even during times of high prey availability. Where dingoes, foxes and feral cats co-existed at Quinyambie Station, all increased their activity with increasing prey activity post rainfall. However, fox activity did not increase to levels found at sites where dingoes were absent. This supports a baseline density concept: that responses by foxes to increasing prey are limited by dingoes, thus dingoes are able to maintain lower densities of foxes over the long term.

Macropod activity was higher where dingoes were absent, while rabbits and small mammal activity was lower where fox activity was high. Activity of reptiles also decreased under high fox activity. No significant relationship was found between prey and feral cat activity. Recent rainfall and site productivity influenced prey, with recent rainfall increasing the activity of rabbits and small mammals, with more dramatic increases occurring in areas of high productivity and lower fox activity. Both rabbits and small mammals were most active where dingoes were highly active and productivity was high. This suggests that by reducing predation by foxes, dingoes may enable these prey species to maintain higher densities.

An important consideration is that most previous studies examining the interactions between dingoes, foxes and feral cats have been carried out on grazing lands, and this may have affected the relationships found between these species. The existence of livestock provides a supplementary food source and enables higher dingo densities to be sustained during drought (Corbett and Newsome, 1987). At Finniss Springs, which has no stock, low productivity and limited water, dingoes did not appear to be suppress fox activity as effectively. This appears to be related to water availability, habitat and productivity, all which may affect the temporal and spatial movement patterns of dingoes. This is further explored in Chapters 5 and 6.

Chapter 5: Habitat use by dingoes, foxes and feral cats and select prey under different dingo management strategies

5.1 Introduction

There is increasing evidence shown from both correlative (Johnson *et al.*, 2007; Johnson and VanDerWal, 2009) and experimental studies (Letnic *et al.*, 2009a; Letnic *et al.*, 2009b) that dingoes are able to suppress fox abundance in arid ecosystems of Australia. Although many additional studies have examined intraguild interactions between mammalian carnivores in other parts of the world, particularly between sympatric canids (see review in Ritchie and Johnson (2009)), most studies do not identify the behavioural response of the mesopredator to such interactions (Thompson and Gese, 2007). Similarly, the mechanisms behind how dingoes may suppress populations of mesopredators remain unclear.

Previous research on interspecific interactions between sympatric mammalian carnivores suggests that limitation of mesopredator populations by apex predators may occur through direct effects, including intraguild predation, aggression or suppression of reproductive success (Creel and Creel, 1996; Fedriani *et al.*, 2000; Ralls and White, 1995), or indirect effects, such as resource partitioning, competition or initiating avoidance behaviours (Moseby *et al.*, 2012) leading to temporal or spatial segregation (Gosselink *et al.*, 2003). In the presence of an apex predator, smaller predators may change their behaviour or foraging strategies to reduce the risk of potentially dangerous encounters (Polis *et al.*, 1989; Thompson and Gese, 2007). Such changes in behaviour may directly influence use of habitat, spatial patterns in prey mortality and spatiotemporal patterns in predator population densities (Giraldeau and Caraco, 2000).

Dingoes, as the apex predator in arid ecosystems, may initiate avoidance behaviours and change spatial activity patterns of foxes and feral cats, such as altering habitat use (Durant, 2000; Palomares *et al.*, 1996). Predator and prey species use of habitat may be influenced by such variables as population density, competition with other species, or predation. Predation effects on predators include smaller predators seeking habitats which contain favourite prey, or avoiding habitats regularly used by larger, more dominant predators that may predate on them. Limited research suggests that foxes may avoid encounters with dingoes on a fine scale or temporal scale (Mitchell and Banks, 2005), and that feral cats and foxes may exploit different habitats as a mechanism of avoiding dingoes (Southgate *et al.*, 2007).

Spatial partitioning the use of the landscape, including habitats, is a common method employed by subordinate carnivores to minimise the chance of potential encounters with dominant carnivores. For example, spatial partitioning has been found between wolves and coyotes (Carbyn, 1982), coyotes and bobcats (Litvaitis and Harrison, 1989; Major and

Sherburne, 1987; Neale and Sacks, 2001b) coyotes and different species of foxes (Gosselink *et al.*, 2003; Harrison *et al.*, 1989; Kamler *et al.*, 2003; Major and Sherburne, 1987; Sargeant *et al.*, 1987; Theberge and Wedeles, 1989a; Voigt and Earle, 1983), red foxes and hyenas (Mukherjee *et al.*, 2009), between different species of foxes (Johnson and Franklin, 1994) and between other carnivores (Prigioni *et al.*, 2008). Habitat partitioning may therefore be important process in moderating interactions between dingoes, foxes and feral cats. Such changes in behaviour may limit the abundance of the two mesopredators by restricting their distribution and access to essential resources.

As dingo management influences activity of dingoes (see Chapter 4), dingo management may also affect the use of habitat by dingoes, and consequently mesopredators. If dingoes are found to occupy resource rich habitats, mesopredators may be forced to occupy less optimal habitats, or those that have greater shelter, in areas where dingoes are not controlled.

This chapter explores avoidance behaviour as a possible mechanism behind dingo, fox and feral cat trophic interactions by examining habitat use by the three predators at the five study sites. Habitat use by select prey categories will also be assessed to provide an assessment of prey resources within each habitat type. By comparing the use of habitat by dingoes, foxes and feral cats under different dingo management strategies, I aim to address the following question:

- What is the effect of dingo management strategy on habitat use by dingoes, foxes, feral cats?

Consistent with the theory that mesopredators change their behaviour in the presence of an apex predator (Polis *et al.*, 1989), it is hypothesised that dingoes will exploit all habitats, while foxes and feral cats will use more sheltered habitats where there is high dingo activity and occupy a wider range of habitats when dingoes are absent. Alternatively, if there is no effect of dingo activity on the habitat use of the smaller predators (foxes and feral cats) then habitat use may instead be influenced by other variables, such as the presence of preferred prey and/or the suitability of the habitat to hunting methods employed by the predator.

5.2 Methods and Data Analysis

In order to assess predator habitat use, major habitat classes at each study site were first categorised, and then field data on predator activity was collected in proportion to each habitat's occurrence.

5.2.1 Habitat classes

Prior to sampling, each study site was stratified by the broad habitat types that occurred at the site. Habitats were then sampled in proportion to their availability within the sampling area at each study site in order to achieve a representative sample of the habitats available to species

(Figure 5.1). Habitat types varied among all five study sites, so were categorised using the two dominating land systems: the North-West Sands land system, dominated by sand dunes and inter-dune areas (found at sites Sturt National Park, Bollards Lagoon and Quinyambie Station) and the Mumpie land system dominated by creek lines, drainage lines and sand plains (found at sites Mundowdna Wilpoorina and Finniss Springs). For the purposes of this study, five habitat classes were defined as follows:

1. Sand dunes (SD): Large sand-dunes 10-15m in height (Figure 5.2)

2. Inter-dunes (ID): Areas of claypans and swamps between large sand dunes (Figure 5.3)

3. Creek lines (CR): Major creek lines characteristically lined by large trees (Figure 5.4)

4. Drainage lines (DL): Drainage depressions that intersect gibber flats (Figure 5.5)

5. Sand Plains (SP): Raised sandy pockets 1-3m in height interspersed sporadically in between gibber flats and swamps (Figure 5.6)

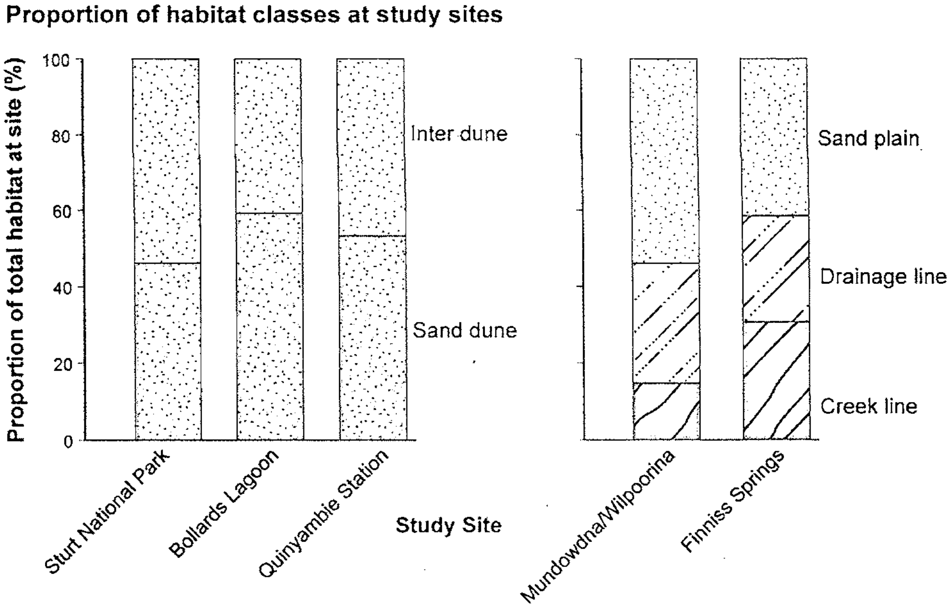


Figure 5.1 The proportion of total habitat that each habitat class represents at the five study sites.

Figure 5.2 Sand dune habitat
(Photograph by R. Brawata 2008)

Figure 5.3 Inter-dune habitat
(Photograph by R. Brawata 2007)

Figure 5.4 Creek line habitat
(Photograph by R. Brawata 2006)

Figure 5.5 Drainage line habitat
(Photograph by R. Brawata 2008)

Figure 5.6 Sand plain habitat
(Photograph by R. Brawata 2006)

5.2.2 Data Analysis

Field methods for collecting the data used to obtain density indices for both predator and prey populations are covered in detail in Chapter 2 (section 2.3). Here I discuss the methods used to analyse data collected from transects and scent station methodologies.

Scent station surveys were limited to binary (presence/absence) data. Both binomial data (presence/absence of a species) and count data (number of crossings per transect) were collected from transects. Data from transects and scent stations were combined to assess habitat use by predators, but only transect data were used for prey categories.

Data analysis was conducted using the statistical software package Genstat (VSN International, 2008). A generalised linear mixed model, with habitat, site and year as fixed effects, and sampling area, year and night as random effects, used binary data to calculate the proportion of the total sampling units in each habitat that target species were detected in at each site.

In addition, the same model as above was used with a Poisson distribution and count data to determine the rate (incidence) of prey species (excluding macropods) within habitat classes at each site. This was done to account for differences in prey densities between habitats. The Poisson distribution was not used for macropods as data were predominantly binomial, with rarely more than one print detected on transects at a time.

Due to variations in rainfall and prey availability between sampling years, the effect of year on habitat class use was examined for each predator species and prey category. When there were no significant differences in habitat use between years, data from both sampling years were combined to assess whether there was a difference in habitat class use between study sites. Sites with different habitat classes were compared separately.

5.3 Results

The effect of habitat, site and year on the presence of predator species and prey categories in different habitats are shown in Table 5.1. The mean proportion of sampling with predator and prey presence for each habitat class and corresponding study site are shown in Table 5.2 and Table 5.3 respectively. Mean proportion results from sites containing comparable habitat classes are graphed for both predator species (Figure 5.7a, b) and prey categories (Figure 5.8a, Figure 5.9a). Incidence of occurrence for each prey category (not including macropods) are shown in Table 5.4 and graphed by sites containing comparable habitat classes in Figure 5.8b and Figure 5.9b. The effects of site and year on the incidence of prey found in each habitat class (not including macropods) are shown in Table 5.5.

5.3.1 Habitat use by predators

5.3.1.1 North-West Sands land system

At sites where dingoes were present (Bollards Lagoon and Quinyambie Station), dingoes were found in both sand dune and inter-dune habitats in similar proportions (Table 5.2). Dingoes were found in slightly more inter-dunes than sand dunes at Quinyambie Station, while at Bollards Lagoon dingoes were found in sand dune more often (Figure 5.7a), but this difference was not significant (p=0.395) (Table 5.1). There was no significant difference in the use of habitat by dingoes between sites (p=0.319) or between years (p=0.566) (Table 5.1).

Results for foxes showed a strong preference for sand dune habitat over that of inter-dunes at all study sites within the North-West Sands land system (Table 5.2). Significantly more fox presence was found in sand dunes than inter-dunes at (p<0.001) (Table 5.1). This pattern of habitat use by foxes did not vary significantly between sites with different dingo management regimes (p=0.999) or years (p=0.443) (Table 5.1).

Feral cats were found in slightly more sand dunes than inter-dunes at both Sturt National Park and Bollards Lagoon, but were found in equal proportions within both habitats at Quinyambie Station (Table 5.2; Figure 5.7a). Results indicate that these differences were not significant (*p*=0.355), and that feral cats did not show a preference for either sand dune or inter-dune. Habitat use by feral cats did not vary between sites with different dingo management strategies (*p*=0.642) or years (*p*=0.392) (Table 5.1).

Table 5.1 The effect of habitat, site and year on the presence of predator species and prey categories in different habitats

Values are given for binomial distribution models, with corresponding residuals and standard error (pooled) values are from the habitat by site model (except where noted). * denotes significant (p < 0.05) and ** denotes highly significant (p < 0.005) result; n.d. indicates statistic not available.× indicates p value for habitat, residual and standard error (pooled) values taken from the habitat by year model due to lack of comparison between sites (only one site contained dingoes).

Species/Category	Habitat Type	Habitat	Site by Habitat	Year by Habitat	R	±s.e
		p value	*p* value	*p* value		
Dingo	SD/ID	0.395	0.319	0.566	0.952	0.05
	CR/DL/SP×	0.09	n.d.	0.213	1.013	0.08
Fox	SD/ID	<0.001**	0.999	0.443	0.886	0.04
	CR/DL/SP	0.003**	0.249	0.152	0.966	0.05
Feral Cat	SD/ID	0.355	0.642	0.392	0.918	0.04
	CR/DL/SP	<0.001**	0.09	0.565	0.934	0.05
Macropod	SD/ID	0.08	0.05*	0.116	0.879	0.06
	CR/DL/SP	0.602	0.461	0.418	1.023	0.09
Rabbit	SD/ID	<0.001**	0.938	0.354	0.970	0.07
	CR/DL/SP	0.002**	0.085	0.589	0.974	0.09
Small Mammal	SD/ID	0.656	0.02*	0.02*	0.953	0.07
	CR/DL/SP	0.430	0.309	n.d	0.902	0.10
Reptile	SD/ID	<0.001**	0.454	0.128	0.847	0.06
	CR/DL/SP	0.016	0.066	n.d	0.606	0.07

5.3.1.2 Mumpie land system

Dingoes were found at only one site within the Mumpie land system (Finniss Springs). There was no significant difference in use of habitat classes by dingoes at this site (*p*=0.09), however results indicate a slight preference for creek lines over other habitats (Table 5.2). However, dingoes were also found regularly in drainage lines and on sand plains (Figure 5.7b). Year did not appear to effect habitat use by dingoes in the Mumpie land system (*p*=0.213) (Table 5.1).

Table 5.2 Results showing the mean proportion (*pr*) of sampling units (scent stations and transect data combined) with predator species present within each habitat class.

Results are shown by site with corresponding 95% confidence intervals.

		Dingo		Fox		Feral Cat	
Site	**Habitat**	*pr*	95% C.I.	*pr*	95% C.I.	*pr*	95% C.I.
SNP	SD	**0**	0	**0.37**	(0.24-0.50)	**0.04**	(0.02-0.08)
	ID	**0**	0	**0.23**	(0.14-0.36)	**0.02**	(0.01-0.05)
BL	SD	**0.14**	(0.09-0.22)	**0.10**	(0.05-0.20)	**0.05**	(0.02-0.11)
	ID	**0.13**	(0.08-0.20)	**0.06**	(0.02-0.13)	**0.03**	(0.02-0.07)
QS	SD	**0.21**	(0.15-0.29)	**0.06**	(0.03-0.11)	**0.05**	(0.02-0.10)
	ID	**0.25**	(0.19-0.33)	**0.03**	(0.01-0.07)	**0.05**	(0.02-0.11)
MW	CR	**0**	0	**0.26**	(0.13-0.44)	**0.24**	(0.12-0.43)
	DL	**0**	0	**0.16**	(0.09-0.27)	**0.04**	(0.02-0.10)
	SP	**0**	0	**0.25**	(0.16-0.38)	**0.05**	(0.02-0.10)
FS	CR	**0.29**	(0.20-0.40)	**0.22**	(0.11-0.40)	**0.20**	(0.10-0.36)
	DL	**0.16**	(0.10-0.26)	**0.05**	(0.02-0.13)	**0.09**	(0.04-0.18)
	SP	**0.17**	(0.11-0.25)	**0.18**	(0.10-0.31)	**0.02**	(0.01-0.07)

Foxes showed a strong preference for creek lines and sand plain habitats at both sites within the Mumpie land system regardless of dingo management (Table 5.2, Figure 5.7b). The preference of creek line and sand plain habitats by foxes was found to be statistically significant for all sites (p=0.003) (Table 5.1). The avoidance of drainage line habitat by foxes appeared more pronounced at Finniss Springs where dingoes were not controlled (Table 5.2, Figure 5.7b), however this difference was found not to be significant (p=0.249). There was also no statistically significant difference in the proportion of foxes found on transects within each habitat class between sampling years (p=0.152) (Table 5.1).

Feral cats showed a strong preference for creek lines over other habitat classes at both sites within the Mumpie land system regardless of dingo management (Table 5.2, Figure 5.7b). Feral cats were found to use creek line habitat significantly more often at both Mundowdna Wilpoorina and Finniss Springs (p<0.001) (Table 5.1). There appeared to be some difference in habitat use between sites, with feral cats detected more often in drainage lines at Finniss Springs, where dingoes were uncontrolled and recorded more often in sand plains at

Mundowdna Wilpoorina where dingoes were controlled (Figure 5.7b).Although habitat use by feral cats at was found not to significantly differ between sites (*p*=0.09), results indicate that there may be some effect of site on habitat use by feral cats. There was no difference in feral cat use of habitat between years (*p*=0.565) (Table 5.1).

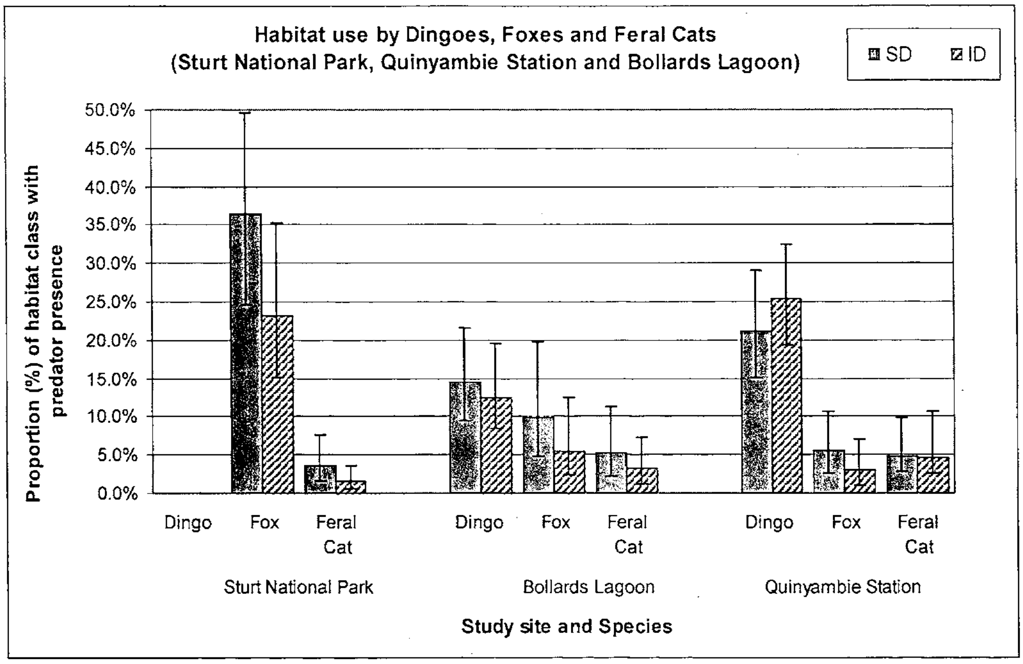
5.3.2 Habitat use by prey

5.3.2.1 North-West Sands land system

At both Sturt National Park (dingoes controlled by exclusion fencing) and Quinyambie Station (dingoes uncontrolled), macropods showed a strong preference for inter-dune habitat, while at Bollards Lagoon (dingoes baited) they were more often found in sand dunes (Table 5.3, Figure 5.8a). This difference is habitat use by macropods was not significant overall (*p*=0.08) and did not vary significantly across years (*p*=0.116) (Table 5.1). However, variations in habitat use by macropods were found to significantly differ between sites over both years (*p*=0.05).

When examining the proportion of transects with rabbit presence, rabbits were found to strongly favour sand dune habitats at both Sturt National Park and Bollards Lagoon (dingoes controlled), but appeared on most sampling units in both sand dune and inter-dune habitats at Quinyambie Station (dingoes uncontrolled) (Table 5.3, Figure 5.8a). This preference for sand dune habitat by rabbits was found to be highly significant (*p*<0.001) and did not differ across sites (*p*=0.938) or between years (*p*=0.354) (Table 5.1). Similarly, the incidence of rabbits on transects was higher in sand dune habitat for all sites (Table 5.4, Figure 5.8b). Rabbits displayed significantly higher activity on sand dunes overall (*p*<0.001), and this pattern did not vary between sites (*p*=0.471) or over years (*p*=0.884) (Table 5.5).

The proportion of transects in each habitat class with small mammal presence at Sturt National Park, Bollards Lagoon and Quinyambie Station differed significantly between sites (*p*=0.02) and over sampling years (*p*=0.02), but not overall (*p*=0.656) (Table 5.1). Small mammals occurred on a higher proportion of inter-dune transects at Sturt National Park and Bollards Lagoon (dingoes controlled), but on a higher proportion of sand dune transects at Quinyambie Station (dingoes uncontrolled) (Table 5.3, Figure 5.8a). When the incidence of small mammals on transects was examined, more small mammal crossings were recorded on sand dunes at both Sturt National Park and Quinyambie Station, but at Bollards Lagoon small mammal occurred at higher rates on transects in inter-dune habitat (Table 5.4, Figure 5.8b). However these differences in habitat use were not significant (*p*=0.296). There was a highly significant difference found in the incidence of small mammals in each habitat class between years (*p*=0.005) (Table 5.5). When data from all years and sites were combined, the incidence of small mammals on transects showed a strong preference for sand dune habitats (*p*=0.010) (Table 5.5).



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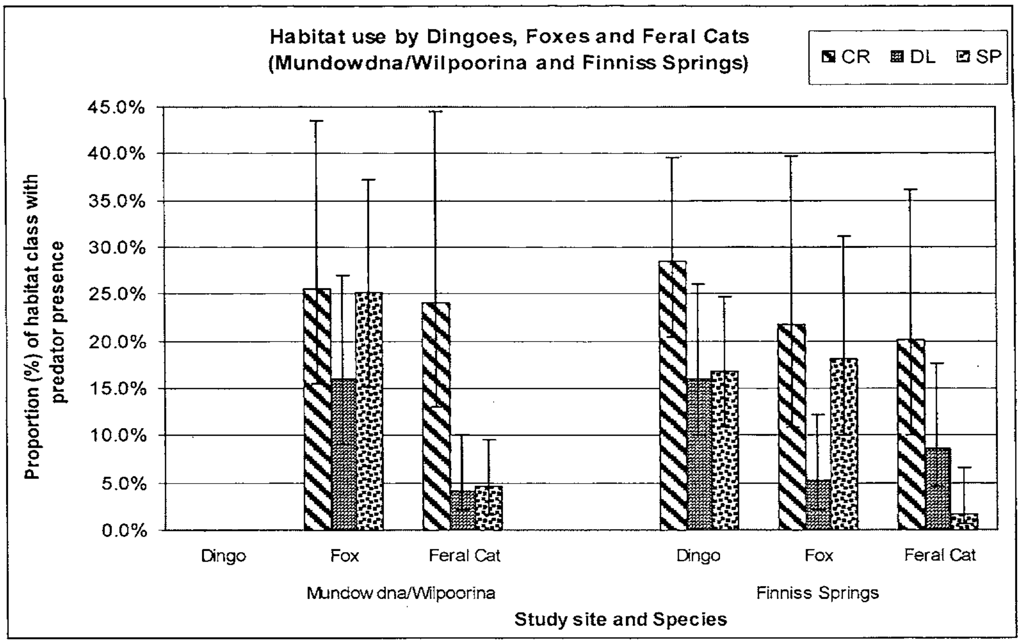


(b)

Figure 5.7 The proportion of each habitat class with predator presence at three study sites within the (a) North-West Sands land system and (b) Mumpie land system (including 95% confidence intervals).

Reptiles were found more often in sand dune habitat at all sites, regardless of dingo management (Table 5.3, Figure 5.8a), Reptiles were present significantly more often on transects in sand dunes than in inter-dunes (p<0.001) and this pattern did not vary across sites (p=0.454) or years (p=0.128) (Table 5.1). Similarly, the incidence of occurrence of reptiles on transects was higher in sand dunes at all sites (Table 5.4, Figure 5.8b) and results showed that sand dunes were strongly preferred by this prey class (p<0.001). However, the incidence of reptiles in sand dune and inter-dune habitats did differ significantly between years (p=0.032). Results also indicate that site may have influenced the incidence of reptiles in each habitat class (p=0.057) (Table 5.5).

5.3.2.2 Mumpie land system

Macropods were detected in all three habitats in the Mumpie land system (creek lines, drainage lines and sand plains) at both Mundowdna Wilpoorina and Finniss Springs (Table 5.3, Figure 5.9a). There was no significant difference in the proportion of transects with macropod presence between habitats (p=0.602), and this pattern was constant across sites (p=0.461) and years (p=0.418) (Table 5.1).

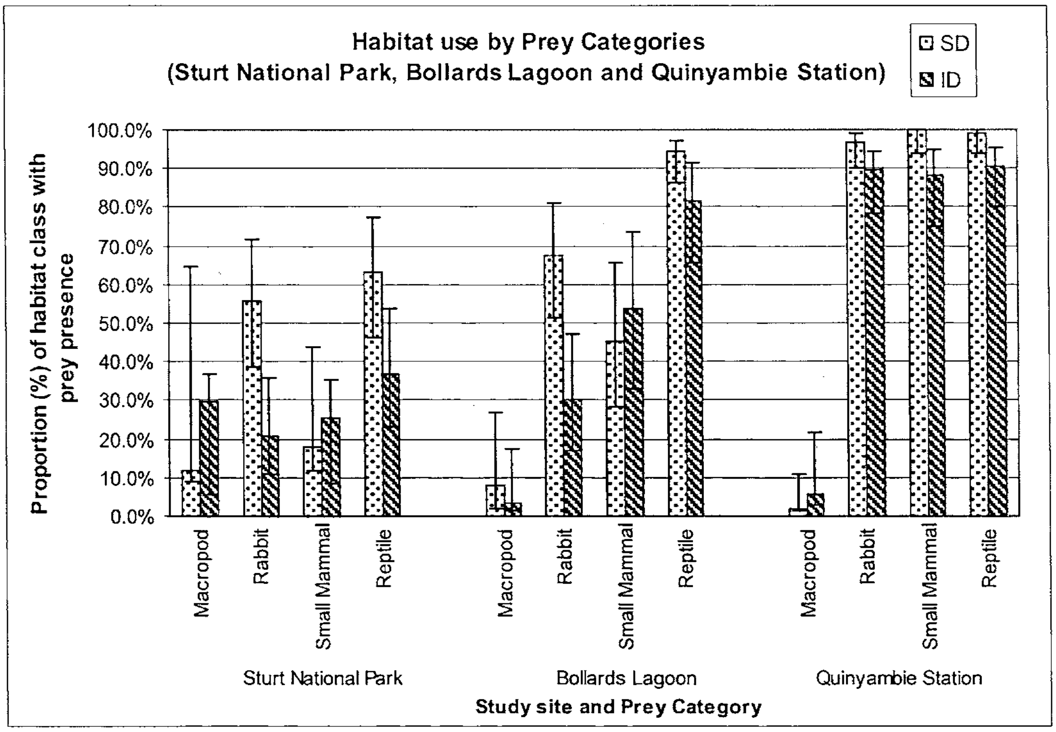
Rabbits showed a preference for creek line and sand plain habitats over that of drainage lines (Figure 5.9a), although this preference appeared to be more pronounced at Mundowdna Wilpoorina (dingoes controlled) than at Finniss Springs (dingoes uncontrolled) (Table 5.3). Overall there was a significant difference in the proportion of transects with rabbit presence across habitats (p=0.002). Results indicate there may be some difference in habitat use by rabbits between sites with different dingo management strategies (Table 5.1), although this difference was not found to be significant (p=0.085). Year was found not to significantly affect the proportion of transects with rabbit presence within each habitat class (p= 0.589) (Table 5.1). Similarly, the incidence of rabbits in each habitat class showed that rabbits prefer creek line and sand plain habitats regardless of dingo management (Table 5.4; Figure 5.9b). The difference in the incidence of rabbits between habitats was found not to be significant (p=0.07); even so, results indicate that lower crossings of transects by rabbits were detected in drainage line habitat at both sites. The incidence of rabbits in each habitat class was not effected by site (p=0.696) or year (p=0.268) (Table 5.5).

Overall, there was no significant difference in small mammals presence in the three habitat classes (p=0.430) (Table 5.1). There appeared to be some differences in habitat use by small mammals between sites with different dingo management. There was no clear preference by small mammals for any habitat class at Mundowdna Wilpoorina, while small mammal presence was more often found on transects in sand plain habitat at Finniss Springs than the other two habitat classes (Table 5.3; Figure 5.9a). However, these between site differences were found to be not significant (p=0.309) (Table 5.1). The incidence of small mammal occurrence in habitats showed a similar pattern to that of proportion estimates (Table 5.4; Figure 5.9b). There was no significant difference found in the incidence of small mammals in habitat classes overall (*p*=0.630), but some differences in the incidence of small mammals in different habitats was seen between sites, although these differences were not found to be significant (*p*=0.09) (Table 5.5).

Similar to small mammals, reptiles appeared to have no habitat preference at Mundowdna Wilpoorina (dingoes controlled) , but were more commonly found in sand plain habitat at Finniss Springs (dingoes uncontrolled) (Table 5.3; Figure 5.9a). Results showed that the proportion of transects with reptile presence in each habitat class differed significantly overall (*p*=0.016) and indicated there were differences in the proportion of transects with reptile presence in habitat classes between sites, although these were found not significant (*p*=0.066) (Table 5.1). The incidence of reptiles showed a strong preference for sand plain habitats at both sites (Table 5.4; Figure 5.9b). The incidence of reptiles was found to differ very significantly between habitat classes overall (*p*<0.001), and between sites (*p*=0.010) (Table 5.5)

Table 5.3 Results showing the mean proportion (*pr*) of sampling units (transect data only) with prey categories species present within each habitat class. Results are given by site with corresponding confidence intervals.

		Macropod		**Rabbit**		**Small Mammal**		**Reptile**	
Site	**Habitat**	***pr***	95% C.I.	***pr***	95% C.I.	***pr***	95% C.I.	***pr***	95% C.I.
SNP	SD	**0.12**	(0.09-0.64)	**0.58**	(0.38-0.72)	**0.45**	(0.12-0.45)	**0.63**	(0.46-0.78)
	ID	**0.30**	(0.03-0.37)	**0.21**	(0.11-0.36)	**0.46**	(0.08-0.35)	**0.37**	(0.23-0.54)
BL	SD	**0.08**	(0.02-0.28)	**0.67**	(0.51-0.81)	**0.41**	(0.27-0.65)	**0.94**	(0.86-0.98)
	ID	**0.03**	(0.01-0.18)	**0.30**	(0.17-0.48)	**0.44**	(0.33-0.73)	**0.82**	(0.66-0.91)
QS	SD	**0.02**	(0.01-0.11)	**0.97**	(0.90-0.99)	**0.99**	(0.93-0.99)	**0.98**	(0.94-0.99)
	ID	**0.06**	(0.01-0.22)	**0.90**	(0.78-0.95)	**0.90**	(0.75-0.95)	**0.90**	(0.80-0.96)
M/W	CR	**0.38**	(0.20-0.60)	**0.95**	(0.70-0.99)	**0.16**	(0.02-0.63)	**0.94**	(0.29-0.99)
	DL	**0.27**	(0.16-0.42)	**0.51**	(0.27-0.74)	**0.25**	(0.10-0.50)	**0.94**	(0.39-0.99)
	SP	**0.24**	(0.15-0.35)	**0.82**	(0.62-0.92)	**0.23**	(0.10-0.44)	**0.97**	(0.54-0.99)
FS	CR	**0.15**	(0.07-0.30)	**0.80**	(0.56-0.93)	**0.09**	(0.02-0.33)	**0.70**	(0.10-0.98)
	DL	**0.19**	(0.09-0.36)	**0.63**	(0.37-0.83)	**0.07**	(0.02-0.27)	**0.73**	(0.12-0.98)
	SP	**0.07**	(0.03-0.18)	**0.70**	(0.46-0.86)	**0.23**	(0.09-0.45)	**0.98**	(0.67-0.99)



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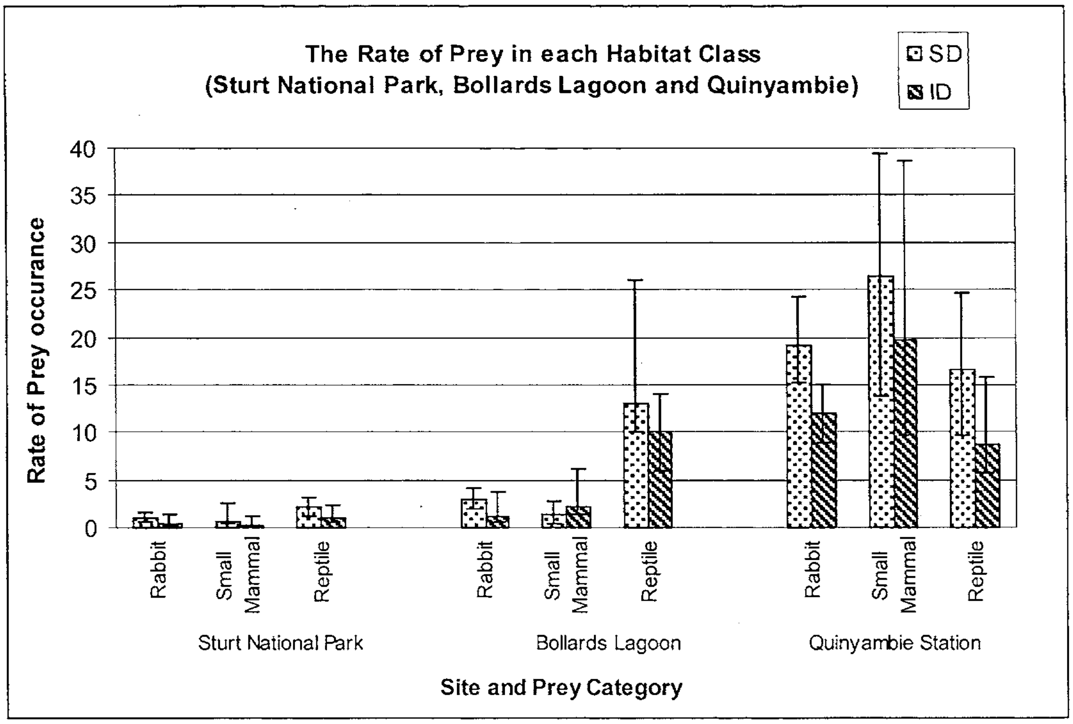


(b)

Figure 5.8 The (a) proportion of each habitat class with prey presence and (b) the incidence (rate) of prey occurrence in each habitat class at study sites within the North-West Sands land system (including 95% confidence intervals).

Table 5.4 Results showing the incidence (rate) of occurrence for prey categories on transects within each habitat class.

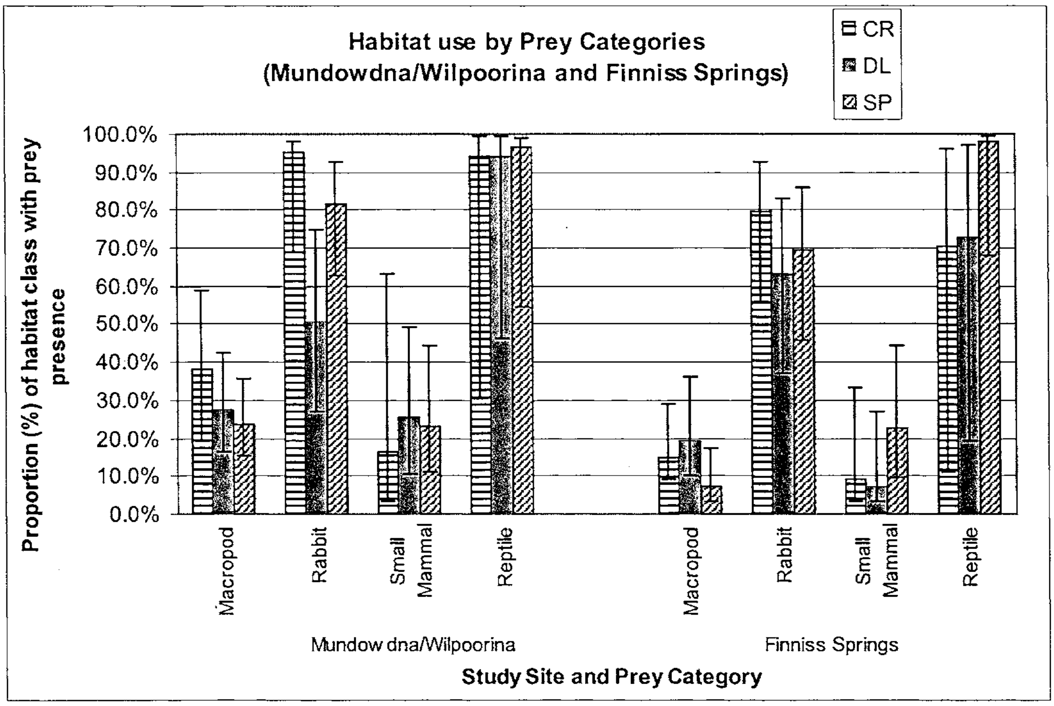
Results are shown by site with corresponding 95% confidence intervals.

		Rabbit		**Small mammal**		**Reptile**	
Site	**Habitat**	***rate***	95% C.I.	***rate***	95% C.I.	***rate***	95% C.I.
SNP	SD	**1.04**	(0.51-2.11)	**0.53**	(0.09-3.22)	**2.08**	(0.92-3.26)
	ID	**0.44**	(0.17-1.19)	**0.26**	(0.06-1.12)	**0.92**	(0.28-1.23)
BL	SD	**3.05**	(2.01-4.62)	**1.31**	(0.46-3.72)	**12.98**	(10.29-26.98)
	ID	**1.20**	(0.58-2.48)	**2.16**	(0.78-5.97)	**10.01**	(5.69-15.58)
QS	SD	**19.21**	(15.00-24.58)	**26.37**	(12.49-55.63)	**16.60**	(10.37-26.77)
	ID	**11.96**	(9.08-15.77)	**19.70**	(9.27-41.91)	**8.72**	(2.69-7.22)
M/W	CR	**5.32**	(2.87-9.86)	**0.46**	(0.11-1.96)	**6.92**	(3.93-12.20)
	DL	**2.86**	(1.53-5.35)	**0.36**	(0.13-1.01)	**5.99**	(3.09-11.59)
	SP	**4.08**	(2.41-6.90)	**0.35**	(0.13-0.91)	**12.07**	(4.39-33.16)
FS	CR	**4.35**	(2.44-7.73)	**0.09**	(0.02-0.49)	**4.72**	(2.21-10.05)
	DL	**3.10**	(1.66-5.80)	**0.07**	(0.01-0.36)	**2.88**	(1.27-6.57)
	SP	**4.44**	(2.55-7.75)	**0.32**	(0.11-0.90)	**13.90**	(7.80-24.78)

Table 5.5 *p* values shown for the effect of habitat type on the incidence of each prey category, and the effects of site and year on the incidence of prey found in each habitat type (macropods not included).

Values shown for Poisson distribution models, with corresponding residuals and standard error (pooled) values from the habitat*site model. * denotes significant ($p < 0.05$) and ** denotes highly significant ($p < 0.005$) result; n.d. indicates statistic not available.

Species/Category	**Habitat Types**	**Habitat**	**Site*Habitat**	**Year*Habitat**	**R**	**±s.e**
Rabbit	SD/ID	<0.001**	0.471	0.884	8.703	0.59
	CR/DL/SP	0.071	0.696	0.268	5.761	0.51
Small Mammal	SD/ID	0.010*	0.296	0.005*	15.54	1.05
	CR/DL/SP	0.630	0.092	n.d	1.095	0.12
Reptile	SD/ID	<0.001**	0.057	0.032*	7.254	0.498
	CR/DL/SP	<0.001**	0.100	n.d	8.629	0.959



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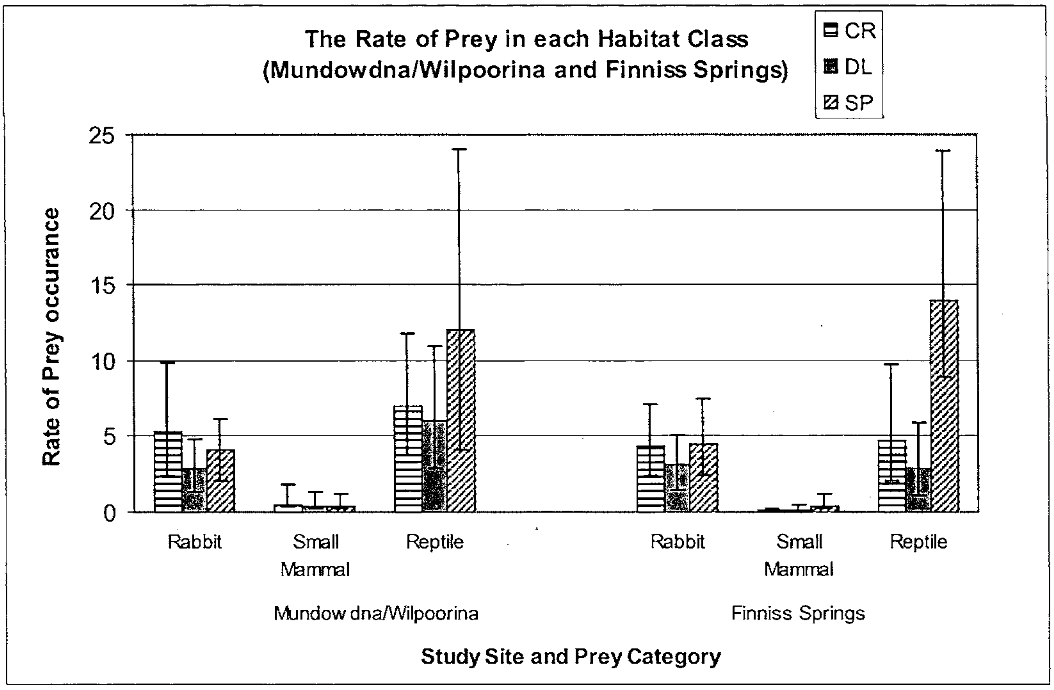


(b)

Figure 5.9 The (a) proportion of each habitat class with prey presence and (b) incidence (rate) of prey occurrence in each habitat class at study sites within the Mumpie land system (including 95% confidence intervals).

5.4 Discussion

5.4.1 Habitat use by sympatric carnivores in the arid zone

Overseas studies examining the habitat use of sympatric carnivores have found habitat partitioning an important process in moderating interactions between competing species. Habitat partitioning has been found between sympatric canid species, including coyotes and red foxes (Gosselink *et al.*, 2003; Theberge and Wedeles, 1989b) and coyotes and grey foxes (*Urocyon cinereoargenteus*) (Fedriani *et al.*, 2000). Such interactions were shown to influence fox densities, perhaps due to coyotes selecting resource- rich habitats, while foxes avoided the areas coyotes inhabited. In Australia, foxes have been found to avoid interactions with dingoes through avoiding habitats, such as drainage areas, favoured by dingoes. Foxes were then found to increase their use of such habitats when dingoes were absent (Southgate *et al.*, 2007).

In contrast, when the use of habitats by bobcats and coyotes was examined, no interaction was found (Fedriani *et al.*, 2000). Similarly, Edwards *et al.* (2002) found feral cat use of habitat did not change with changes in dingo activity, instead, feral cats continually occupied prey-rich habitats. Molsher *et al.* (1999) found behavioural changes in habitat use and diet in feral cats following the control of foxes, but while feral cats may increase their use of open areas, such as roads, in the absence of dingoes (Burrows *et al.*, 2003), they appear to better be able to persist sympatrically where dingoes exist than do foxes.

While findings as reported by Southgate *et al.* (2007) suggest landscape scale avoidance of foxes by dingoes may occur between these species, other studies suggest behavioural interactions are inherently localised (Franke *et al.*, 2004). The decision made by a mesopredator to use a habitat patch may be made through its response to nearby organisms, including other predators and prey. In this study dingoes and foxes were found to overlap in the use of broad habitat types (for example, sand dunes), but data were not collected on fine scale and temporal avoidance in particular habitat patches. Mitchell and Banks (2005) found fine scale exclusion of foxes in the presence of wild dogs, and suggested this may be indicative of temporal rather than landscape scale avoidance. As such, interactions between these predators may vary with productivity of the landscape, resource availability, habitat structure and trophic complexity (Ritchie and Johnson, 2009).

Dingoes are generalist predators, and occupy a wide variety of habitats across Australia (Corbett, 1995; Fleming *et al.*, 2001a). Previous research on habitat use by dingoes in the arid zone has found that they have no apparent preference for habitat type (Edwards *et al.*, 2002; Southgate *et al.*, 2007). In the North-west sands land system sampled in this study, dingoes used both sand dunes and inter-dunal habitats equally. In the Mumpie land system, dingoes did show a preference for creek lines, but were also regularly found in other habitats. Southgate *et al.*

(2007) found dingo presence in a habitat had a positive association with proximity to drainage and rainfall gradient.

A study conducted in the Australian arid zone have found dune crests have been favoured by foxes (Mahon et al., 1998) while other studies report foxes to have the least specific habitat requirements of all three predator species (Southgate et al., 2007) . Similarly, in this study foxes showed a strong preference for habitat type, favouring sand dune habitat in the North-west sands land system, and creek lines and sand plain habitats at within the Mumpie land system. This pattern of habitat use was uniform, regardless of dingo management strategy at the site, suggesting other factors may determine habitat use by foxes in arid areas. Landscape use by red foxes in the semi-arid areas of North Africa has been found dependant on the distribution and availability of water, food patches and suitable digging substrates for dens (Dell'Arte and Leonardi, 2007).

Feral cats appeared to have no preference for either sand dune or interdunal habitats, although a slight preference for the more sheltered sand dunes has been found previously (Mahon *et al.*, 1998; Southgate *et al.*, 2007). Feral cats were more commonly found in sheltered habitats such as drainage areas and creek lines in the Mumpie land system. While there were some differences in habitat use between Mumpie land system sites by feral cats, these differences were not statistically significant, suggesting habitat use by feral cats is not determined by dingo management strategy. Previous studies on the use of habitat by feral cats at similar sites in the arid zone have also shown a preference for more sheltered habitats with denser vegetation cover, such as sand dunes and creek lines (Eldridge *et al.*, 2002; Moseby *et al.*, 2009). When available, feral cats may also favour other sheltered habitats, such as rocky outcrops (Southgate *et al.*, 2007).

5.4.2 Factors that may influence habitat use by predators

Habitat use by foxes and feral cats in this study did not vary significantly between sites with different dingo management regimes, and thus appeared not to be affected to any great extent by the presence or absence of dingoes. Nor did habitat use for any of the predators vary between years, indicating rainfall also had little effect on habitat use. This suggests that other factors may be more important in determining the use of broad habitat types by foxes and feral cats at the study sites.

Previous research on intraguild interactions between terrestrial carnivores have examined vegetation structure and apparent available shelter as a possible selection criteria for mesopredators occupying certain habitats (Major and Sherburne, 1987). In addition to densely sheltered habitats providing a refuge from the sun during the hotter periods of the year, a preference for more sheltered, or 'safe' habitats by mesopredators may suggest an avoidance of open or 'risky' habitats where the chance of being able to avoid an interaction with larger predators is lower (Thompson and Gese, 2007).

The difficulty with examining safe vs. resource rich habitats in this study, and across arid areas in general, is that more open habitats tend to have less prey resources, while in more sheltered habitats (such as sand dunes) many prey items (for example, rabbits, small mammals and reptiles in this study) are generally more abundant. The confounding nature of these two variables means that it is difficult to assess what factors may influence foxes to prefer sand dune habitats; whether it is prey availability, shelter or both. Furthermore, it may be an interaction between these two variables that increases habitat suitability: rabbit burrows might provide enough shelter for mesopredators away from dingoes so that all three predators can readily occupy the same habitats. Similarly, trees may provide feral cats with shelter in creek lines, while also providing an alternative food resource: birds.

The assessment of the distribution of different prey classes across habitats in this study allows some insight as to whether prey distribution may be an alternative explanation to mesopredator habitat use. Similar to predators, prey distribution across habitats may be associated with resource availability, but may also be related to predation pressure. The occupation of habitats by prey species may therefore not necessarily indicate preference, but as with predators may be a reflection of the interaction between food availability, other microhabitat variables (such as grazing pressure/distribution), shelter from predation and abundance of different predators or prey species at the site.

For example, when examining the proportion of transects with rabbit presence, rabbits were found to strongly favour sand dune habitats at both Sturt National Park and Bollards Lagoon, but appeared on most sampling units in both sand dune and inter-dune habitats at Quinyambie Station. While sand dunes may offer better substrate for warrens, in addition to increased shelter, the more even distribution of both small mammals and rabbits across both habitats at Quinyambie Station may reflect higher densities of these prey classes overall. These results may be indicative of density dependant habitat selection, in that as populations increases, the range of habitats used increases, including the occupation of less favourable habitats (Pulliam, 1988; Pulliam and Danielson, 1991). Alternatively, more evenly distributed food resources, and higher availability of alternative prey species may have led to less predation pressure on one particular prey type at this site.

In the Mumpie land system, rabbits showed a preference for more sheltered habitats such as creek lines and sand plains over that of drainage lines, and this preference was more pronounced where foxes were at higher densities. It is possible that selecting habitat that has protection from predators becomes more important to prey when predators are at higher densities, and prey at lower densities.

Small mammalian prey occurred on a higher proportion of inter-dune transects at Sturt National Park and Bollards Lagoon, but on a higher proportion of sand dune transects at Quinyambie Station. While the incidence of occurrence of small mammals at all these sites suggests a preference for sand dune habit by small mammals, high predation pressure by foxes, and possibly feral cats, at sites where dingoes are controlled or absent, appears to have reduced the presence (and probably density) of small mammals on sand-dunes. This difference in habitat use by prey between these sites may indicate an effect of dingo management, in that prey used open habitats to a greater extent in the presence of dingoes, or are less susceptible to intense predation pressure through a reduction in mesopredator activity.

Southgate *et al.* (2007) suggest that dingo dominance in more productive habitats leads to feral cats and foxes making use of prey resources in lower productive habitats, (such as reptiles). Predator hunting styles are an important consideration when examining the use of habitats by predators, and the effect of predator presence on the use of habitats by prey. Carnivore hunting behaviour is often suited to specific vegetation types and stereotypical within taxonomic families (Murray *et al.*, 1995).

Carnivores forage in two main ways. Feral cats are stalking/ambush predators and use cover within habitats to get close to chosen prey, thus tend to occupy habitats with dense cover, such as creek lines, drainage areas and sand dunes (Edwards *et al.*, 2002; Molsher *et al.*, 2005). In this study, despite an even distribution of small mammals throughout all habitats in the Mumpie land system, feral cats were more common in sheltered creek lines. Rabbits, a favoured prey of feral cats (see review in Chapter 1, section 1.2.3) were found to favour creek lines, and the dense vegetation suited the hunting tactics of feral cats. Conversely, canids (including foxes and dingoes) make less use of vegetation and instead use running/chasing tactics to pursue prey (Murray *et al.*, 1995). This means that canids can occupy more open habitats where they have often have clearer pursuit paths.

A further consideration to habitat use between sympatric predators is territoriality, which often determines the availability of habitats and prey resources within them (Andrewartha and Birch, 1954). The availability of required resources is rarely uniform across the landscape (Manly *et al.*, 2002), and patchiness of resources may lead to territorial domination of apex predators in optimal habitats. Sargeant *et al.* (1987) found that territoriality played a part in patch use of red foxes in the presence of coyotes (Sargeant *et al.*, 1987). Red foxes were absent from large, central portions of coyote territories, and young dispersing foxes avoided establishing new territories in coyote ranges. They suggest that such inter-specific territoriality has led to a decline in red fox populations.

The nature of a food supply will also determine the way a territory is used; if target prey is mobile (such as macropods in this study), then the predator will move between habitats within its territory (Lendrem, 1986). As such, use of a wide variety of habitats by dingoes may be a reflection of a wider variety of target prey species, including macropods that are more often found in open areas, and rabbits which were more common in sheltered habitats in this study. In contrast to dingoes, which are more mobile, occupy larger home ranges and depredate a broader range of prey sizes, foxes focused their activity in sand dunes where rabbits and small mammals were abundant. It is interesting to note that even when these prey were common in both interdunes and on sand dunes, fox activity remained higher on sand dunes. This restriction may have been due to increased shelter for protection from dingoes, and it is unknown as to whether foxes would have broadened their use of different habitats where rabbits were more evenly distributed (such as at Quinyambie Station) if dingoes were not present at this site. In a previous study, feral cat home ranges have been found to contain a mixture of habitat types that provided both shelter from larger predators and adequate prey resources (Molsher *et al.*, 2005). Thus mesopredators may be effectively "boxed into" habitats that meet both their resource and shelter needs by the larger and more competitive apex predator (Pianka, 1978).

The question of habitat selection by a species in space and time remains highly complex. Habitat selection may be affected by individual attributes, such as age, sex, or social status, season, vegetation structure and habitat complexity (Thompson and Gese, 2007; Manly *et al.*, 2002), all of which were beyond the scope of this study. Furthermore, in the arid zone of Australia, predators are faced with fluctuating and unpredictable availability of food and water resources which may change habitat patch suitability over time (Pulliam, 2000). In addition, the impact of human activities, including livestock grazing, will undoubtedly influence habitat patch suitability and use. Finally, the temporal mobility of a species around its home range will undoubtedly influence its detection and ultimately its presence in a habitat at the time of sampling.

5.5 Conclusion

This study found dingo management was not a single determinant of the use of broad habitat classes by foxes and feral cats. Instead habitat use by mesopredators appears to be a determined by a number of inter-related variables, including prey availability, adequacy of shelter and suitability of the habitat to the predator's characteristic hunting method. While dingoes may exclude mesopredators temporarily on a local (patchy) scale, no evidence was seen in this study for a large landscape scale exclusion from resource-rich habitats.

The aim of this research was to conduct a broad comparison of habitat use by three predators under varying dingo management regimes. One limitation of the data collected in this study is that it cannot be used to determine the amount of time predators spent in each habitat class, or where temporal activity was focused, both which may enlighten more subtle interspecific interactions. Research into the temporal activity of sympatric dingoes, foxes and feral cats is needed, and this is further examined in Chapter 7 of this thesis.

Chapter 6: The effect of dingo management on the distribution of dingoes, foxes and feral cats around water points in arid Australia.

6.1 Introduction

There is increasing interest in the closure of artificial water points in the water remote areas of arid Australia for the restoration of biodiversity. Artificial watering points are common throughout the Australian rangelands for the provision of water to livestock (James *et al.*, 1999). In addition to providing water for domestic animals, artificial water points may support native fauna and increase survival rates of local consumer species (Sabo and Power, 2002). Predators are major beneficiaries of artificial water points in arid environments (DeStefano *et al.*, 2000), and in particular, the use of artificial waters by introduced predators is an important consideration in the development of remote water management and predator control strategies. An increase in artificial water availability across arid areas may enable introduced species, including exotic herbivores and predators, to expand their range into previously water remote areas (James *et al.*, 1999; Davies *et al.*, 2010).

The majority of research on artificial water points in Australia has focused on the impact of livestock and introduced herbivores on native vegetation (Landsberg *et al.*, 2002; Landsberg *et al.*, 2003; Pringle and Landsberg, 2004; Tynan *et al.*, 1999). Interactions between predators and native prey species at water points are especially important considerations in artificial water management, but remain largely overlooked when formulating management plans for water points in arid areas. Intraguild interactions around water points in arid regions may play a significant role in structuring mammalian predator assemblages and influence spatial predation on some native prey species. In Australia, predation by two exotic mesopredators, the red fox *Vulpes vulpes* and the feral cat *Felis catus*, has been identified as a primary cause of dramatic declines in native fauna in many ecosystems (Burbidge and Manly, 2002; Johnson *et al.*, 2007; Short and Smith, 1994; Smith and Quin, 1996; Burbidge and Mckenzie, 1989) (see Chapter 1, section 1.3). Strategies that restrict the access of mesopredators to water may reduce their abundance, distribution and impact on native prey species, both in the long term and by decreasing predation around artificial waters.

The influence of a naturalised top-order predator, the dingo, on reducing the impact of foxes and feral cats on native biodiversity has been the focus of much debate. Traditionally, the dingo has been managed as a pest across much of the continent, with the species heavily controlled in many areas to reduce conflict with livestock (Fleming, 2000). However, there is increasing evidence from both correlative analysis (Johnson *et al.*, 2007; Johnson and

VanDerWal, 2009) and field studies (Letnic *et al.*, 2009a; Letnic *et al.*, 2009b) that dingoes may provide a positive benefit to native biodiversity through limiting fox abundance in arid Australia. The mesopredator-release hypothesis (Crooks and Soule, 1999) predicts that a decline in top-order predators will lead to an increase in the abundance of smaller predators, and consequently increased predation on smaller prey. While dingoes may limit the numbers of foxes, and perhaps feral cats, the mechanisms of how dingoes are able to suppress the abundance of these smaller predators remain unclear (Glen and Dickman, 2005).

Previous research on intraguild interactions between sympatric mammalian carnivores suggests that limitation of mesopredators by larger carnivores may occur through direct predation (Creel and Creel, 1996; Fedriani *et al.*, 2000; Ralls and White, 1995), or indirect effects such as resource partitioning, and temporal or spatial segregation (Gosselink *et al.*, 2003), including avoidance behaviour (Moseby *et al.*, 2012). For example, in the presence of an apex predator, mesopredators may change their use of space to reduce the risk of potentially harmful encounters (Polis *et al.*, 1989; Thompson and Gese, 2007). Such changes in behaviour often restrict both the abundance and distribution of the mesopredators (Durant, 2000; Palomares and Caro, 1999) and directly influence spatial patterns in prey mortality, and spatiotemporal patterns in predator population densities (Giraldeau and Caraco, 2000).

Diet studies of dingoes show limited presence of fox or feral cat remains (Corbett and Newsome, 1987; Thomson, 1992a; Whitehouse, 1977), with some studies recording no predation at all (Robertshaw and Harden, 1985; Triggs *et al.*, 1984). Similarly feral cat remains are not commonly found in the diet of foxes (Lunney *et al.*, 1990; Molsher *et al.*, 2000), suggesting nominal inclusions may be due to opportunistic aggressive encounters rather than predation (Corbett, 1995; Corbett and Newsome, 1987; Paltridge, 2002). Limited research on intraguild avoidance behaviour suggests that foxes avoid encounters with dingoes on a fine spatial or temporal scale (Mitchell and Banks, 2005; Southgate *et al.*, 2007).

As in the previous chapter, this chapter explores avoidance behaviour as a possible mechanism behind trophic interactions between dingoes, foxes and feral cats. Here I examine how dingo management influences the distribution of dingo, foxes and feral cats around water points at the five study sites. Through comparing the activity of dingoes, foxes and feral cats in proximity to water points under different dingo management strategies, I aim to address the following question:

- What is the effect of dingo management strategy on the spatial distribution of dingoes, foxes, feral cats around water points at the study sites?

I hypothesise that dingoes will dominate areas near water, displaying increased activity in these areas, thereby inducing avoidance behaviours in foxes and feral cats close to water points. If dingoes do have this effect, they could provide a potential means of limiting access of smaller predators to water resources. In this way dingoes may indirectly reduce survival rates of mesopredator populations, thereby reducing impacts on native prey species vulnerable to fox and feral cat predation.

6.2 Methods and Data Analysis

Data on water resource locations and predator activity were collected from each study site during summer between the years 2006 and 2008 (see Chapter 2, section 2.1.3). This time of the year is when resources, in particular water, are most likely to be in short supply.

6.2.1 Identification of water points

A transect 20 km in length was defined at the centre of each sampling area, and water points within 10km radius of the transect were included in the analysis (Figure 6.1). The number of water points at some sites varied slightly between sampling years due to both rainfall events and movement of stock. To increase consistency, where access permitted, an attempt was made to locate and all accessible water resources within the sampling area. This included permanent and semi-permanent artificial waters, in addition to non-permanent and natural waters. Permanent artificial water points consisted of stored surface water (including catchment tanks and open dams) and bore troughs, while springs formed the majority of permanent natural waters. Locations of permanent water points within the sampling area were provided by property managers. The number of and distances between permanent water points varied between sites depending on management (reserve or pastoral property) and grazing practices (sheep or cattle). Non-permanent water included flowing creeks and surface water depressions filled from episodic rains. Non-permanent waters were located by driving along all available access roads in the sampling area and using binoculars to scan surrounds. We recorded the location of all water resources using a Global Positioning System (GPS).

6.2.2 Sampling of predator activity in proximity to water points

Predator activity in proximity to water resources was determined using track counts from sand transects (Allen *et al.*, 1996; Mahon *et al.*, 1998) and scent stations (Linhart and Knowlton, 1975; Roughton and Sweeny, 1982; Sargeant *et al.*, 2003; Smith *et al.*, 1994b) (see Chapter 2, section 2.1.3). Distance of transects and scent stations from water points varied between 100 m to 15 km. Each predator species was recorded as either present or absent at every sampling unit. The location of all sampling units was recorded using a GPS. Transect, scent station and water point locations were mapped and then the distance between each sampling unit and the closest water point was calculated using ArcGIS 9.

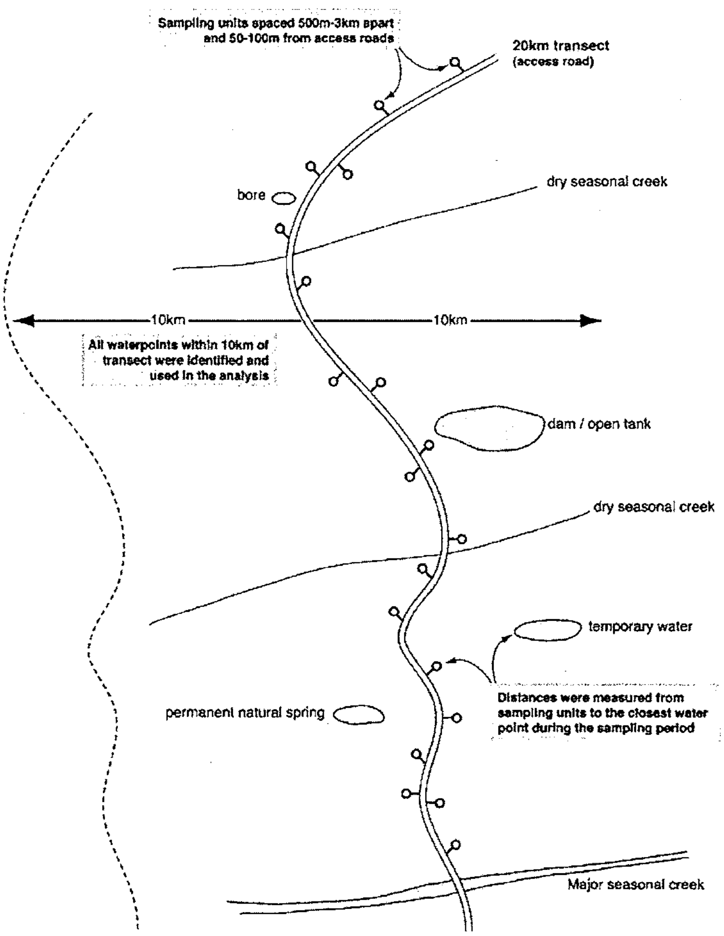


Figure 6.1 Conceptual diagram of study design, using the Finniss Springs study site as a model.

The diagram shows the relative distributions of sampling units (transects and scent stations), water points and access roads. Note: The reference to all water points indicates an effort to use all water points located during the sampling session, within logistical limitations. Diagram is approximate and not to scale.

6.2.3 Data Analysis

Analyses were conducted using the statistical software package Genstat (VSN International, 2008). The probability of predator presence was modelled for the three predator species for distance to water at each site. Initially the polynomial functions of distance to water (Distance, Distance^2) were considered as covariates, however distance to water produced the best fitting model. The final model included site and distance to water as fixed effects and sampling area within each site and night within sampling area as random effects. Year was used initially in the model but was not significant for all species, so data from both sampling years were combined.

The average effects on the probability of predator presence at sampling units by distance to water under different dingo management regimes was modelled. In this model sites were categorised into three dingo management strategies, including no dingo control (Finniss Springs and Quinyambie Station), exclusion fencing (Sturt National Park and Mundowdna) and baiting (Bollards Lagoon).

To compare accuracy of model findings to observed predator activity, an activity index was calculated for each species. Predator activity indices were estimated using the observed proportion of sampling units with the presence of each predator species for each distance to water category under different dingo management regimes. Four cut-off points were used to categorise distance to water: <500 m, 500 m > 2.5 km, 2.5 km > 5 km and > 5 km. Distances for the four categories were selected taking into account both the minimum spacing distance for sampling units (500m) and the home range size of mesopredators in arid regions (Edwards *et al.*, 2001; Marlow, 1992b). The Hosmer-Lemeshow goodness of fit was then used to test how well the models fit the observed data.

6.3 Results

6.3.1 The effect of distance to water on predator presence

Dingoes were more likely to be found near water than further away ($p < 0.001$); this pattern was consistent across all sites where dingo populations occurred (Figure 6.2a), with no evidence of a site by distance interaction ($p = 0.355$) (Table 6.1).

Distance to water was also a determinant of fox presence, and this relationship was highly significant ($p = 0.001$). There was also a significant difference in fox presence in proximity to water between sites ($p < 0.001$) (Table 6.1). At both Sturt National Park and Mundowdna Wilpoorina, where dingoes were absent, the model showed that fox presence decreased with increasing distance from water. In contrast, at sites with dingoes (Bollards Lagoon, Quinyambie Station and Finniss Springs), modelled fox presence increased with increasing distance to water (Figure 6.2b).

The effect of distance to water on feral cat presence was significant ($p = 0.03$). There was an increase in feral cat presence as distance to water increased at all sites with the exception of Bollards Lagoon, although this pattern was strongest at Sturt National Park (Figure 6.2c). At Bollards Lagoon the opposite occurred and feral cats were more likely to be detected closer to water, although this difference in slopes between sites was found not to be significant ($p = 0.09$) (Table 6.1).

When the average effect of distance to water on the probability of predator presence was modelled for sites with different dingo management regimes, similar results were found. Distance to water had a highly significant effect on the probability of dingo presence ($p < 0.001$), as did dingo management strategy ($p = < 0.001$). However, no site by distance to water interaction was found. Both distance to water ($p = 0.006$) and site ($p = 0.009$) were significant in determining the probability of fox presence, and a distance to water and site interaction was found ($p = < 0.001$). Foxes were much more likely to occur close to water points at sites with no dingoes than at sites with either uncontrolled or baited dingo populations. Feral cat activity was low at all sites, but results indicated that the probability of cat presence was affected by distance to water ($p = 0.02$) but not by dingo management strategy ($p = 0.82$). There was, however, an interaction between distance to water and site ($p = 0.02$) (Table 6.1).

Table 6.1 The modelled association between distance to water and the probability of predator presence (slope) with corresponding standard errors.

Negative (-) slopes indicate that predator prevalence decreases as distance to water increases. Results for the Hosmer-Lemeshow goodness of fit are shown separately for both models (site and dingo management category) for each predator species.

By Site	**Dingo**		**Fox**		**Feral Cat**	
	Slope	*SE*	Slope	*SE*	Slope	*SE*
Sturt National Park	-	-	- 0.18	0.05	0.22	0.13
Bollards Lagoon	- 0.15	0.07	0.12	0.07	- 0.22	0.13
Quinyambie Station	-0.23	0.07	0.08	0.14	0.16	0.14
Mundowdna Wilpoorina	-		- 0.42	0.11	0.15	0.16
Finniss Springs	- 0.11	0.04	0.04	0.05	0.13	0.07
Slope by site interaction (p-value)	0.355		<0.001		0.09	
Hosmer-Lemeshow goodness of fit	χ^2_9 = 9.26, p= 0.41		χ^2_9 = 10.09, p=0.34		χ^2_9 =13.17, p=0.16	
By Dingo Management						
No management	- 0.11	0.03	0.09	0.07	0.14	0.06
Baiting	- 0.15	0.07	0.09	0.05	- 0.22	0.12
Exclusion fencing	-	-	- 0.22	0.05	0.16	0.09
Slope by site interaction (p-value)	0.627		<0.001		0.02	
Hosmer-Lemeshow goodness of fit	χ^2_9 = 15.7, p= 0.07		χ^2_9 =6.97, p= 0.64		χ^2_9 = 15.21, p= 0.09	

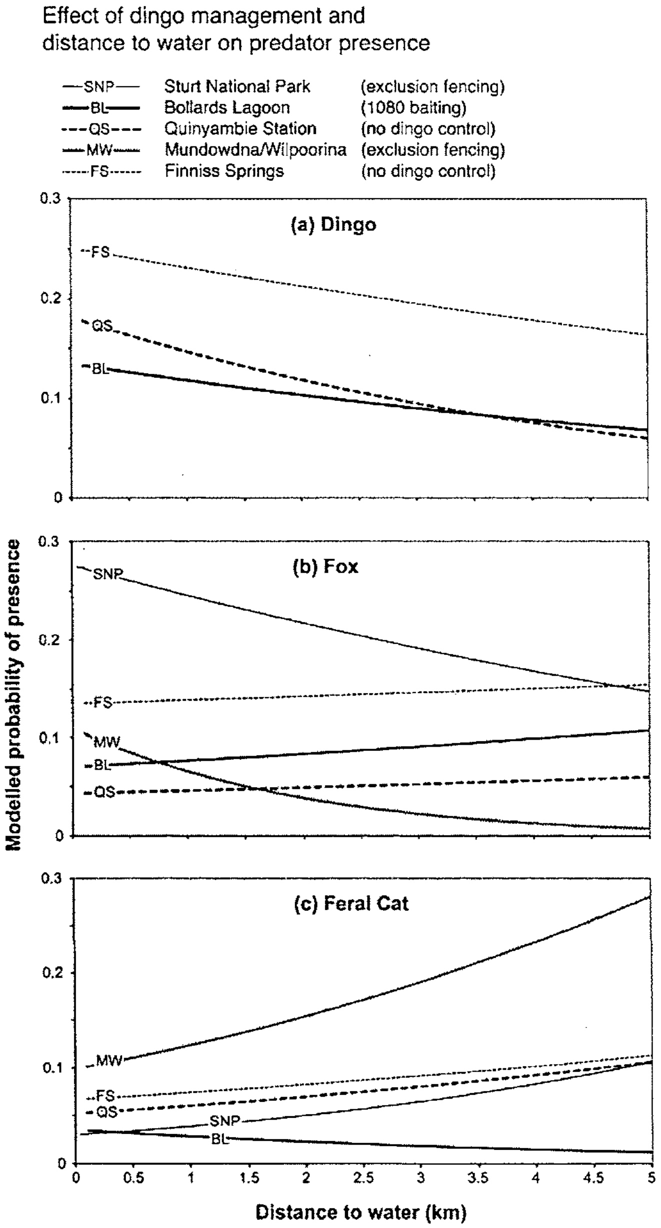


Figure 6.2 (a-c) The modelled probability of (a) dingo, (b) fox and (c) feral cat presence in proximity to water points at five study sites.

The modelled percentage of observations with predator presence by site and distance to water were in close agreement to observed values (Table 6.2). The observed dingo presence on sampling units was highest within 500 m of water where dingoes were not controlled, while at sites where dingoes were controlled either by baiting or exclusion fencing, observed dingo presence increased further from water (Table 6.2; Figure 6.3a). Where dingoes were not controlled, observed fox presence was highest < 5 km from water points (Figure 6.3a). In comparison, at sites where dingoes were controlled by exclusion fencing, observed fox presence was greatest within 500 m of water (Figure 6.3c). At the study site where baiting occurred, the observed presence of feral cats was highest within 500 m of water points (Figure 6.3b). At sites with uncontrolled dingo populations or where dingoes were controlled by exclusion fencing, the observed presence of feral cats was higher further away from water (Figure 6.3a, c).

Table 6.2 The observed percentage of observations with predator presence. Results shown for each predator species by distance to water and dingo management regime: n indicates total number of observations over the sampling period.

Dingo management (site)	Distance category	*n*	Dingo		Fox		Feral Cat	
			(%)	*SE*	(%)	*SE*	(%)	*SE*
Sturt National Park	< 500m	81	0	0	40	5.4	1	1.2
	500m < 2.5 km	96	0	0	33	4.8	2	1.5
	2.5 < 5km	86	1	1.2	34	5.1	2	1.6
	> 5km	78	0	0	15	4.1	5	2.5
Bollards Lagoon	< 500m	32	41	8.7	3	3.1	9	5.2
	500m < 2.5 km	63	10	3.7	8	3.4	8	3.4
	2.5 < 5km	96	9	3.0	8	2.8	5	2.3
	> 5km	105	11	3.1	10	3.0	1	0.9
Quinyambie Station	< 500m	48	42	7.1	6	3.5	0	0
	500m < 2.5 km	130	26	3.9	2	1.3	5	1.8
	2.5 < 5km	198	19	2.8	7	1.8	7	1.8
	> 5km	33	21	7.1	0	0	3	3.0
Mundowdna Wilpoorina	< 500m	51	0	0	39	6.8	2	1.9
	500m < 2.5 km	195	0	0	25	3.1	10	2.2
	2.5 < 5km	132	0	0	15	3.1	5	1.8
	> 5km	3	0	0	0	0	0	0
Finniss Springs	< 500m	20	40	11	10	6.7	5	4.9
	500m < 2.5 km	42	33	7.3	10	4.5	5	3.3
	2.5 < 5km	19	5	5.1	21	9.4	21	9.4
	> 5km	232	17	2.5	16	2.4	10	2.0

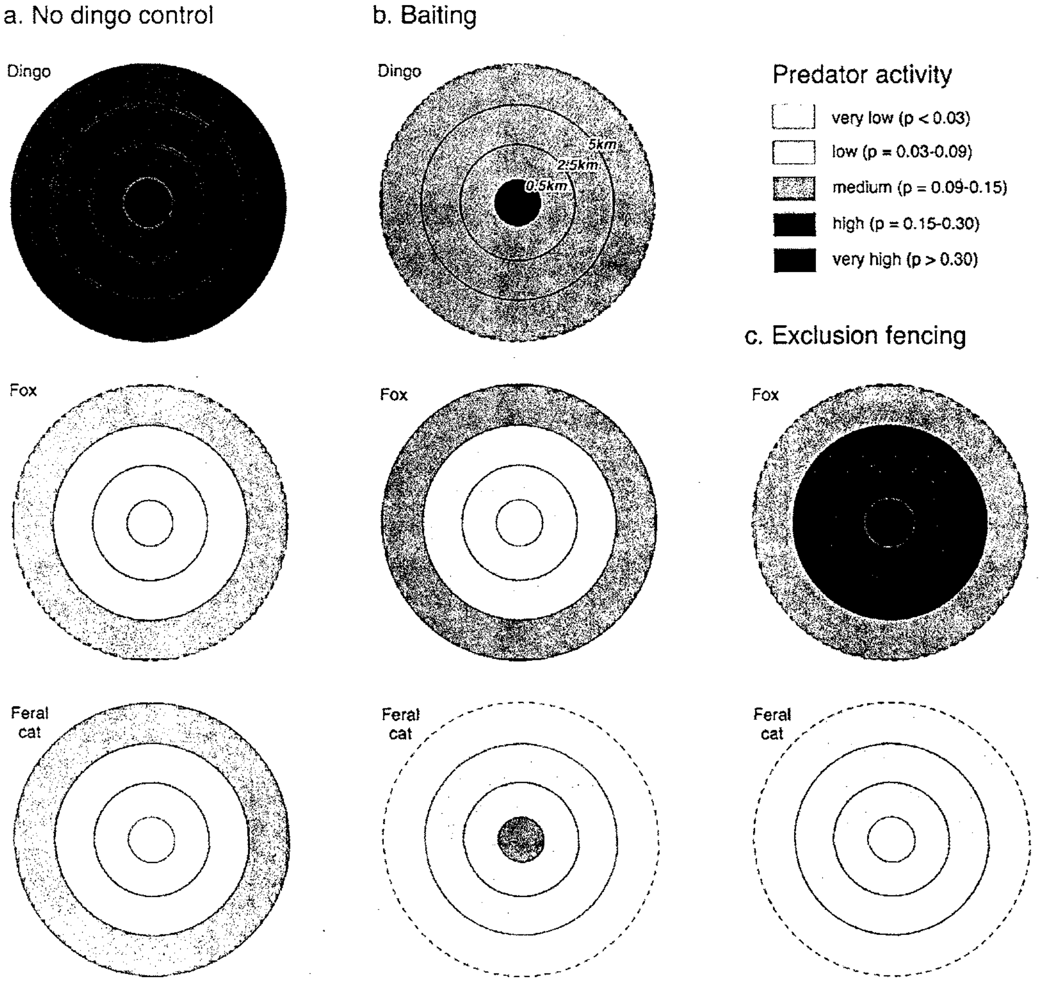


Figure 6.3 (a-c). The average effect of distance to water on observed predator activity by dingo management category.
No dingo control (a), baiting (b) and exclusion fencing (c): p indicates observed predator activity index.

6.4 Discussion

6.4.1 Spatial avoidance of dingoes by mesopredators around water points

Spatial avoidance behaviour by sympatric members of the genus *Canis* and *Vulpes* has been well documented (Sargeant and Allen, 1989; Sargeant *et al.*, 1987; Voigt and Earle, 1983). In this study, differences in the presence of red foxes and proximity to water points at sites with and without dingoes suggest that foxes avoid areas near water if dingoes are present. At sites where dingoes were uncontrolled, foxes were less likely to be found within 5 km of water points; conversely, where dingoes were controlled using exclusion fencing, fox activity was highest near water. Feral cats were more likely to be found closer to water where 1080 baiting was conducted and dingoes (and non-target foxes) were controlled. Such spatial distribution of these predators suggests that the presence of dingoes around water points instigates avoidance behaviour by foxes and feral cats, and through doing so may limit the use of artificial waters by mesopredators.

Consistent with these findings, observations by other authors have noted the ability of dingoes to exclude foxes from some areas during drought, in particular from around water points (Eldridge *et al.*, 2002) and other shared resources such as carcasses (Corbett, 1995). Feral cats showed an avoidance response to both canid species. Other studies which have included felid/canid interactions have also found less intense interactions than those reported between members of the Canidae (Major and Sherburne, 1987; Fedriani *et al.*, 2000).

Artificial water points may facilitate competitive interactions between carnivores in arid regions, with mesopredators actively avoid areas surrounding water resources when there is a perceived high risk of interaction with larger predators (Valeix *et al.*, 2008). However, while findings from this chapter indicate that mesopredators avoided areas around water points occupied by dingoes overall (and did so consistently across years of varied rainfall and prey availability), the study did not examine any detailed difference in avoidance patterns between permanent and non-permanent waters.

The strength of competitive interactions between predators may also fluctuate with season or other environmental influences. For example, variability in prey abundance and water resource availability, driven by seasonal change or by extreme climatic events, may increase or decrease competitive interactions. During drought, when predator populations are under resource stress, competitive interactions may increase substantially. In contrast, during periods when surface water is plentiful and prey widespread, reliance on permanent water points may lessen and lead to less spatial segregation between predator species. It may be that while dingoes are highly effective in limiting mesopredator access to permanent water points, an increase in the availability of surface rainwater during 'good' years may allow the smaller predators to redistribute across the landscape and avoid encounters with dingoes.

Ranging and hunting behaviours of dingoes may also play a role in limiting access to water by mesopredators. Competitive interactions between dingoes and mesopredators may be dependent on dingo spatial and temporal activity, with mesopredator access to water points restricted only when dingoes are locally present (Catling and Burt, 1995; Mitchell and Banks, 2005). In arid and semi-arid landscapes, predators tend to occupy areas surrounding permanent water points as they provide both reliable access to water and a focused search area for hunting, as prey species also aggregate around water (Valeix *et al.*, 2010). In arid areas of Australia, access to water is an important factor determining dingo spatial distribution; dingoes rely heavily on surface water for survival when prey is scarce. Even when prey is plentiful dingoes are rarely more than 5 km from water (Corbett, 1995). While predation may not necessarily occur at the water point (Rosenstock *et al.*, 2004), by targeting prey within close vicinity (2 – 5 km) of water (Shepherd, 1981), search effort is reduced and energy efficiency of the predator is maximised. In times of low prey availability, dingoes may disperse further away from permanent waters to meet metabolic needs and adequate energy intake. Their absence during hunting forays may allow mesopredators increased temporal access to water points.

The spatial distribution of reliable water points at a site is therefore likely to be important for predator interactions. At pastoral sites where dingoes are heavily controlled south and to the east of the DBF, the predominant land use is sheep grazing and the average distance between watering points is from 5.5 to 7 km (James *et al.*, 1999). Such uniform water distribution would provide easy access to water for most fox individuals, with daily movements rarely exceeding 10 km (Saunders *et al.*, 1995). At sites where dingo populations remain north and to the west of the DBF the major livestock grazing enterprise is cattle and the average distance between water points is around 11 km (James *et al.*, 1999). Larger distances between waters mean that there is less overall area close to water points. With areas within 2.5 km of water points dominated by dingoes, reduced access to permanent water may lead to lower densities, lower reproductive rates and lower juvenile survival in mesopredator populations.

6.4.2 The role of artificial water points in facilitating competitive interactions between predators

Through avoiding areas surrounding water points which are dominated by dingoes, mesopredators may experience a substantial reduction in access to water resources. While foxes and feral cats can exist with little surface water (Dell'Arte and Leonardi, 2007; Paltridge *et al.*, 1997; Paltridge, 2002) and gain enough water intake through adequate and selective prey intake (Dell'Arte and Leonardi, 2009), access to artificial water points is likely to reduce physiological stress and enhance survival in arid landscapes. Reduced access to water may lower survival rates and population densities of mesopredators over the long term.

The results of this study suggest artificial water points may play a key role in facilitating competitive interactions between dingoes and foxes in arid Australia. The role artificial water points play in facilitating interactions between dingoes and feral cats is less clear. In addition to avoidance behaviour, feral cat distribution may be strongly influenced by environmental factors or site-specific characteristics, such as proximity to adequate habitat and shelter (see Chapter 5). Previous studies on the habitat use by feral cats in the arid zone show a preference for sheltered habitats with dense vegetation cover (Edwards *et al.*, 2002; Molsher *et al.*, 2005; Moseby *et al.*, 2009) which are suited to stalk and ambush hunting methods and may also provide shelter from larger predators. A lack of vegetation cover close to water points may reduce feral cat activity in these areas.

Through reducing mesopredator populations, dingoes may also indirectly minimise the impact of mesopredators on native prey. Avoidance mechanisms that change spatial behaviour of mesopredators in response to dingo presence around water resources are likely to influence spatial predation patterns. As a result, the presence of dingoes in areas surrounding artificial water points may have positive flow-on effects to local prey species susceptible to fox predation (Sabo and Power, 2002). Dingoes, through creating refugia around water points, may be critically important for the survival of some native arid zone species where artificial watering points exist.

It follows that the removal of dingoes may have the unintended consequence of encouraging mesopredator predation on native fauna. Ground baiting of dingo populations is often conducted around water points (Twigg *et al.*, 2001). The removal of dingoes from such areas may lead to increased mesopredator access to water and local activity. While 1080 baiting may also reduce fox populations, it is likely that with dingo activity centred around water points, dingoes would be most susceptible to baiting activities around water. If baiting activities removed dingoes with little impact on fox populations, foxes would be able to occupy areas surrounding water points and exist at much higher densities, increasing predation pressure on prey species in the absence of dingoes. If non-target baiting also reduced fox densities, in the absence of the larger predators feral cats may have more opportunity to target birds and other small prey such as reptiles and small mammals that frequent artificial waters.

While the preservation of dingoes across arid regions may be beneficial to some native species, such as small mammals (Letnic *et al.*, 2009a; Letnic *et al.*, 2009b), birds and reptiles, others may be at a disadvantage. For example, predation on macropods by dingoes is often focused around water resources (Shepherd, 1981). A further consideration is that livestock grazing and activity, which is often focal around water points, leads to trampling, dust and a reduction in vegetative cover in these areas (see review in James et al. 1999). Little is known about the impact of dingoes on livestock grazing patterns, but it may be that dingoes act to moderate the impact of foxes and feral cats on native species already vulnerable to predation through habitat loss.

There has been debate in Australia over the benefits of limiting watering points in the arid zone to increase the amount of water remote areas for the purpose of biodiversity conservation. For the conservation of native biodiversity, it may prove beneficial to maintain intact dingo populations due to their suppressive effect on mesopredators. The results of this study highlight the importance of including predator-prey and predator-predator spatial interactions in such management discussions and analyses.

Chapter 7: Temporal visitations and behaviour of dingoes, foxes and feral cats under different dingo management strategies

7.1 Introduction

Behaviour of species and individuals have wide-reaching consequences in ecosystem function (Schmitz *et al.*, 2008). Animal behaviour may be a major shaping force in structuring species assemblages (Dawkins and Krebs, 1979; Palomares and Caro, 1999), yet is often overlooked in many ecological studies. Studies on competitive interactions within predator guilds have reported effects on the distribution, abundance and population dynamics of both predators and prey populations (Holt and Polis, 1997; Linnell and Strand, 2000; Palomares and Caro, 1999). As such, intraguild interactions have important implications for the behaviour, ecology and long-term demographics of sympatric carnivore populations (Linnell and Strand, 2000) and may exert a broader influence on trophic cascades within ecosystems and communities (Switalski, 2003).

Mesopredators may suffer reduction in feeding times and poorer hunting success, leading to reduced densities and increased mortality, through behavioural interactions with a more competitive, dominant predator (Creel and Creel, 1996; Durant, 1998; Linnell and Strand, 2000). Vulnerability of mesopredators to interspecific competition may be reduced through changes in mesopredator behaviour and activity patterns (Switalski, 2003). Mesopredators may partition the use of shared resources across different dimensions to avoid competitive interactions, including changing their use of habitat or geographical area (space), food-type (diet) and activity budgets (time) (Schoener, 1974).

Competition avoidance is a common cause of temporal partitioning in activity between dominant and subordinate species (Hayward and Slotow, 2009). While temporal partitioning of a niche space is a less common method of avoidance employed by species in general, it is more frequently encountered between predators (Schoener, 1974). Temporal activity of predators may evolve through the influence of a number of factors (Hayward and Slotow, 2009). One driving force is maximised hunting efficiency and prey capture rates, targeted to the activity patterns of favoured prey species. However, subordinate predators with low competitive ability may avoid areas with dominant predators due to risks of decreased fitness even when prey density is high (Creel and Creel, 1996; Mills, 1993). Sympatric predators that share a high dietary overlap, and thus similar optimal hunting times, are at increased exposure of interference competition. Under such circumstances, mesoporedators may instigate temporal partitioning as a means to facilitate coexistence with the apex predator(s) (Fedriani *et al.*, 1999). Temporal partitioning away from optimal hunting times would, however, only be advantageous to the subordinate predator if the risk of attack during feeding was significant enough to limit capture rates of prey (Schoener, 1974).

Most interspecific competition occurs at carcasses (Gese *et al.*, 1996) and in poorer environments where food and water may be limited, increasing the potential for interactions (Scheinin *et al.*, 2006). The presence of dingoes, the apex predator in Australian arid ecosystems, may initiate avoidance behaviours and increase vigilance in smaller predators (foxes and feral cats), thereby restricting mesopredator access to shared resources such as carcasses or watering points when dingoes are present.

While the previous two chapters examined spatial partitioning between dingoes, foxes and feral cats, this chapter explores partitioning of temporal activity as a possible mechanism used by mesopredators to avoid interactions with dingoes. To examine the effect of dingoes on shared resource use and temporal activity of mesopredators, I ask the following question:

- How do different dingo management strategies affect the behaviour and temporal visit rates of dingoes, foxes and feral cats at shared resources?

Consistent with the theory that mesopredators may avoid or change their temporal behaviour in the presence of an apex predator (Polis *et al.*, 1989), it is hypothesised that dingoes will dominate shared resources at sites where they are present, while foxes and feral cats will temporally avoid dingoes and exhibit increased vigilance when accessing shared resources. Increased vigilance may include behaviours displaying increased alertness and/or reduction in total visitation time, in addition to a decrease in confident behaviours such as play and rest. Alternatively, at sites where dingoes are controlled, foxes and feral cats will increase visitations to shared resources and display more confident behaviours, such as increased visitation times and relaxed posture. If there is no effect of an apex predator (dingoes) on the behaviour of the smaller predators (foxes and feral cats) then temporal visitations by foxes and feral cats at shared resources will not vary between dingo management strategies, and confident behaviours (less vigilance) will be uniformly displayed across all sites.

7.2 Methods and Data Analysis

To address this question, temporal visit rates and behaviour of dingoes, foxes and feral cats at shared resources were monitored at sites with different dingo management strategies. Study site details are covered in Chapter 2.

Predator temporal visitations and behaviour were recorded using a combination of observational methodologies, including automated thermal video, still digital cameras and direct (human) observation. Data on temporal visitation rates was collected using all three methods, while behavioural data were only collected from the automated thermal video.

Observational data are difficult to obtain on carnivore species, due to their large home ranges, predominantly nocturnal habits and shy, cryptic natures. Due to such limitations for data collection, a new method for collecting behavioural data was developed specifically for this study. Details of this new method, automated thermal video recording, including hardware, software and system design, are given in Chapter 3, thus only a brief summary of the application of this sampling method is included here.

A further method, not included here, of assessing shared resource use by counting predator tracks at water points (Best *et al.*, 1974) was trialled but was not continued due to trampling of pads around waters by domestic stock.

7.2.1 Automated thermal video recording

Predator temporal visitations and behaviour were monitored using a thermal video camera, a device similar to a normal video camera that records heat, not light. The camera was programmed using a remote system designed to activate video recording when animals of interest (that is, feral cats, foxes and dingoes) came into its field-of-view (see Chapter 3 for details of hardware and software design).

Data were collected using the thermal video camera at two study sites: Sturt National Park and Finniss Springs. Details of these study sites are given in Chapter 2. Sturt National Park, being south of the dingo fence, has no or few dingoes, in comparison to Finniss Springs, where dingoes are uncontrolled. Thus Sturt National Park is hereafter referred to as the 'no dingo' site, and Finniss Springs as the 'dingo' site.

At each study site, the thermal video camera was placed near a shared resource (water points and carcasses) to monitor predator visitations, interactions and broad behaviours displayed at the resource. The camera was set up during the evening and functioned though the night, until sunrise. This meant data collected by the thermal video camera was restricted to nocturnal activities of the predators, from approximately 8pm through to 7am.

Predator temporal visitations and behaviour at shared resources were monitored for three nights at each site using thermal video. At the completion of sampling, thermal video recordings were reviewed for predator visitations. For each predator species, visitations were categorized by hourly timeframes and study site. Data from all three nights were then combined, and standardised as the number of individual visitations per sampling hour for each species. Observations were also made on the length of time between species visitations on each sample night, although no analyses were conducted due to limited data.

7.2.1.1 Assessment of behaviour

Behaviours displayed in thermal video images were categorised into 'confident' behaviours or 'vigilant' behaviours, based on an approach by Switalski (2003). An individual animal was considered 'confident' if it displayed the following behaviours: relaxed walking/wandering or eating, resting (including sitting, sleeping and lying down), grooming, digging/scratching and playing/interacting with other individuals. Increased vigilance behaviours included running, alert postures (such as lifting the head in an alert manner while feeding), agitated movements, stopping to survey surrounds, cautious approach and cautious sniffing.

The time spent at the resource for each individual was also estimated from the recordings. An individual appeared more confident if they spent greater than two minutes in the area surrounding the lure without displaying increased vigilance behaviours. An individual at a lure that displayed increased vigilance behaviours was usually present less than two minutes in the area surrounding the lure. Two minutes was a time chosen by the author's judgement, as most individuals that displayed confident behaviours remained in the lure vicinity for a longer period of time.

7.2.2 Infrared digital cameras

Infrared digital cameras (often referred to as camera traps or remotely-triggered cameras) (Figure 7.1) were used to monitor temporal activity of predators and visitation rates to shared resources at all five of the study sites (see Chapter 2). These data were intended to supplement the behavioural information collected with the thermal video camera (see Chapter 3). Infrared digital cameras such as these have been used with some success to monitor behaviour of cryptic and shy species (Claridge *et al.*, 2004; Moruzzi *et al.*, 2002).

Three remotely triggered digital cameras (Talon Basic® model) were set up in each sampling area at either food lures (carcasses) or watering points, and then left at the same sampling point for up to 10 days. All three cameras were continually operational in the field during all sampling at the study site, which varied from 2-4 weeks depending on the sampling year. The first year of sampling at all of the five sites site was of longer duration as sampling areas and sampling plots needed to be established.

The infrared digital cameras were attached to a branch or fence 7-10m from the lure and aimed using an internal laser beam. The cameras were activated through motion sensitivity, and collected still, black and white photographs labelled with time and date of the image. The digital cameras had a near-infrared flash to enable night photography with minimal disturbance to the predators. They were powered by six D-cell batteries and stored up to 60 pictures using a 64KB memory card.

As both the time and date were recorded, photographs supplied information on the temporal use of resources by different species. Data collected by these cameras also aided in assessing whether or not there was any overlap of individual dingoes between study areas, and also helped determine the number of dingoes at each study site, with individuals distinguished by size, colour and markings where possible. One photograph was counted as one visitation to the resource, and the visitation was categorized by species and time of visitation. For the purpose of assessing and comparing temporal visitations by predator species, sites were classified as either 'dingo' (dingoes present: Bollards Lagoon, Quinyambie Station and Finniss Springs) or 'no dingo' (dingoes absent or very low density: Sturt National Park and Mundowdna Wilpoorina). As with the thermal video data, visitation times were categorized into hourly timeframes for each predator species at dingo and no dingo sites. Data were combined over years.

Figure 7.1 Digital camera used for collecting predator visitation data.

7.2.3 Direct Observation

Direct observation was conducted opportunistically during other field activities, including during recording with the thermal video camera (see Chapter 3), but also during other sampling, such as spotlighting and checking of scent stations and transects. However, data collected by direct observation during the use of thermal videos (in human observation thermal video efficiency comparisons, see Chapter 3, section 3.5.2) could not be used in this analysis as it was only conducted at one site (Sturt National Park).

At both Sturt National Park and Finniss Springs, spotlighting was conducted for three consecutive nights in two sample areas during both sampling years. Details of this method are covered in Chapter 2, section 2.3.2.1. Spotlighting was conducted for a total of 12 nights at each study site. While spotlighting has been found to be a less accurate method for measuring predator density (Sharp *et al.*, 2001) than for prey species, and was therefore primarily used for estimating prey activity in this study, any opportunistic observations of predators at shared resources were recorded. When a predator was identified by green eye-shine, the vehicle was stopped and binoculars used to identify the species. In some cases, the location was marked and the following day tracks were sought to confirm correct species identification. Both the predator species and time of activity were recorded. Opportunistic observation data collected by spotlighting was combined over nights and over years.

As spotlighting was only conducted over a 2-3 hour period during the evening (usually between 9pm and 12am), it represented a restricted time period to collect data on temporal activity. As such, opportunistic observation was also conducted during other sampling and field activities, such as checking of scent stations and transects. At each field site, 40 scent stations and 30 transects were established across two sample areas and checked for three consecutive mornings in each sample area. Typically, data collection was carried out from 6am through until around 11am. This meant a total of 8 mornings per study site per sampling year, which including three sampling mornings plus one morning for setting up sampling units in the study area.

As with data collected by digital cameras, sites were classified as either 'dingo' (dingoes present: Bollards Lagoon, Quinyambie Station and Finniss Springs) or 'no dingo' (dingoes absent or very low density: Sturt National Park and Mundowdna Wilpoorina), and visitation times were categorized into hourly timeframes for each predator species at dingo and no dingo sites. Data were combined over years.

Due to the difficulties of gathering data on predator behaviour, *n* was small for data sets collected by each individual method. As such, observational data from all methods were combined and exploratory data analysis conducted. Through combining data it was hoped that a broader sample of temporal activity would be captured for a more complete picture of temporal activity of each species.

7.3 Results

A total of 38 dingo, 365 fox and 3 feral cat visitations to lures were recorded by automated thermal video. A further 105 dingo, 68 fox and 26 feral cat visitations were recorded by other methods.

7.3.1 Temporal visitations at a shared resource

For temporal visitation assessment, data from all observational methods were combined. Results for temporal visitations are based on a total of 143 dingo visitations, 433 fox visitations and 29 feral cat visitations to shared resources. Results were graphed firstly by predator species (Figure 7.2a-c) and then by site characteristics (dingo or no dingo: Figure 7.3a and Figure 7.3b, respectively)

Dingoes were found to be active at shared resources throughout the day, with the exception of the afternoon period from noon until 4pm, when no visitations were detected. Most dingo visitations were detected between 8pm and 12am, with a peak in activity at 10pm. A second peak in activity then occurred at 3am, with visitations to shared resources reducing from 6am (Figure 7.2a).

Temporal visitations of foxes to shared resources appeared to be more restricted than those of dingoes. At sites without dingo populations, foxes became active around 9pm and visitations steadily increased toward a peak at 11pm. As with dingoes, a second peak in activity was found between 1am and 2 am, with a steady decline in visitations until 6am, after which fox activity appeared to almost cease. At sites with dingoes, very few foxes were recorded at shared resources (n= 10), however as with sites with no dingoes, these foxes appeared to be most active from 9pm until 11 pm (Figure 7.2b).

While some dingoes and foxes were found to be active during daylight hours, feral cat temporal visitations to shared resources were exclusively nocturnal. Feral cats were detected at shared resources from 7pm at night through until 1am in the morning, with a distinct peak in activity at 10pm for both dingo and no dingo sites. Feral cat activity was similar between dingo and no dingo sites, with two major differences. Firstly, the peak in visitations at 10pm was found to be much more pronounced at sites with dingo populations. However, while there appeared to be a distinct lack of feral cat visitations at shared resources at 9pm at no dingo sites (Figure 7.2c), low sample sizes limits the ability to draw inference regarding dingo or fox avoidence from these results.

When comparing temporal visitation rates of all three predators at sites with and without dingo populations, the differences in visitation rates for both dingoes and foxes vary greatly. In the absence of dingoes, fox visitations to shared resources increased 20-fold to almost 120 visitations within a two hour period (from 10pm until midnight), in comparison to only 5 visitations recorded at dingo sites (Figure 7.3a, b). Conversely, feral cat visitations to shared resources decreased, although marginally, at no dingo sites.

The limited data from thermal video recordings taken at Finniss Springs suggest that both feral cats and foxes temporally avoided attending resources when dingoes were present. At Finniss Springs, a fox was recorded at a carcass approximately two hours after dingoes had finished feeding on it. At the same site a feral cat attended a carcass three hours prior to dingoes visiting the same lure. At Sturt National Park, in the presence of foxes and no dingoes, feral cats attended the shared resource (large dam) in the presence of foxes, but did so when fewer foxes were at the site, and from the opposite approach angle to where foxes were at the time of visitation (authors' personal observation).

7.3.2 Behaviour at a shared resource

Behavioural results are given for automated thermal video visitations only. There were too few feral cat observations from thermal video recordings (n=3) to construct comparative graphs in the behavioural analysis. However, all three behavioural results for feral cats showed cautious vigilant behaviour, including the two feral cats recorded at sites with no dingoes, and the feral cat observed at a site with dingo populations. Only one fox recording was captured on automated thermal video at the dingo site, and this individual also displayed uniformly vigilant behaviour.

When dingoes and foxes were alternatively 'top predator' at a site, they displayed similar proportions of confident and vigilant behaviours (Figure 7.4a, b). Approximately 10% of total behaviours recorded for both predators were vigilant, while most (approximately 90%) were categorised as confident. Confident behaviours recorded included walking, feeding, resting, scratching, interacting with other individuals, investigating the area (both species), feeding lying down (dingoes only) and sleeping (foxes only). Vigilant behaviours recorded included alert postures (such as raising the head in an alert manner while feeding), a cautious approach and cautious sniffing (both species), agitated movements, running and stopping to survey surrounds (foxes only). Dingoes and foxes sometimes displayed both confident and vigilant behaviours in a single visitation, while feral cats displayed vigilant behaviours only.

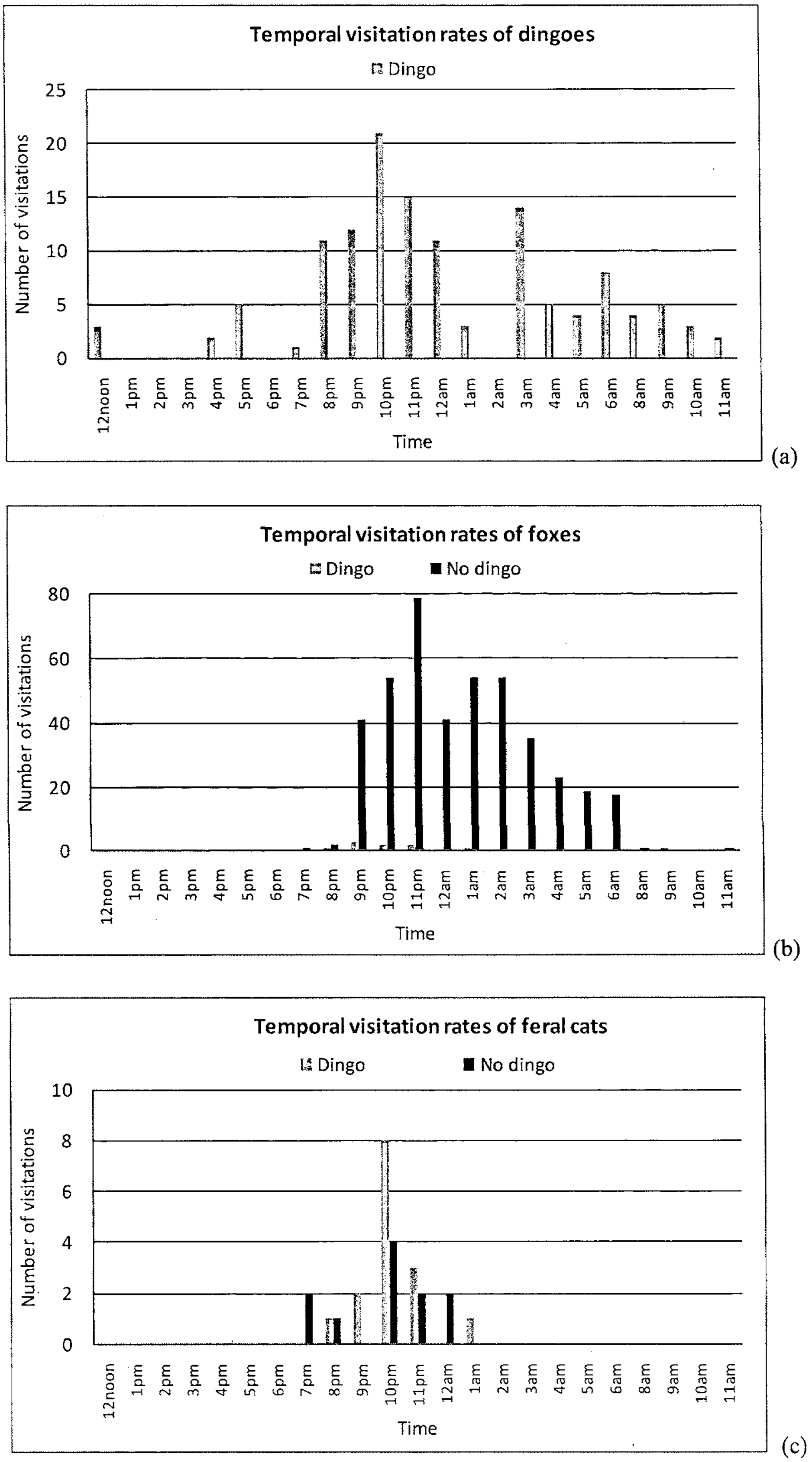
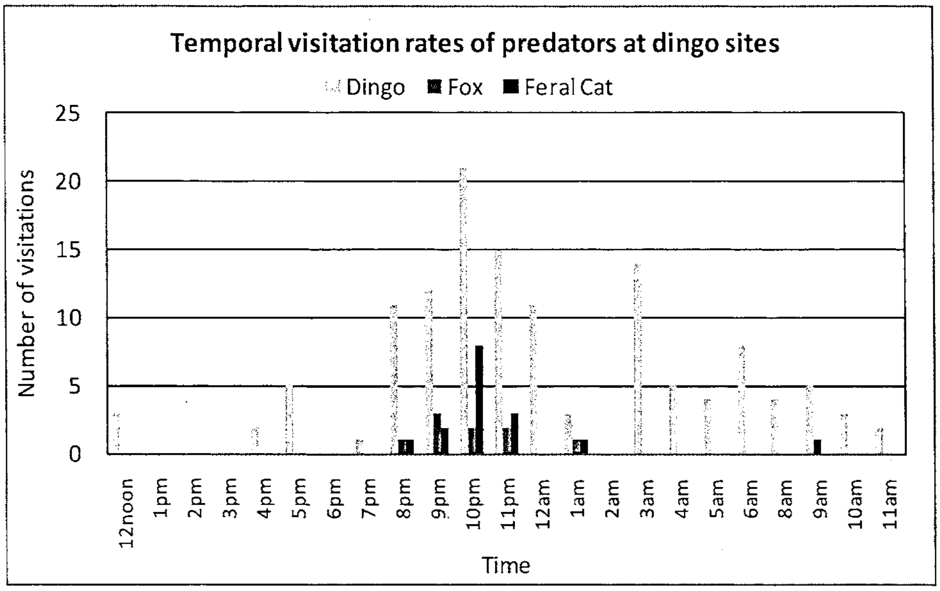
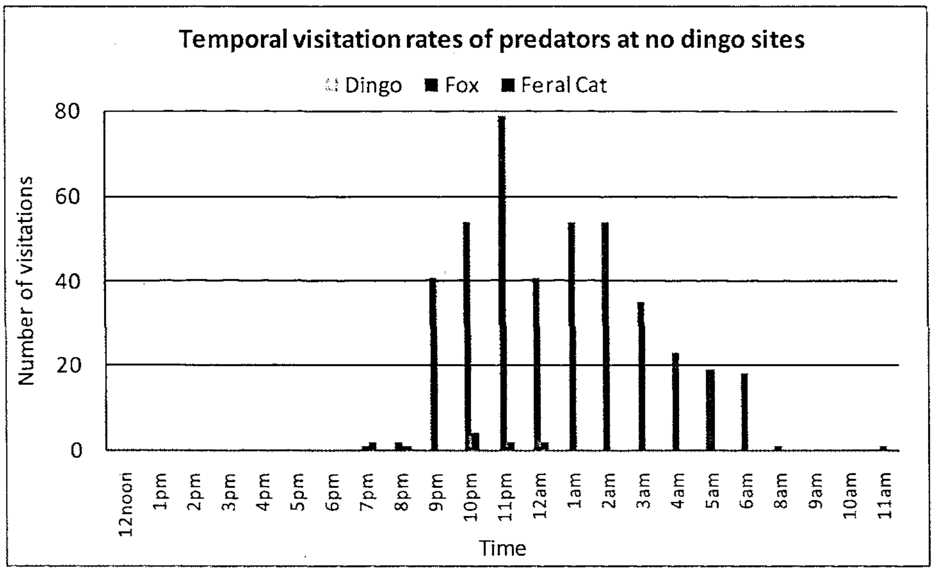


Figure 7.2 (a-c). Temporal visitation rates of dingoes (a), foxes (b) and feral cats (c) to shared resources at dingo and no dingo sites.



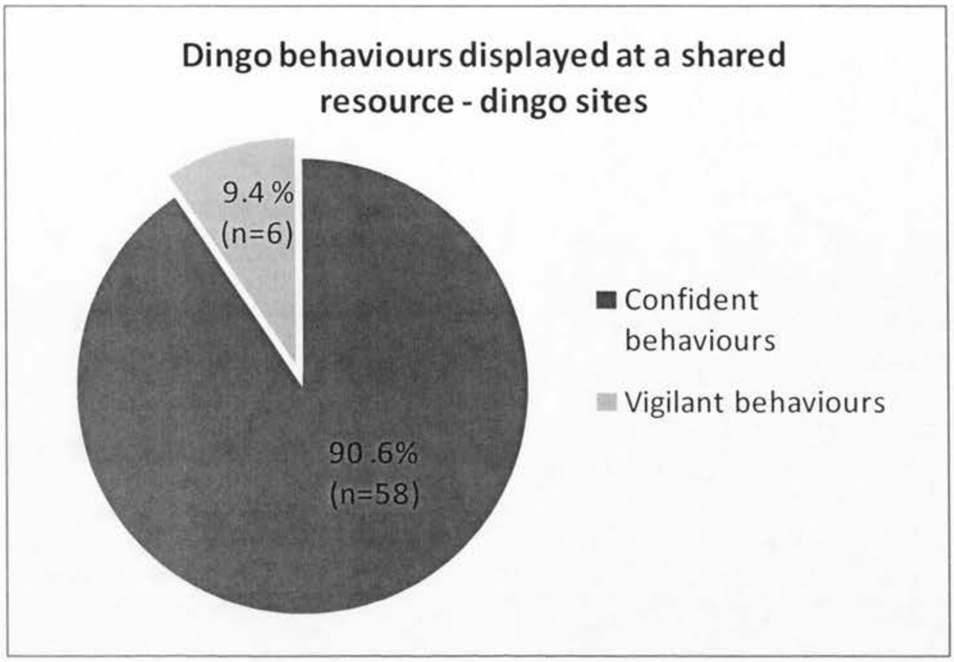
(a)



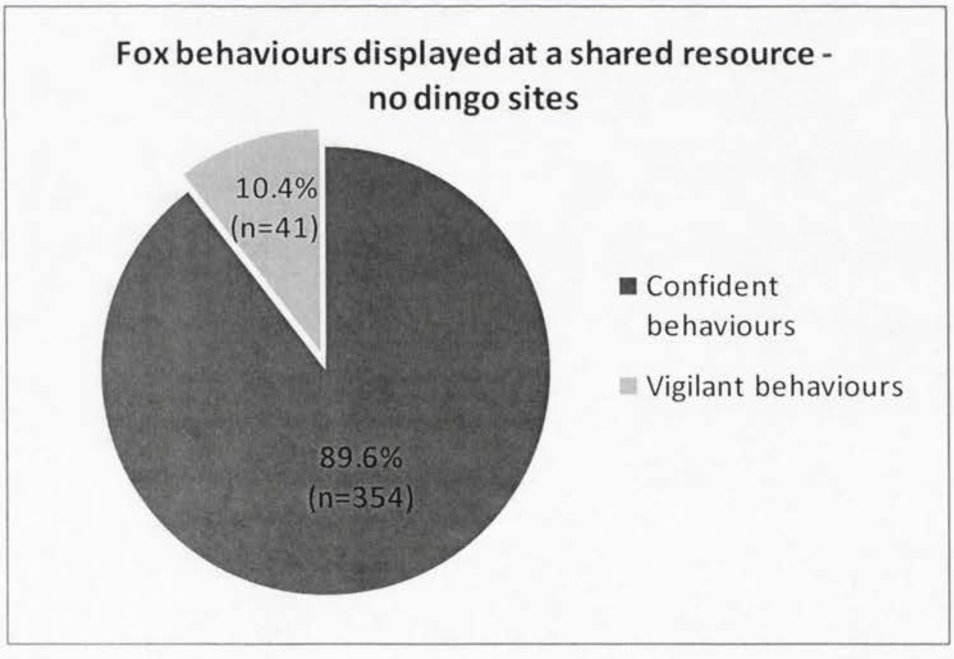
(b)

Figure 7.3 (a, b). Temporal visitation rates of three predators to shared resources at dingo (a) and no dingo (b) sites.

Foxes were recorded attending water resources in large numbers (up to 5 individuals interacting at one time) but attended food resources only as individual animals. Dingoes were only recorded in singles or pairs at both carcasses and water, while feral cats were always recorded singly.



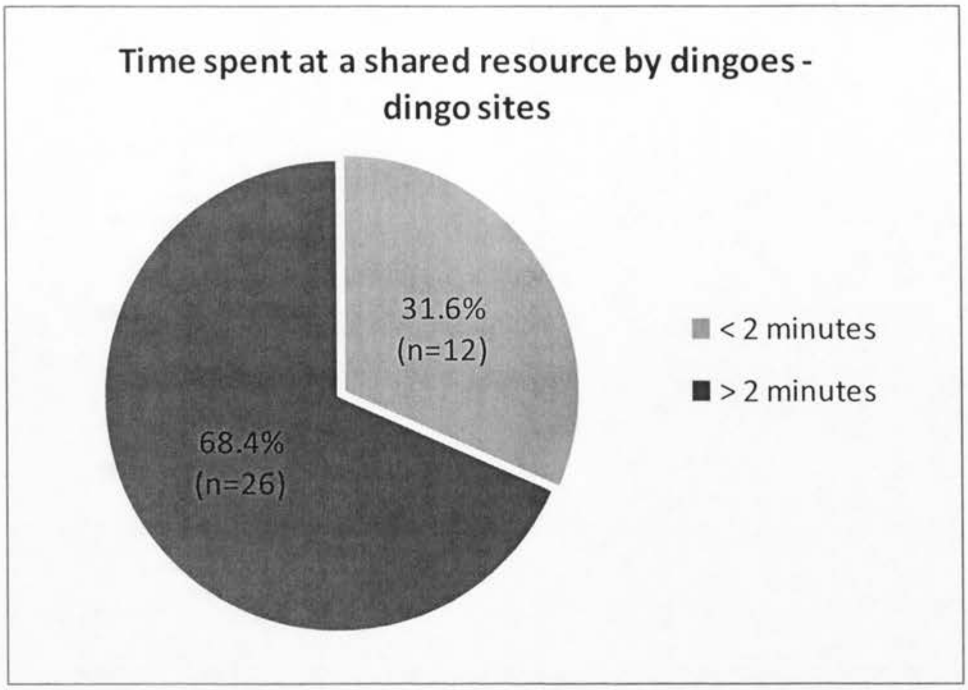
(a)



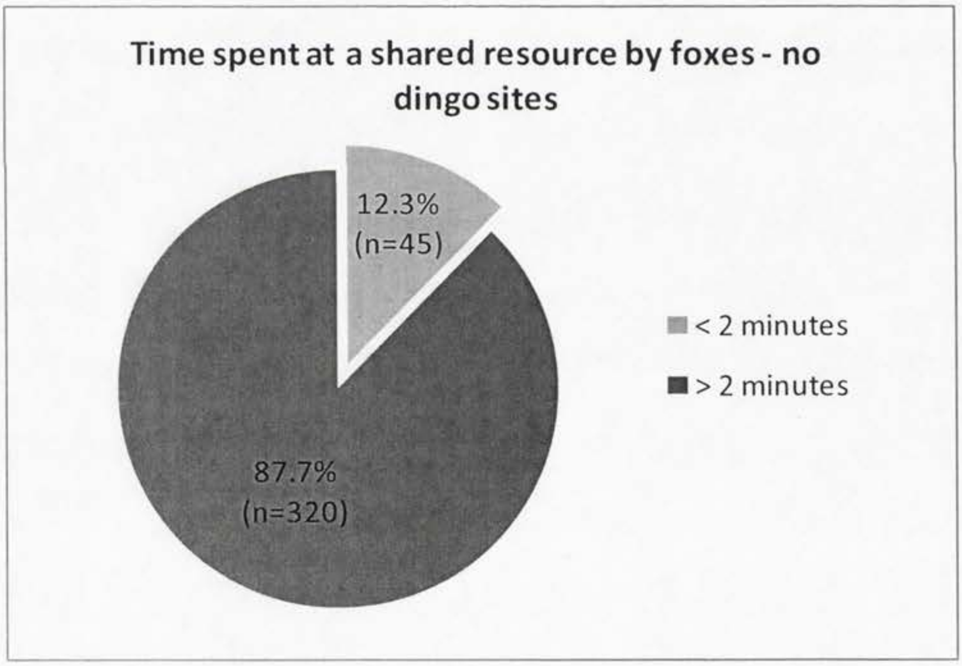
(b)

Figure 7.4 (a, b). Behaviour of dingoes and foxes at shared resources, including confident vs. vigilant behaviours.

Results shown only for sites where (a) dingoes and (b) foxes are the dominant predator, respectively.



a)



(b)

Figure 7.5 (a, b) Time spent at a shared resource by (a) dingoes at sites where they were present and uncontrolled and (b) foxes at no dingo sites.
Results shown only for sites where (a) dingoes and (b) foxes are the dominant predator, respectively.

One third of dingoes (31.6%) were found to spend less than two minutes at the shared resource, compared to only 12.3 % of foxes (Figure 7.5a, b). The average time spent at a resource by dingoes at dingo sites was 5.5 minutes, with a median duration of 2.5 minutes. The longest recorded time for an individual dingo at a resource for any one visitation was 26 minutes. The average time spent by foxes at a shared resource at dingo sites was 6.2 minutes, with a median duration of 4 minutes. The longest recorded time for an individual fox at a resource for any one visitation was 101 minutes, where the individual was seen to drink, explore, sleep and interact with other individuals.

7.4 Discussion

7.4.1 The effect of dingo management on predator visitation rates to shared resources

Dingoes were found to have the broadest activity patterns, with visitations detected at resources throughout most times of the day. Foxes were more restricted in their activity; only a few individuals were detected visiting resources during daylight hours. Limited data on feral cats showed them to be exclusively nocturnal in their visitations to shared resources. All three predators shared a common peak activity period between 9pm and midnight.

Dingoes maintained some activity throughout the day. This was somewhat unexpected given the high diurnal temperatures at the study sites during sampling (summer). The most probable explanation for these results was that dingoes often rested close to water, and were observed sheltering in the coolness between watering tanks as well as swimming in the dams on a number of occasions (Figure 7.6). By remaining in close vicinity to water, dingoes have regular access for drinking as required during the hotter parts of the year. Water points may also provide dingoes with increased opportunity to target prey species as they accessed water resources. Such continual occupancy of areas surrounding water would have increased detection of dingoes by cameras placed around water points during this study.

Figure 7.6 A dingo cooling off in a watering point at Bollards Lagoon
(Photo R. Brawata 2006)

While dingoes were recorded at shared resources during the day, most visitations to shared resources occurred in the early night hours, prior to midnight, with a second peak of activity in the early morning hours. Dual activity peaks have been found previously, with dingoes active during similar time periods as found in this study (8-11pm, then 4am-7am: P. Bird, unpublished data). However temporal activity patterns may also be site-specific (P. Bird, unpublished data). The reason for differences in temporal activity patterns of dingoes is unknown, but may be associated with the activity of their prey or anthropogenic influences at the study sites (Beckmann and Berger, 2003).

Foxes were less active during the day than dingoes, even when dingoes were not present, and did not show such pronounced peaks in activity during the night. Temporal visitations to shared resources by foxes were more constant than those of dingoes over a six-hour period from 9pm – 3am. Fox activity patterns recorded at a shared resource in a different study, carried out at a site with dingoes in the arid zone (Lake Eyre) found a peak in activity from 1-3am (P. Bird, unpublished data.). During the same study, dingoes were observed chasing foxes away from water resources (P. Bird pers. comm. Feb 2006).

At Sturt National Park, foxes came to the water point throughout the night, often in pairs and sometimes in interacting groups of up to 5 (authors personal observation). Early in the evening foxes came mainly to drink, and then left again, presumably to hunt. In the early morning hours, the number of fox visitations appeared to decline, but those foxes recorded at the water point spent more time exploring and interacting. It is probable that many of the individuals recorded during this time were returning for a second or third drink before the heat of the day. At Sturt National Park, thermal video recordings were conducted at the only water resource available for more than 100 km (Quartpot Tank). Here, forays by foxes would have been greatly restricted to areas surrounding the dam. The aggression associated with typical social/territorial encounters between individual and family groups of foxes appeared to be minimal in the immediate vicinity of the water. However the chance of aggressive encounters may have prevented foxes from hunting extensively in the area surrounding water points (White and Harris, 1994).

In this study, sample sizes for visits to resources by foxes in the presence of dingoes and feral cats at all sites were too small to draw strong inferences about temporal interactions, but some general observations were made. Results suggest that both feral cats and foxes temporally avoided attending resources when dingoes were present, and feral cats locally avoided foxes when temporal avoidance was not possible. Furthermore, a direct observation of a feral cat at a water resource fleeing from dingoes when they came into view (author's personal observation), indicates that it is probable that feral cats also actively avoid dingoes on a local scale. Other studies have reported incidents of aggressive encounters between dingoes and foxes (Marsack and Campbell, 1990) and foxes and feral cats (Read and Bowen, 2001). Evidence from diet studies has found direct predation of feral cats by dingoes (Marsack and Campbell, 1990)..

Feral cat visitations to resources did not appear to differ with dingo management. Interspecific competition appears to be strong between foxes and dingoes, but interactions were not so evident between dingoes and feral cats. This may have been due to larger differences in body size and taxonomy (Gehrt and Prange, 2007). However, this result may also have been due to low feral cat activity in general and the difficulty of enticing feral cats to lures (low sample size). One curious difference in feral cat activity between sites with and without dingoes was the distinct lack of activity of feral cats around 9pm at no dingo sites. While it may have been solely a lack of data that left this gap, it is interesting to note that fox activity rose significantly at this time, and such a result may therefore be indicative of avoidance of foxes by feral cats. It was also noted that feral cat activity increased on nights when dingo activity was much lower, even though the same habitats (creek lines) were commonly used (author's personal observation, see Chapter 5).

7.4.2 The effect of dingo management on predator behaviour at shared resources

Due to minimal data, including very low visitation rates of foxes at dingo sites, and very low visitations by feral cats at both dingo and no dingo sites, it is difficult to determine the effect, if any, of dingo management on predator behaviour at shared resources. However, the absence of foxes and feral cats from shared resources at sites with dingo populations may be an indication in itself that mesopredators may actively avoid encounters with dingoes.

Dingoes attended lures in singles and pairs (Figure 7.7), while foxes were recorded at lures in singles (Plate 7.4), pairs and groups of up to 5 individuals. Both species displayed similar proportions of confident and vigilant behaviours when they were top predator at each site. While most behaviours were classified as confident (90%), vigilant behaviours were still displayed. Vigilance behaviours, such as scanning the surrounds, may serve to lower the success rate of an attacking larger predator by giving subordinate predators time to escape (Switalski, 2003). The presence of vigilant behaviours in the absence of a superior competitor, such as displayed by foxes at Sturt National Park and dingoes at Finniss Springs, may be for other purposes, including guarding against conspecifics or anthropogenic threats.

At Finniss Springs, where dingoes are the apex predator, fox visitation rates to shared resources were dramatically reduced compared to sites without dingo populations (Sturt National Park and Mundowdna Wilpoorina). Only one fox was recorded at a shared resource during the entire sampling period. Such a result could lead to a conjecture that such a low visitation rate by foxes is the result of lower fox densities at Finniss Springs in comparison to no dingo sites. However, moderate fox activity was recorded at Finniss Springs during the same sampling period (see Chapter 4). Low temporal visitation rates by foxes therefore do not appear to reflect recorded fox activity at the site; foxes visit shared resources less often than fox activity would suggest. This result indicates that in the presence of a dominant predator (dingo), foxes may actively avoid using shared resources. Supporting this interpretation, mesopredators showed no confident behaviours in the presence of dingoes, and the few thermal video recordings from Finniss Springs also revealed that mesopredator visitations at lures were separated from dingo visitations by a number of hours.

Bird (1995) monitored dingo behaviour around water points at three study sites in arid South Australia (Lake Eyre, Quinyambie Station and Frome Downs). He found dingoes used the same defined pathways to access water, showing a preference for certain approaches to drinking sites. Dingoes spent 3-6 minutes drinking and then spent time investigating the surrounding area. Dingo activity around water points appeared to be influenced by a combination of population density, seasonal conditions and food availability, with an increase in activity at waters during periods of high dingo densities and lower prey availability (Bird, 1995). Similarly, the average time spent at resources by dingoes in this study was 5.5 minutes, but almost one third of individuals spent less than two minutes at a resource (usually a carcass). While it has been suggested that territoriality may prevent dingoes foraging extensively around resources (Bird, 1995), a review of thermal video footage revealed that disinterest or repeat attendance rather than vigilance meant that some confident individuals, particularly dingoes, left the vicinity of lures within a two minute time-frame (see section 7.4.4 of this chapter) .

7.4.3 Temporal and behavioural responses in sympatric carnivores

Temporal avoidance and increased vigilance have been found in other sympatric carnivore species. Studies of intraguild competition and predation for predators of the African savannah have found evidence of temporal partitioning by subordinate carnivores to avoid interference competition and kleptoparasitism by dominant carnivores (Creel and Creel, 1996; Durant, 1998; Hayward and Slotow, 2009). While all of the predator species in such studies exhibited crepuscular behaviour (synchronised with prey activity to maximise hunting success), subordinate predators temporally avoided an area when dominant predators were in the immediate vicinity. Such localised avoidance behaviour (both spatial and temporal) by mesopredators was coupled with a reduction in mesopredator activity (Durant, 1998; Hayward and Slotow, 2009).

Encounters between sympatric wolves and coyotes have found that coyotes change their spatial movements and temporal activity budget (including time spent resting, feeding and on vigilance) to avoid encounters with wolves. Wolf abundance and the degree of wolf use of an area influenced coyote activity budgets, with more time spent on vigilance and less on rest, and an increase in nocturnal activities when wolves were present (Arjo and Pletscher, 1999; Berger and Gese, 2007; Switalski, 2003). Changes in coyotes activity budgets were particularly evident when wolves were present in the immediate vicinity (Switalski, 2003).

In the summer months, evidence suggests that dingoes focus their activity within 2.5km of water resources (see Chapter 6). In areas of higher productivity and prey availability, including supplementary prey such as livestock, dingoes may not be required to move far from water points to meet metabolic requirements. However at sites such as Finniss Springs, water resources are distributed further apart than those of pastoral properties, and both productivity and prey availability are lower (see Chapters 2, 4 and 6). In this situation dingoes may need to move further afield to find adequate food. Under these circumstances mesopredators may gain temporary access to shared resources (such as water points or carcasses) through employing a combination of temporal and localised spatial avoidance. Greater access to resources may in turn lead to an increase in mesopredator density and activity, despite decreased productivity. Through initiating avoidance behaviours, mesopredators are thus able to "fill in the gaps" between activities of dingoes, and are able to coexist successfully, albeit at low densities, with the larger, more dominant carnivore.

Figure 7.7 Still digital image of two dingoes visiting a water resource at Finniss Springs in the early morning
(Photo R. Brawata 2007)

The risk of encounters between mesopredators and dingoes may be influenced by a number of factors. For example, a certain age or social standing of individuals within the mesopredator population may make them more vulnerable to aggressive encounters with dominant predators Research has shown that aggressive interactions between wolves and coyotes involve predominantly young, transient coyotes. Wolves effectively reduced coyote densities through differential effects on survival and dispersal rates, (Berger and Gese, 2007). Gese *et al.* (1996) suggest age may also determine the vulnerability of red foxes to coyote predation.

Environmental conditions may also play a role in determining the risk of intraguild interactions, and consequently affect behaviour of mesopredators. Both moonlight (Mukherjee *et al.*, 2009) and visibility (Creel and Creel, 1996) have been shown to influence the ability of subordinate predators to detect the presence of dominant predators, and thus affect mesopredator temporal activity and behaviour.

Avoidance behaviour, including changes in daily activity patterns of mesopredators, may be influenced by season (Arjo and Pletscher, 1999; Johnson and Franklin, 1994). Johnson and Franklin (1994) examined daily activity patterns in sympatric grey foxes (*Dusicyon griseus*) and culpeo foxes (*Dusicyon culpaeus*) in Chile. While both species were primarily nocturnal, the subordinate grey foxes appeared to increase their daily activity in summer/autumn to avoid the dominant culpeo foxes, which are more active during winter and spring. Similarly, spatial separation of red foxes and coyotes is more pronounced during spring and summer, as foxes avoid breeding near coyote territories (Voigt and Earle, 1983). Seasonal avoidance has also been found in coyotes and wolves, where coyotes appear to have taken advantage of a change in wolf behaviour induced through anthropogenic influences. While wolves avoid humans during daylight hours, the more brazen coyotes have move into the temporal (diurnal) niche in order to successfully coexist (Carbyn, 1982).

Due to logistical restrictions in sampling design, this study was unable to examine the influence of season on avoidance behaviour by mesopredators under different dingo management regimes. Results presented in this study are for observations taken across three summer sampling sessions, when diurnal temperatures in the arid zone are high. An increase in diurnal activity for all three predators may be found in the cooler winter months and an increase in avoidance behaviour may be employed by mesopredators during breeding season. Future research should consider such seasonal changes in behaviour.

Mesoporedators may resort to fine scale spatiotemporal separation if temporal separation is not the optimal means to avoid encounters with dominant carnivores. While no evidence of temporal avoidance was found between coyotes and swift foxes, there was fine-scale spatiotemporal differences in activity patterns between the two species (Kitchen *et al.*, 1999). Coyotes travelled more during diurnal hours, while foxes remained closer to den sites during the day. Swift foxes have also been found to employ local avoidance behaviour to reduce antagonistic interactions with coyotes (White *et al.*, 1995). Cougars have also been shown to avoid areas used by wolves on a fine temporal scale, in that they allow more time to elapse before using locations where wolves had been (Kortello *et al.*, 2007). In the present study, feral cats were seen to access water resources in the presence of foxes, but did so when fewer foxes were at the site, and from the opposite approach to where foxes were at the time of visitation. One feral cat was also seen fleeing a water point only minutes before a dingo pack came into view (author's personal observation).

It has been suggested that foxes may respond to and actively avoid areas where dingoes have placed scent and territorial markers (Wallach *et al.*, 2009a). While such markers may provide effective means of intraspecific communication, there is little evidence from this and previous studies that avoidance behaviour by foxes can be attributed to such markers. Instead, captive mesopredators have been found to respond only to visual cues and the actual presence of the apex predator. These behavioural interactions have been found between Indian foxes (*Vulpes bengalensis*) and domestic canids (Vanak *et al.*, 2009) and between red foxes and golden jackals (*Canis aureus*) (Scheinin *et al.*, 2006). In both these studies, urine and scent did not appear to alter mesopredator behaviour, but the presence of a live apex predator reduced visitation rates to food resources as well as total feeding times, and greatly increased vigilance behaviour. This result suggests that mesopredators are able to coexist with the presence of an apex predator in an area, but avoid direct contact with them to reduce potentially lethal encounters (Scheinin *et al.*, 2006).

Figure 7.8 Still digital image of a fox visiting a shared resource (carcass) at Mundowdna Wilpoorina
(Photo R. Brawata 2007).

One problem with interpreting predator behaviour and temporal activity is that interactions between species are not always constant (see review in Linnell and Strand (2000). Changes in predator interactions, avoidance behaviour or activity patterns may be very subtle, even inconsistent. For example, Gese *et al.* (1996) noted that of 66 interactions recorded between red foxes and coyotes, foxes were tolerated in around half of all encounters, and deterred or displace in the others. Simple changes in activity in the dominant predator led to increased tolerance towards the mesopredator. Resting and travelling coyotes tolerated foxes more, while feeding coyotes were much more aggressive. The number of coyotes feeding also influenced whether foxes would avoid the area or not (Gese *et al.*, 1996).

Changes in the density of both predator and prey populations may play a part in determining behavioural interactions. Density of both apex and mesopredators may influence the encounter rate between the two and consequently the impact on mesopredator populations (Creel and Creel, 1996). When the density of top predators becomes lower, competition with conspecifics becomes more important when determining behaviours (Durant, 1998), such as between foxes at Sturt National Park in this study.

Prey availability may be another factor affecting behavioural interactions. Mesopredators may opt to utilise areas of lower prey density to avoid potentially dangerous encounters with apex carnivores (Durant, 1998). Alternatively, high prey availability may increase tolerance between predator species which compete for food resources.

The choice of spatial or temporal occupancy of an area by mesopredators may be a trade-off between the availability of prey and other resources (such as water) and perceived predation risk from apex predators (Mukherjee *et al.*, 2009). It is therefore probable that avoidance behaviour employed by mesopredators in the presence of dingoes may be both site and situation specific. In addition, temporal partitioning (Schoener, 1974) between sympatric carnivore species may be more subtle than significant changes in behaviour, such as altering peak activity times. It likely that most mesopredators, including foxes in this study, practice a blend of temporal and spatial avoidance (Durant, 1998) or "close proximity avoidance", where subordinate predators remain active at similar times, but actively avoid the immediate vicinity of dominant predator activity.

7.4.4 Methodological considerations

Behavioural data on carnivore species is difficult to obtain but is essential for studying trophic interactions. Understanding interactions between predators is challenging due to their low densities, large home ranges and cryptic, shy behaviour. Most modern studies that examine predator behaviour, particularly those that monitor habitat use and movement, use radio tracking (either GPS or VHF radio collars) to collect behavioural data (Mech and Barber, 2002). In addition, radio collars on animals are able to collect accurate information on home range size, some spatial interaction between individuals (Merrill and Mech, 2003), and whether individuals are active or resting (Mech and Barber, 2002). Radio tracking was not used in this study for three reasons. First, the method requires time and funding that were not available. Second, because of its cost the method is restricted to gathering data on only a few individuals, which may or may not interact. Third, radio tracking is unable to record detailed behaviour at a particular point in time and space (for example, defensive behaviours between species or individuals at food resources) (Anderson and Lindzey, 2003).

Due to the focus of this study, I selected methods suitable for recording detailed interspecific behaviours at a selected site. These methods, thermal video, still digital infrared cameras and human observation, also had limitations.

The thermal video had a limited field-of-view (FOV) of 10-15m around the lure point. When individuals entered the FOV they triggered recording, and when they exited, recording ceased (see Chapter 3). Using this method, when individuals moved out of the field-of-view of the camera even for a brief period, this would trigger separate recordings, many less than 2 minutes in length. In the case of dingoes, individuals would often leave the immediate area around the lure for a brief period, possibly to investigate surrounds, before returning to the carcass within minutes. Each visitation had to be classed as a separate visitation, due to the inability to recognise individuals. However, due to the territoriality of dingoes and lower dingo activity at Finniss Springs (see Chapter 4) it is likely that the same individual dingoes were attending lures repeatedly within the hour and at different stages during the night.

Still digital infrared cameras were used as a supplementary method in this study to record temporal visitations at lures. As only one thermal video was available, using still digital cameras enabled alternative lure sites to be set in different locations within the study area. However, the digital cameras used were found to be inefficient with a very low rate of capture (images) compared to visitations of species recorded at lures using print identification. This could be explained by the camera triggering too late to record the species and blank frames were consequently recorded. These inaccuracies meant that the same sampling effort at each site yielded very varying results, with many sites having few or no photographs and others with a substantial amount of data collected. The still digital infrared cameras had approximately 18% success rate during the course of this study; inaccuracies were not uncommon when using this method (see review in Henschel and Ray (2003).

Finally, there was limited ability to collect behavioural data on feral cats at lures. Feral cats were present at all sites, but appeared to avoid lures. Feral cats are notoriously difficult to entice with lures (Clapperton *et al.*, 1994; Edwards *et al.*, 1997). It is possible that feral cats were more active than detected and active for longer periods, but were not detected because they did not visit camera traps and scent stations as frequently as the other two predator species.

7.5 Conclusion

At sites where dingo populations are present, they dominate all shared resources (both food and water). Foxes and feral cats were still found at shared resources, but foxes did not use resources to the extent that their activity would suggest. In addition, foxes displayed an increase in vigilance behaviour at sites that contained dingo populations. Conversely, at sites with no or low dingo activity, foxes dominated shared resources and display predominantly confident behaviours. Therefore the results support the hypothesis that dingoes influence the behaviour of mesopredators. It follows that human manipulation of dingo populations, such as the removal of dingoes from a site, are also likely to affect mesopredator behaviour.

The extent of avoidance behaviour employed by mesopredators varied with both site and situation. Behaviour may vary with dingo activity, prey availability, season, weather, moonlight and other environmental factors. When dingoes are required or chose to be more active throughout their territory, this may enable mesopredators to access a resource by filling the temporal gaps dingo movements have created. Mesopredators may also increase vigilance behaviours to decrease the risk of attack by dingoes.

Behavioural avoidance of dingoes by foxes and feral cats is most likely to be at a fine temporal and locally spatial scale. It is likely that these mesopredators actively avoid the immediate vicinity of dingo activity, minimising competitive interactions and enabling coexistence with the apex predator, albeit at lower densities. Understanding the relationship between behaviour and abundance of these sympatric carnivore species is important for future ecosystem management.

Chapter 8: A Synthesis. Top–down or bottom-up? Using Bayesian analysis to understand the role of dingoes in trophic regulation of arid ecosystems.

8.1 Introduction

Two opposing theories attempt to identify the drivers of ecosystem structure, composition, and diversity in arid ecosystems. “Bottom-up” regulation identifies primary productivity as the driving force behind trophic dynamics in arid areas (Jaksic *et al.*, 1997). Wildlife populations in arid ecosystems fluctuate greatly in response to environmental perturbations (Morton *et al.*, 2011), of which the most significant is rainfall (Fensham *et al.*, 2005; Haythornthwaite and Dickman, 2006; Letnic *et al.*, 2005; Previtali *et al.*, 2009). Changes in the availability of water are responsible for a high variability in vegetative productivity, animal abundance and spatial distribution (Grant and Scholes, 2006; James *et al.*, 1999). “Boom-bust” cycles of native vegetation and prey populations (Dickman *et al.*, 1999; Letnic and Dickman, 2006) may drive predator populations to expand and decline in response to rapid changes in food availability (Jaksic *et al.*, 1997).

Alternatively, the “top-down” regulation hypotheses stipulates that large predators exert regulatory forces on mesopredators and prey populations through direct or indirect mechanisms (Terborgh and Estes, 2010). The removal of an apex carnivore may therefore have cascading effects down through the food web (Soulé *et al.*, 2005), altering ecosystem function (Bruno and Cardinale, 2008) and increasing susceptibility to invasion by exotic species (Hooper *et al.*, 2005). Following this, mesopredator release theory (Soulé *et al.*, 1988) suggests that eradication or reduction of apex predators will result in an increase in mesopredator populations and consequently an increase in predation pressure on smaller prey (Crooks and Soule, 1999).

Australia has the highest rate of mammal extinctions in the world, and their recent demise has been primarily attributed to predation by exotic mesopredators (Burbidge and Mckenzie, 1989; Short and Smith, 1994; Smith and Quin, 1996). There is increasing evidence that the dingo is able to suppress populations of introduced mesopredators in arid ecosystems (Letnic *et al.*, 2009a; Letnic *et al.*, 2009b; Kennedy *et al.*, 2011) and other bioregions (Johnson and VanDerWal, 2009; Letnic *et al.*, 2010). Where dingoes persist, native prey species, particularly those at high risk of predation by foxes and feral cats (medium-sized mammals and small vertebrates) (Burbidge and Manly, 2002; Risbey *et al.*, 2000) have been found to be in higher abundance (Johnson *et al.*, 2007; Letnic and Koch, 2010; Smith and Quin, 1996; Wallach *et al.*, 2009a). Dingoes are thought to be beneficial in some ecosystems as they utilize a much broader range of prey, particularly larger prey such as macropods (Robertshaw and Harden, 1986; Brook and Kutt, 2011; Thomson, 1992a), placing less predation pressure on smaller native species that are vulnerable to extinction (see review in Chapter 1).

The persistence of dingoes in arid regions may have important implications for native fauna conservation. However, natural variability within ecosystems presents researchers and managers with many difficulties when trying to teasing out the possible effects of, and interaction strengths between species, habitat resources and other ecosystem variables (Lima *et al.*, 2002). In addition, many ecosystem variables also exhibit complex temporal and spatial variation (Letnic and Dickman, 2010). As it is likely that both top-down and bottom up forces play a part in the function of arid ecosystems (Pianka, 1978), determining the impact of a top-order predator on biodiversity in rangeland ecosystems remains a fundamental but complex undertaking (Glen *et al.*, 2007a; Visser *et al.*, 2009).

Bayesian statistical methods provide ecologists and decision-makers with a means of analysing field data from multiple sources, making sense of trophic interactions and ecosystem dynamics and gaining insights of practical value (Wade, 2000; Reckhow, 2003). Bayesian statistics combine field data with expected distributions to determine the probability of an event occurring. In ecological studies, Bayesian statistics have been previously used to construct habitat suitability models (McNay *et al.*, 2006; Smith *et al.*, 2007), conduct population viability analysis (Marcot *et al.*, 2001; Wade, 2000), determine extinction probability (Ludwig, 1996), and to carry out ecological risk assessment (Pollino *et al.*, 2007). McCarthy (2007) provides a detailed review of the use of Bayesian statistics in ecological research.

Understanding the trophic effects of apex predators in terrestrial ecosystems is an example of a research problem that, due to logistic constraints, often relies on small data sets with inadequate replicates relative to the challenge of trying to understand broad-scale, complex ecological interactions (Allen, 2011). Predators are notoriously difficult to detect because they usually occur at low densities and occupy large home ranges. Field experiments on predators are therefore compelled to be conducted over large spatial scales (Karanth *et al.*, 2011). In these circumstances, Bayesian statistics have the advantages of not requiring design sampling, randomisation or replication of data sets (Reckhow, 1990), or sampling within assumed temporal or spatial scales (Ellison, 1996; Smith *et al.*, 2007). This allows for stronger inference to be gained from field studies conducted in uncontrolled environments with few replicates (Ellison, 1996; Smith *et al.*, 2007).

Due to most carnivore species being cryptic of habit, indices of predator activity are often calculated from low counts (*n*) and may be taken from populations that have been susceptible to some form of predator control. Techniques used to calculate population indices can also be prone to imprecision (Allen *et al.*, 1996; McCarthy, 2007; Karanth *et al.*, 2011). Bayesian statistics are advantageous in analysing such field data as they are robust even with small sample sizes (Gazey and Staley, 1986; Ter Braak and Etienne, 2003), data inaccuracies (McCann *et al.*, 2006) and incomplete data sets (Walton and Meidinger, 2006), including those collected from populations that may be controlled or previously manipulated (McNay *et al.*, 2006). Bayesian methods also allow for knowledge gained from different sources, such as empirical data from different field methods including personal observation be incorporated into an analysis (Ver Hoef, 1996). This means that researchers can effectively combine small data sets collected from a number of different field methods into a single model.

A further benefit to using Bayesian analysis in predator research is the ability to incorporate many years of field experience and expertise into the model (Marcot *et al.*, 2001). While sometimes criticised for its subjectivity (Dennis, 1996), the inclusion of expert opinion and findings from previous research can be used fill knowledge gaps in the model (Ellison, 1996; McCann *et al.*, 2006; Wolfson *et al.*, 1996). A distinct advantage that Bayesian statistics have over the use of frequentist statistics is that they enable the incorporation of human thought patterns, insights and reasoning into the model (Olson *et al.*, 1990). The use of experts to review prior distributions used in calculations may also help validate model accuracy for other researchers, managers and decision makers (Cohen, 1988; Winkler, 1967).

In this chapter Bayesian analysis is used to aid in understanding complex interactions between dingoes, foxes, feral cats and select prey at the five study sites (see Chapter 2). A Bayesian Belief Network (Pearl, 1988) was constructed to examine the most likely cause of predator and prey species activity found at the study sites and to help determine whether top-predator management plays a key role in trophic interactions within these arid ecosystems.

8.2 Methods

8.2.1 Construction of a Bayesian Belief Network

Bayesian Belief Networks, (hereafter BBNs) are directed graphical models that use Bayesian statistical inference (Heckerman *et al.*, 1995; Morawski, 1989; Olson *et al.*, 1990). BBNs model complex interactions within ecosystems by calculating the relative probabilities of competing hypotheses, given a particular set of conditions (Ludwig, 1996), and from these calculations, identify the most probable hypothesis (Taylor *et al.*, 1996). Each variable in the model is represented by a "node" (Charniak, 1991), which in ecological studies may represent either predictor variables (McCann *et al.*, 2006), such as key environmental drivers (Marcot *et al.*, 2001) and disturbance factors or response variables such as change in prey density (McNay *et al.*, 2006). Directional arrows are then used to link the nodes and indicate causal relationships between them (Morawski, 1989; Olson *et al.*, 1990). To enable parameter relationships to be analysed, each node in the BBN is allocated a series of discrete "states" in a summary table (McCann *et al.*, 2006). For parent (input) nodes, each of these states has a "prior" (expected) probability associated with it (Morawski, 1989), and for each child (intermediate or output) node, a conditional probability distribution is specified in the table. The conditional probability distributions are the probability of the child node taking on a different value for each combination of values of the parent nodes. A more detailed overview of Bayesian analysis is given in Appendix 3.

This research used the commercially available software package Netica^{TM} (Version 4.16, Norsys Software Corporation) to construct a BBN representative of the five sites used in this study. The BBN was used to model causal relationships between key ecosystem variables, including introduced predators, select prey, environmental conditions and dingo management regimes. A BBN was the ideal model for the ecosystems under study first because the visual nature of BBNs means results are presented in a highly interpretable format for managers, an advantage in environmental decision-making (Crome *et al.*, 1996; Taylor *et al.*, 1996). Second; BBN's enable scenario testing and are very useful for identifying major levers within the ecosystem (Hart and Pollino, 2008).

The first step towards forming a BBN was to develop a conceptual model in the form of an influence diagram (Figure 8.1). The influence diagram used in the current chapter was the ecosystem model of presumed interactions introduced in Chapter 1 of this thesis (Figure 1.3). The influence diagram mapped interactions between variables which were thought to have significant influence on predator and prey populations through affecting their distribution or abundance (see Marcot *et al.* (2001) and Smith *et al.* (2007) for similar constructions). This included environmental correlates, disturbance factors and response conditions within the system. The influence diagram was developed drawing upon results and conclusions from analogous studies published in peer reviewed literature. The variables included in the influence diagram were: *Habitat, Distance to Water, Site Productivity* and *Rainfall* (environmental correlates), *Dingo Management Regime, Livestock* and *Shooting* (disturbance factors), and predator and prey activity and predator behaviour (response conditions). The influence diagram also included important density-dependant feedback loops (e.g., predation) that reinforce or stabilize responses.

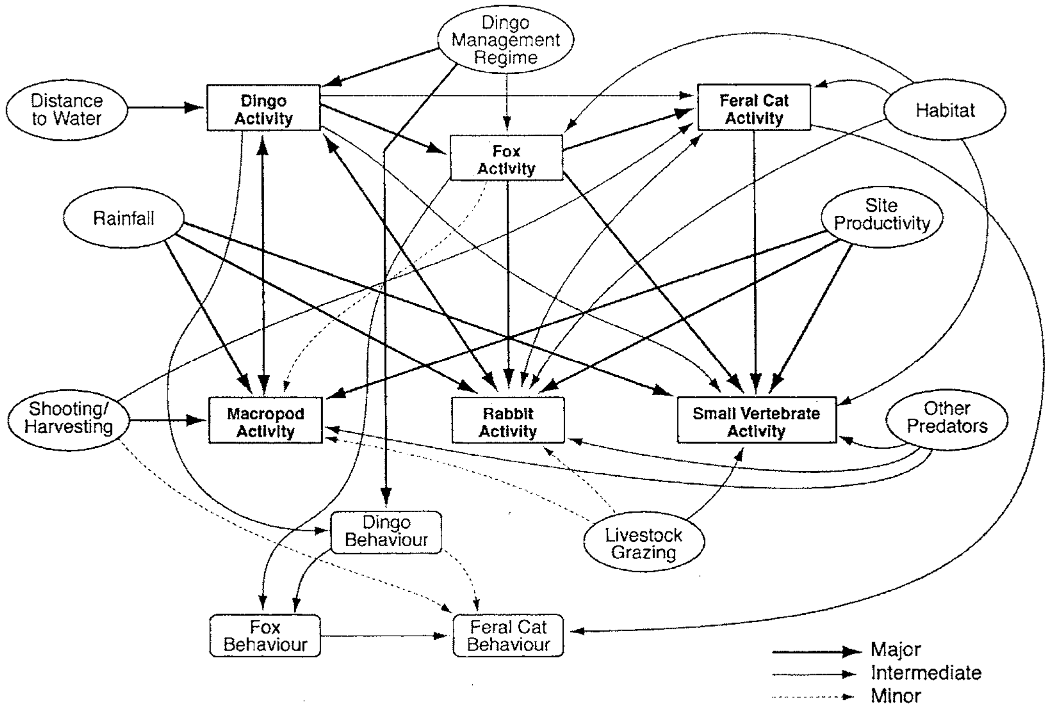


Figure 8.1 The influence diagram (conceptual model) of the ecosystem under study, used to form the basis of the BBN model.
Arrows indicate major, intermediate and minor interaction strengths predicted between ecosystem variables prior to the BBN model outcomes.

While the influence diagram was used to inform the structure of the BBN, not all variables and interactions in the influence diagram were included in the final model (Figure 8.2). The aim was to form a BBN that was representative of critical ecosystem characteristics but simple so that it matched data availability and was computationally un-cumbersome. Predictor variables (including environmental correlates and disturbance factors) formed the parent nodes of the BBN and are given by site in Table 8.1. *Shooting* referred to the annual harvesting of macropods (~ 1200 per annum) and culling of feral cat populations (~ 200 per annum) at one study site (Mundowdna Wilpoorina) (P. Litchfield pers. comm. 2006). *Site Carrying Capacity* replaced *Site Productivity* as it was deemed a more relevant term and *Livestock* was modified to form the input node of *Supplementary Food.* While livestock grazing may have some impact on selected prey populations (Read and Cunningham, 2010; Kerley, 1992) its primary relevance to our model was the role livestock carcasses play in sustaining predator populations during times of low prey availability (Lopez-Bao *et al.*, 2008). Supplementary food was also supplied by an abundance of macropod carcasses at one study site (Sturt National Park).

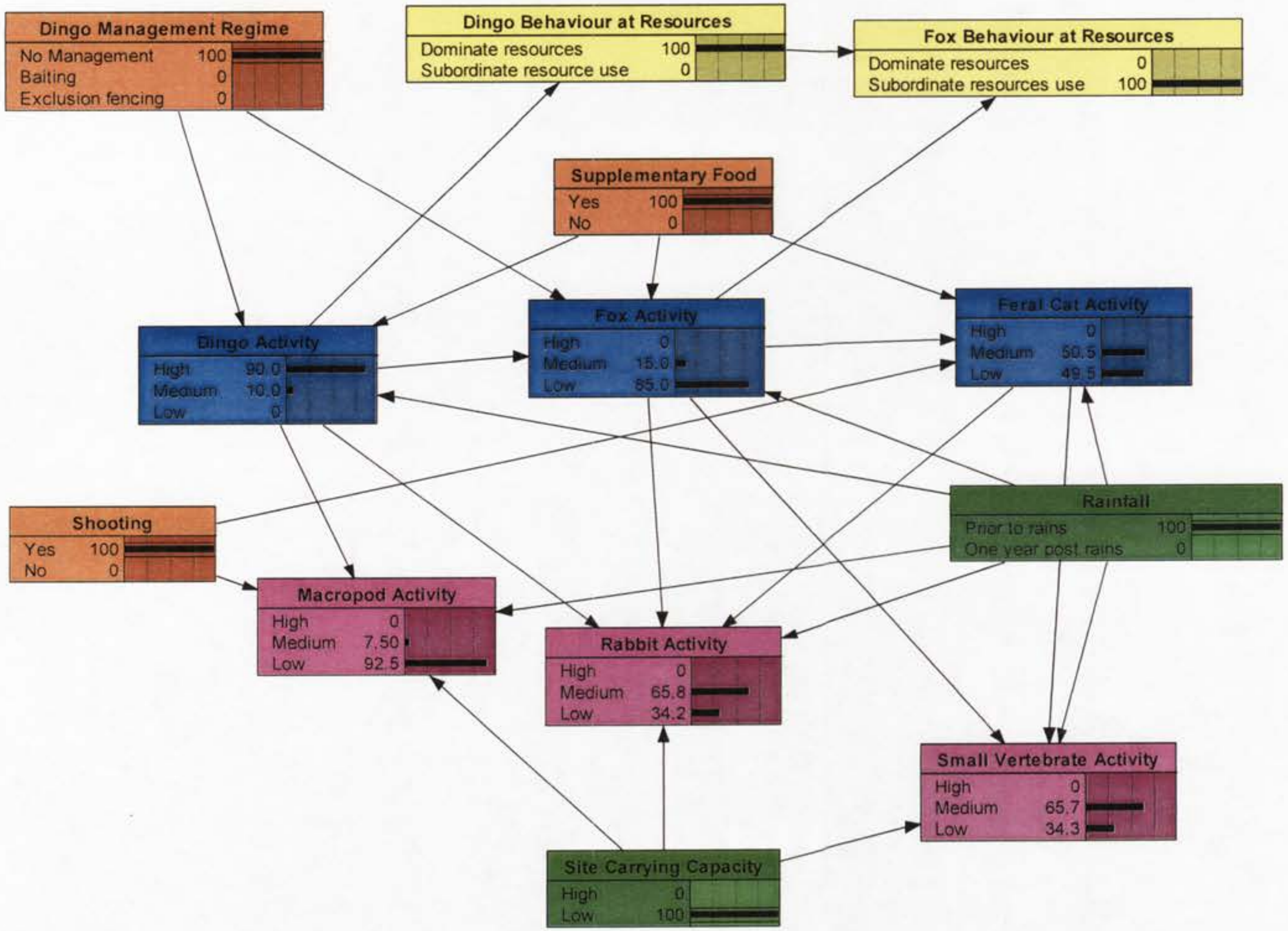
The nodes of *Habitat* and *Distance to Water* were removed from the BBN as the model was constructed to look at overall trends in activity across a site, rather than spatial segregation of activity within a site. Three nodes of predator activity (*Dingo Activity, Fox Activity* and *Feral Cat Activity*) formed the intermediate nodes of the BBN, while three nodes of prey activity (*Large Prey Activity, Medium-sized Prey Activity* and *Small Vertebrate Activity*), in addition to two nodes of predator behavior (*Dingo Behavior* and *Fox Behavior*) formed the output nodes (Figure 8.2).

Table 8.1 States of predictor variables for the five study sites.

Site	Dingo Management	Shooting	Carrying capacity	Supplementary Food
Sturt NP	Exclusion fencing	No	High	Yes
Bollards Lagoon	Baiting	No	High	Yes
Quinyambie	No management	No	High	Yes
Mundowdna/W	Exclusion fencing	Yes	Low	Yes
Finniss Springs	No management	Yes	Low	No

8.2.2 Incorporating temporal dynamics of ecosystem states

Feedback loops that represent density dependant interactions are important in predator-prey systems (Davey *et al.*, 2006; Stenseth *et al.*, 1998). A major limitation of using BBNs in ecology is that they do not permit the explicit representation of feedback loops (Pearl, 1988). Feedback loops cannot be included in a BBN due to software limitations associated with propagation algorithms that require the model to have an ‘endpoint’. While the model can represent a complex web of interactions that influence the endpoint, there cannot be an interaction that provides a feedback between the end point and primary nodes. It also follows that a BBN can only capture interactions between variables at one point in time, making it difficult to model ecosystem flows over multiple time period and thus show temporal or spatial ecosystem dynamics (Marcot *et al.*, 2001).



Note: Author defines an impossible scenerio of high site carrying capacity and shooting.

Figure 8.2 Bayesian Belief Network (BBN) of the system under study. Parent nodes are in orange (management) and green (environmental), intermediate variables in blue (predator activity), and output nodes in pink (prey activity) and yellow (predator behaviour). In this example, numbers in tables indicate probabilities of events occurring, given 1) no dingo management; 2) shooting conducted at the site; 3) supplementary food is available; 4) site carrying capacity is low and; 5) prior to rainfall event as defined in model.

The model developed here, the limitation of the BNN to represent feedback loops was overcome by incorporating a temporal environmental trigger into the model structure. *Rainfall* was chosen as a driving variable (parent node) due to its important role in the mediation of prey abundance in arid zone systems (Shenbrot *et al.*, 2010; Thibault *et al.*, 2010). To enable the temporal nature of predator-prey dynamics to be reflected in the BNN, *Rainfall* was categorised to represent two major periods in predator-prey interactions. The first stage was 'Prior to Rains', when both predators and prey were at low densities. The second stage was 'One Year Post Rains'. Post-rainfall, a rapid increase in primary productivity (i.e. plant growth) has cascading effects up through the food web, with an initial increase in prey activity and a delayed increase in predator response to prey (Holmgren *et al.*, 2006). Whilst predators may increase their activity sooner, changes in their densities often occur after the following breeding season, where higher prey availability may lead to increased juvenile survival in predator species (Tannerfeldt *et al.*, 2002). In the developed model, a rainfall event occurred when > 30mm fell within a one month time period.

8.2.3 Discretisation of continuous variables

All nodes representing continuous variables were made discrete by categorisation, to comply with the BNN modelling requirements. *Site Carrying Capacity* was calculated by estimating the gross primary productivity (GPP, mol CO_2 m^{-2} $month^{-1}$) of each site during both sampling periods, as well as historical productivity (previous 7 years) (GPP, mol CO_2 m^{-2} $year^{-1}$) to estimate overall annual productivity (Berry *et al.*, 2007). The GPP estimates were calculated using MODIS 16-Day L3 Global 250m (MOD13Q1) satellite imagery data (LPDAAC/CSIRO) (see Chapter 2, section 2.1.4.1). Productivity of the sites was categorised as high (post rainfall peaks in GPP, mol CO_2 m^{-2}/day > 40 on average) or low (post rainfall peaks in GPP, mol CO_2 m^{-2}/day < 40 on average).

The categorisation of other continuous data was determined from the numerical distribution of field data collected during the study. The PAI for each predator species and prey class, calculated using transect data, was used to classify activity at each site as either low (PAI < 0.1), medium (PAI 0.1 < 0.4) or high (PAI > 0.4). Details of PAI estimates by predator species and prey categories are given in Chapter 4 (section 4.3). Nodes that represented variables that were not continuous (*Dingo Management Regime, Supplementary Food* and *Shooting*) were readily categorised into states by the presence or absence of these factors at study sites (Table 8.1)

Data used as input data into the Bayesian Belief Network was derived from previous chapters in this thesis. Details of study sites used in the analysis are given in Chapter 2, and methods for field data collection and analysis of animal activity are described in Chapters 2 and

4. Methods for collection of field data on predator behaviour are described in Chapters 3 and 7. Details on analysis of behavioural data are given in Chapter 7. For the purpose of the Bayesian analysis, each predator's behaviour was further classified as dominant or sub-ordinate at the resource. A species dominated shared resources at the site if it had (i) the highest number of visitations per hour and (ii) spent the longest time in the vicinity of the resource.

Where field data were not available to estimate priors (i.e. populate the summary tables for each nodes), findings from previous and similar research in other arid ecosystems were drawn upon (Table 8.2). The model generated was then independently reviewed by two experts (T. Newsome and C. Pavey pers.comm., August 2011) using criteria outlined in Wolfson *et al.* (1996). Both experts are experienced arid zone ecologists with particular expertise in dingo management and prey species ecology. The process of review involved introducing each reviewer to the BBN model, then supplying the model and relevant data to the reviewer to run through different scenarios upon request. The reviewer then assessed model outcomes to determine how realistic the model was and how well the BBN captured relationships between ecosystem variables. Feedback from experts was then used to validate and improve the model. Both reviewers were supportive of the model, with positive comments such as "I really enjoyed the process" and "it is a well-rounded piece of work." Feedback was mainly focused on the importance of considering the influence of variables that were not included in the final model, such as disease, habitat structure, fire and native predators. Such feedback was then dealt with in the text of this chapter.

The BBN model was then used to test ten different scenarios that represented each of the five study sites under two temporal circumstances: prior to rains and one year after rainfall. A sensitivity analysis was then conducted. The sensitivity analysis ranks evidence nodes (Pollino *et al.*, 2007) and helps determine the relative strength of interactions between predictor variables within the BBN. The metric used for sensitivity analysis was Root Mean Squared as outlined in (Korb and Nicholson, 2004).

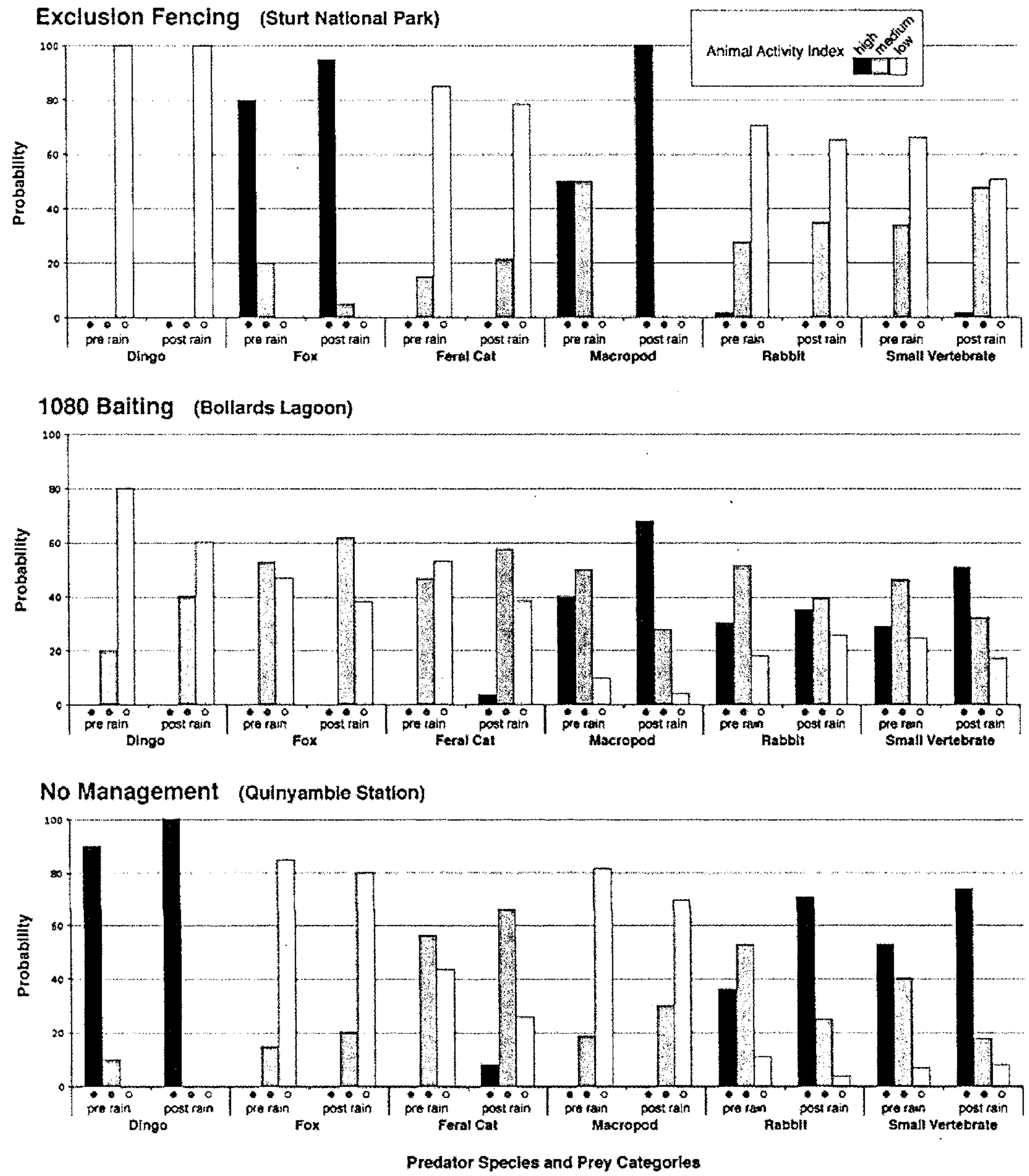
Table 8.2 Definitions and data sources for nodes within the BBN.

Node	Description	States	Data Source
Dingo Management	The dingo management regime practiced.	No management, Baiting, Exclusion fencing	Site management data
Supplementary Food	Whether or not large animal carcasses are available as alternative food during drought.	Yes/No	Site management data
Shooting	Whether or not shooting was carried out regularly (macropods and feral cats only).	Yes/No	Site management data
Rainfall	Indicates time period in relation to large rainfall event at the site (> 30ml fell during one month)	Prior to rains, one year post rains	Historical rainfall data from Bureau of Meteorology Climatic Services (2008)
Site Carrying Capacity	The potential primary productivity and livestock carrying capacity of the site.	High/Low	Calculated from gross primary productivity estimates (GPP, mol CO_2 m^{-2} $month^{-1}$) using data from MODIS satellite imagery.
Dingo Activity	The passive activity index (PAI) calculated for dingoes, as determined by track counts.	High/Medium/Low	Activity index calculated from empirical transect data using a linear mixed model. Post rainfall data expert opinion for Finniss Springs
Fox Activity	The passive activity index (PAI) calculated for foxes, as determined by track counts.	High/Medium/Low	Activity index calculated from empirical transect data using a linear mixed model. Post rainfall data is expert opinion for sites Sturt National Park, Finniss Springs and Mundowdna/Wilpoorina
Feral Cat Activity	The passive activity index (PAI) calculated for feral cats, as determined by track counts.	High/Medium/Low	As above
Macropod Activity	The passive activity index (PAI) calculated for macropods, as determined by track counts.	High/Medium/Low	As above. Estimated prey responses in conditions not found at sites, e.g. all predators high activity.
Rabbit Activity	The passive activity index (PAI) calculated for rabbits, as determined by track counts.	High/Medium/Low	As above. Estimated prey responses in conditions not found at sites, e.g. all predators high activity.
Small Vertebrate Activity	The passive activity index (PAI) calculated for small mammals and reptiles, as determined by track counts.	High/Medium/Low	As above. Estimated prey responses in conditions not found at sites, e.g. all predators high activity.
Dingo Behaviour	Behaviours displayed by dingoes at resources shared with other predators	Dominate resources/Subordinate resource use	Calculated using empirical data from thermal videos at study sites and determined by both the number of visitations per hour and time in the vicinity of the resource.
Fox Behaviour	Behaviours displayed by foxes at resources shared with other predators	Dominate resources/Subordinate resource use	As above

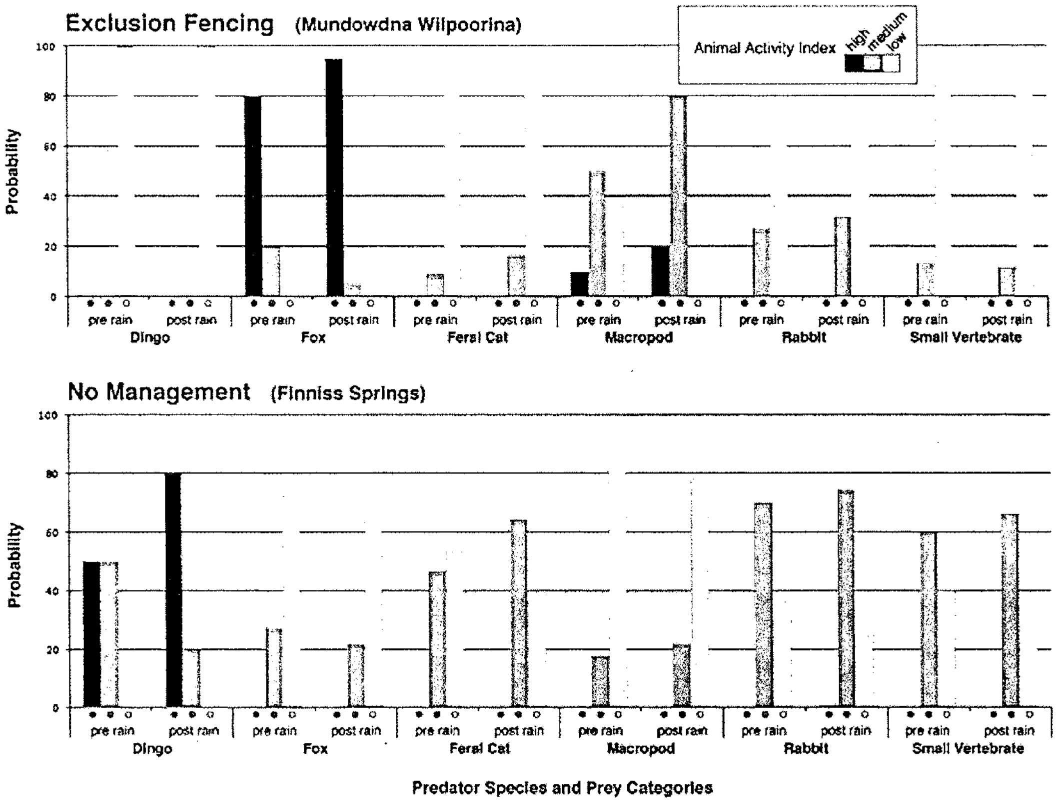
8.3 Results

8.3.1 Animal Activity

Model outputs demonstrate that the response of prey species to rainfall differed between high carrying capacity sites and low carrying capacity sites and between sites under different dingo management regimes (Figure 8.3a, b).


Exclusion Fencing (Sturt National Park)
Animal Activity Index
high
medium
low
1080 Baiting (Bollards Lagoon)
No Management (Quinyamble Station)
Probability
0
20
40
60
80
100
pre rain
post rain
Dingo
Fox
Feral Cat
Macropod
Rabbit
Small Vertebrate
Predator Species and Prey Categories

3(a)



3(b)

Figure 8.3 (a, b) The modelled probability of predator and prey activity prior to and one year post rains at (a) high carrying capacity sites and (b) low carrying capacity sites.
Results given by site (dingo management regime).

At the sites where dingoes are controlled through exclusion fencing our model gave a high probability of high fox activity both prior to and post rainfall and feral cat activity was uniformly low, with little response to rain. The model also showed large prey were more likely to increase activity post-rainfall. In contrast, medium-sized and small prey had a much less pronounced response to rainfall. A high probability of very low activity of both medium-sized prey and small vertebrates was found prior to rains. There was a small increase in the probability of medium activity for both prey categories one year post rainfall at high carrying capacity sites (Figure 8.3a) but little response to rains for either prey category at the low carrying capacity site (Figure 8.3b).

Baiting of dingoes led to a high probability of low activity of dingo populations both prior to and post rains. This pattern was similar to modelled results for fox activity, which was most likely to be medium or low, with only a small increase post rains. Feral cat activity had the highest probability of being medium both prior to and after rains, while a moderate response to rainfall was detected in all prey categories. Small vertebrate activity and activity of large prey was most likely to increase from medium to high post rainfall, while medium-sized prey and small vertebrate activity was also likely to increase (Figure 8.3a).

Sites with no dingo control showed a high probability of medium to high dingo activity prior to rains and an increase in dingo activity post rains. Fox activity at sites with no dingo control was uniformly low, with only one site showing the probability of increasing fox activity after rains. At sites with no dingo control feral cat activity had the highest probability of being medium or low both prior to with little response to rainfall. Activity of large prey was also uniformly low. In comparison, other prey categories (Medium-sized prey and small vertebrates) showed the highest probability of medium to high activity prior to rains, with an increase to high activity in response to rains at higher productivity sites (Figure 8.3a) but with minimal response to rainfall at lower productivity sites (Figure 8.3b).

In summary, our model showed an inverse relationship between dingo and fox activity, dingo and large prey activity, fox and feral cat activity and fox activity and smaller prey (including medium-sized prey and small vertebrates) under different dingo management regimes (Figure 8.3a, b). These relationships were uniform across sites of different carrying capacities and rainfall periods (Table 8.3).

Table 8.3 General trends in the probability of activity of predator species and prey categories.
Clear arrows indicate a trend towards the probability of increasing activity, while filled arrows indicate a trend towards the probability or decreasing activity in comparison to other dingo management regimes. Horizontal lines indicate a trend towards moderate activity or no clear pattern.

Species or category	Exclusion fencing	1080 Poison baiting	No management
Dingo	▼	▼	△
Fox	△	—	▼
Feral cat	▼	△	△
Macropod	△	△	▼
Rabbit	▼	—	△
Small vertebrates	▼	—	△

8.3.2 Sensitivity to model parameters

In the model, both dingo activity and fox activity were most sensitive to dingo management, while feral cats had weaker links to the other two predators. The model showed that activity of all three predators was more strongly associated with prey activity than with other environmental variables, such as rainfall or supplementary food (Figure 8.4).

Similarly, activity of prey was most sensitive to predator activity in most cases. Large prey activity was most sensitive to dingo activity and dingo management. Activity of medium-sized prey was most strongly influenced by fox activity, particularly when prey activity was low, followed by dingo activity and then site carrying capacity. Of the three prey categories, small vertebrates were most sensitive to site carrying capacity, however, site carrying capacity was not as important as fox activity in determining small vertebrate activity (Figure 8.4).

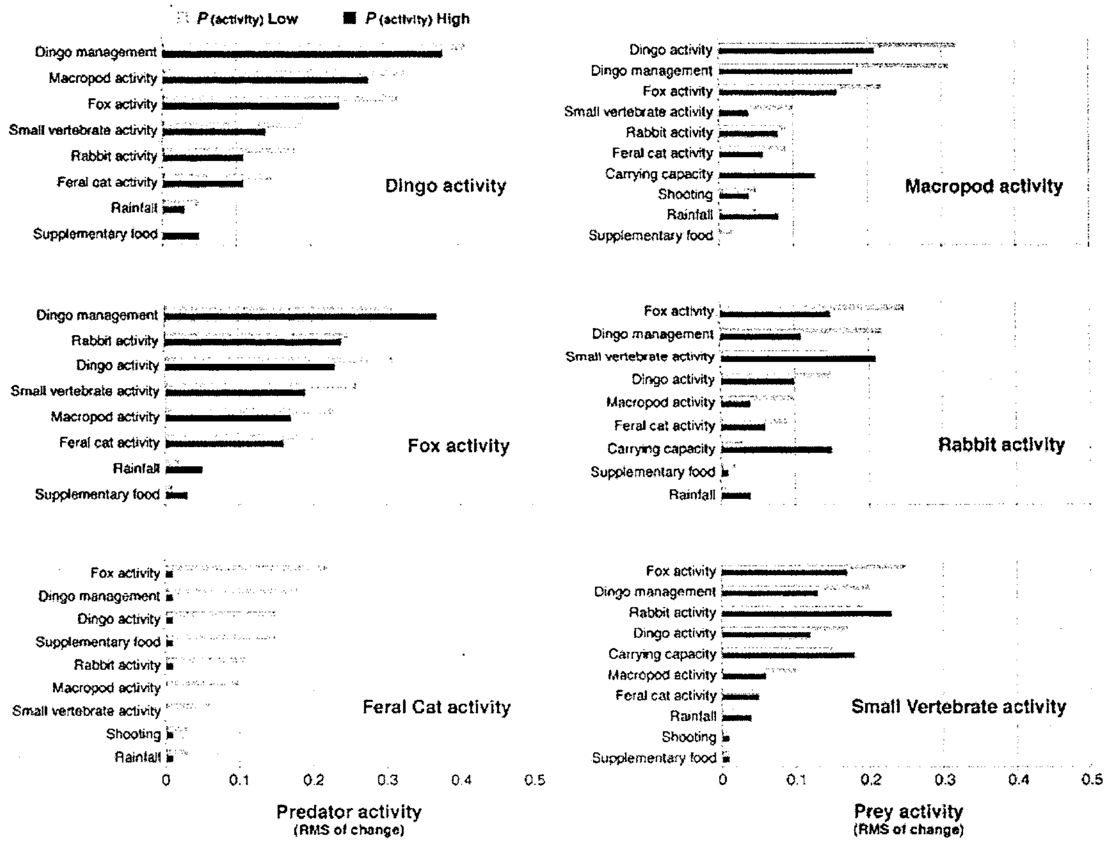


Figure 8.4 Graph showing the sensitivity of BBN parameters to changes in other nodes.
The sensitivity of variables to other nodes was estimated using the root mean squared (RMS) of change (difference between the minimum and maximum probabilities) for the probability of high and low activity for each predator species and prey category.

8.3.3 Predator behaviour

The behaviour of dingo and foxes at resources was strongly associated. Dingoes dominated resources at sites with no dingo management while fox behaviour was subordinate. At sites where dingoes were controlled through exclusion fencing, foxes dominated resources. The control of dingoes using 1080 baiting modified this pattern, so that interactions between dingo and fox behaviour were influenced by rainfall and the availability of supplementary food. Foxes were more likely to dominate resources prior to rains. One year post rains, the probability of dingoes dominating resources increased, although foxes still dominated when supplementary food was not available. With supplementary food available, the probability of dingoes and foxes dominating resources was uniform. Only one video recording of a feral cat was captured during the study, most likely due to the difficulties in luring cats to baits (Edwards *et al.*, 1997). Due to this inability to monitor feral cat behaviour in the field, feral cat behaviour was not included as a node in the BBN.

8.4 Discussion

8.4.1 Top down - The role of an apex predator in determining activity of mesopredators and prey

Many decisions in wildlife management are made with incomplete knowledge of ecosystem function. However, an understanding of trophic interactions is paramount when trying to identify optimal strategies for biodiversity conservation (Salo *et al.*, 2010). The Bayesian model used in this chapter revealed the management of an apex carnivore plays an important role in determining predator and prey activity in the arid environments sampled. Dingo activity was a key predictor of fox and large prey activity and an important predictor small vertebrate activity and activity of medium-sized prey at high and low carrying capacity sites, both prior to and post rainfall.

In agreement with findings from other studies, the model showed a strong inverse relationship between dingo and fox activity (Letnic *et al.*, 2009a; Letnic *et al.*, 2009b; Johnson and VanDerWal, 2009; Letnic *et al.*, 2010). Even post rainfall, foxes exhibited reduced activity in response to increased dingo activity in comparison to sites where dingoes were excluded. Fox activity was also strongly associated with the activity of medium-sized prey and was particularly important when prey activity was low. This strong link between foxes and their primary prey (rabbits) has been demonstrated across other bioregions (Pech *et al.*, 1995; Pech *et al.*, 1992; Davey *et al.*, 2006; Pavey *et al.*, 2008; Dell'Arte *et al.*, 2007).

Populations of feral cats have been found to increase with the removal of larger predators (Burrows *et al.*, 2003). In the model used in this study, increased fox activity was associated with low feral cat activity and reduced response to rainfall by feral cats. Such an inverse relationship between activity of foxes and feral cats has been found in other studies (Molsher, 2006; Risbey *et al.*, 2000). Evidence of a relationship between feral cat and dingo activity was less clear. In the presence of dingoes, feral cat activity appeared similar to activity levels predicated in the presence of controlled dingoes and foxes, particularly at high carrying capacity sites where prey was plentiful. Recent research into feral cat activity in the presence and absence of dingoes suggests that dingoes do impact on feral cat populations (Kennedy *et al.*, 2011; Pettigrew, 1993), and our model suggests that feral cats activity is more sensitive to dingo activity than the activity of prey. However, it may be that some other environmental variable not included in the BBN, such as microhabitat, also plays an important role in determining feral cat activity in arid areas (Southgate *et al.*, 2007; Hayward, 2010). Alternatively, top-down effects from interactions with a canid apex predator may be less intense on members of Felidae than between members of the Canidae (Major and Sherburne, 1987; Fedriani *et al.*, 2000).

While many environmental variables influence prey, our model identified predator activity as the most important parameter in determining prey activity. Previous research has also identified predator activity as a key determinant in the activity of small prey (Risbey *et al.*, 2000). In the absence of dingoes an increase in macropod activity, coupled with a reduction in small mammal activity, has been demonstrated in other studies of arid zone systems (Fillios *et al.*, 2010; Letnic *et al.*, 2009a; Letnic and Koch, 2010; Letnic *et al.*, 2009b; Newsome *et al.*, 2001).

The impact of predators on prey was particularly important at sites with supplementary food resources. At sites without dingoes and in the presence alternative food resources (large herbivore carcasses), fox populations persisted at high densities regardless of rainfall (Banks *et al.*, 2000; Krebs, 1996; Pech *et al.*, 1992). This is most likely due to the availability of supplementary food sources that enable fox populations to be sustained at artificially elevated levels during times of low prey availability (Courchamp *et al.*, 1999). Sustained high densities of predators can then suppress prey populations to an extent that they are unable to increase, even in response to rains (Smith and Quin, 1996).

Accordingly, the model showed that medium sized prey and small vertebrate activity was most sensitive to fox activity when prey activity was very low (Pech *et al.*, 1992; Salo *et al.*, 2010). At Sturt National Park, where fox activity was atypically high, the prolonged low activity and lack of response to rains by both rabbits and small vertebrates suggests that these prey may remain trapped in a "predator pit" due to continuous predation pressure by mesopredators kept at artificially high levels from the consistent availability of macropod carcasses as an alternative food source (Krebs, 1996; Pech *et al.*, 1992). Conversely, in the presence of dingoes, there may exist more stable baseline populations that allow these prey to increase rapidly in response to rainfall (Banks, 2000; Pech *et al.*, 1992; Letnic and Koch, 2010). Survival of small mammals is the key driver of population increases during fluctuations (Korpimaki *et al.*, 2004) therefore by reducing predation pressure by mesopredators, retaining dingo populations may lead to higher activity of these smaller prey over the long term.

Dingo control through 1080 baiting appeared to modify interactions between predators and prey (Wallach *et al.*, 2010). In addition to reducing dingo activity, 1080 baiting also reduced fox activity, most likely due to fox uptake of baits. With reduced activity of dingoes and foxes, the model showed a higher probability of increased feral cat activity in comparison to other sites. Competitive release of feral cats in the absence of larger predators has been shown in other arid zone studies (Pettigrew, 1993; Kennedy *et al.*, 2011). Large prey activity also increased under dingo control (Fleming *et al.*, 1996). Medium-sized and small vertebrate activity were higher than at sites with dingo control through exclusion fencing but not as high as at sites that retained stable dingo populations. These results suggest that 1080 baiting of dingoes may have an important effect on the levels of activity of mesoporedators and consequently the activity of medium-sized and smaller prey (Wallach and O'Neill, 2009), but effects may not be as severe as complete eradication of dingoes through exclusion fencing.

Finally, the model showed that dingo management is an important variable in determining dingo and fox behaviour. Where dingo populations were not baited, dingoes dominated shared resources. Baiting or removal of dingoes through exclusion fencing increased the use of shared resources by foxes. Such competitive behavioural mechanisms may play a key mechanism in effectively reducing mesopredator activity (Cupples *et al.*, 2011; Brawata and Neeman, 2011).

8.4.2 Bottom Up - The effect of rainfall and site carrying capacity on predator and prey activity

The "bottom-up" response of desert-dwelling vertebrates to large rainfall events varies between immediate increases in activity and dispersal to productive "hot-spots" (Grant and Scholes, 2006; Abere and Oguzor, 2011) through to reproductive stimulation in response to sudden increases in primary productivity, as found in many small mammal (Masters, 1993; Medger *et al.*, 2010; Soliman and Mohallal, 2009) and even some reptile (James, 1991) species.

In this study, increases in dingoes activity post rains were found at all sites which retained dingo populations, but whether increases in activity were a result of a numerical response to increased prey resources or the dispersal of individuals in search of mobile prey was unclear (Corbett, 1995). At sites which retained dingo populations, our model indicated decreases in fox activity following rains. Similarly, a reduction in fox activity at these sites may have been either a response to increases in dingo activity, or alternatively, a result of individuals dispersing to previously water remote areas. In the absence of predation by dingoes, large prey responded to rainfall at both low and high carrying capacity sites, but showed a decrease in activity in response to rainfall where dingoes were abundant (Pople *et al.*, 2000). As with foxes, it was unclear from the model as to whether a reduction in activity macropods was due to increases in dingo activity or movement of individuals to patches of high quality food resources (Hill, 1982; Grant and Scholes, 2006).

Medium-sized prey and small vertebrates showed the highest increase in activity in response to rainfall at sites with uncontrolled dingo populations, but this response appeared to be moderated where dingoes were controlled by baiting (Wallach *et al.*, 2010), and minimised even further at sites where dingoes were excluded (Letnic and Koch, 2010). However, the model did not differentiate between rainfall amounts other than the threshold amount used in calculations (30mm), therefore it is possible that higher amounts of total rainfall across study areas that differ in dingo management may have influenced this response. For example, species respond differently to different sized rainfall events, with the larger eruptions of prey species occurring when >100 mm fall over a period of 2-3 months (C. Pavey, pers. comm. September 2011). The incorporation of other stages in predator-prey dynamics, such as immediately post rains or during initial prey declines, could improve future models when such field data are available.

The model identified carrying capacity as an important variable in determining the response of small vertebrates, and to a lesser extent medium-sized prey, to rainfall, but this response was modulated by predator activity. Post-rainfall predator activity generally increased, likely intensifying predation on increasing prey. It is probable that the forces of top-down regulation are attenuated at such times until prey declines, when competition for scarce food resources between elevated predator populations strengthens (Holmgren *et al.*, 2006; Letnic and Dickman, 2006). As arid ecosystems may experience extended periods of drought between large rainfall events this reversal from bottom-up to top-down regulation may be a critical factor in determining prey activity over the long term (Letnic *et al.*, 2005). The model estimated that medium-sized prey and small vertebrates have higher activity and an increased response to rainfall at sites where dingoes are present in comparison to other sites of the same carrying capacity. Such a result may be due to the extended effects of top-down regulation during dry periods within these systems.

Conversely, in the absence of dingoes, medium-sized prey and small vertebrates had a minimal response to rainfall at high carrying capacity sites, and even less response to rainfall at low carrying capacity sites. Increased fox activity in the absence of dingoes is one probable cause of a suppressed response by these prey to rainfall (Letnic and Dickman, 2006). While fox predation may be selective of some species (Dickman *et al.*, 2001; Haythornthwaite and Dickman, 2006), studies from other arid regions indicate that preferred prey (rabbits and small mammals) are generally targeted, even at low densities (White *et al.*, 1996; Pavey *et al.*, 2008) and this may delay or reduce the ability of targeted prey species populations to increase to densities typical of an environment (Jaksic *et al.*, 1992). Alternatively, the impacts of disease outbreaks, such as Rabbit Haemorrhagic Disease (RHD), may result in lower prey densities irrespective of predator activity (C. Pavey pers. comm. September 2011).

Activity of prey species may also be affected by other environmental variables not included in the model. Livestock grazing may impact on some small mammal species (Kerley, 1992) although previous studies in the Australian arid zone have found predation to be a greater determinant of small vertebrate activity (Read and Cunningham, 2010). In other arid ecosystems, intraspecific competition also plays an important role in the dynamics of small mammal populations (Previtali *et al.*, 2009). Variation in activity and dispersal may occur between periods within boom-bust cycles (Dickman *et al.*, 2010) and the impact of predation has been found to differ between cyclic and non-cyclic species (Salo *et al.*, 2010). In addition, it is recognised that other predators such as raptors and larger reptiles, whose activity was not measured, occur within the study ecosystems and may have significant impact on prey populations (Lloyd, 2007; Sutherland *et al.*, 2011).

8.4.3 Model limitations

While much effort goes into collecting field data in ecological studies, much less success is achieved in transferring data into practical management strategies (Varis and Kuikka, 1999). BBNs can serve as useful decision support tools for environmental management as they enhance the ability to focus on key questions that are of practical concern to natural resource managers, explore probable scenarios, and then evaluate the consequences of different management actions. The ocular nature of a BBN also provides an ideal means for ecologists to transparently communicate the conservation implications of results to land managers and policy makers (Taylor *et al.*, 1996; Wade, 2000). This enables managers to identify and make more informed decisions about practical management strategies (Ludwig, 1996; Nyberg *et al.*, 2006; Reckhow, 2003). Furthermore, new research findings can be used to iteratively refine BBNs, subjecting the model to continual improvement as part of an adaptive management process (Howes *et al.*, 2010; McCann *et al.*, 2006; Nyberg *et al.*, 2006). In this way, BBNs can contribute to the design of future research experiments through identifying data gaps in current research (Chaloner and Verdinelli, 1995).

These are all significant advantages for the use of BBN's in the environmental decision making process. In support of this, the BBN was very useful in understanding complexity within these case study ecosystems, but it is noted that the usefulness of BBNs in ecological research may be limited in some cases. As with any models, BBN's are just one of the many tools available to managers and they should be used with prior knowledge of their limitations.

One criticism of using BBNs in ecology is the need to make continuous variables discrete, that in turn may lead to reduced complexity and oversimplified state responses (Nyberg *et al.*, 2006). For the purpose of this study, the categorisation of continuous variables was an advantage as it led to a parsimonious BBN model that was sufficient to establish causal relationships between critical system variables. However, some sites did display subtle differences and inconsistencies that could not be captured in the BBN. For example, the response of feral cats to high fox populations differed greatly between sites of high fox activity. The reason for such inconsistency could not be captured in the model, but one possibility is that the BBN was unable to capture the spatial dynamics of populations, such as immigration into baited areas or areas from which individuals had been removed through hunting activities, or alternatively, the impact of habitat structure on survivorship in feral cat populations.

Such inconsistencies may therefore be due to the effects of other variables that were not factored into the model. When modelling ecosystems using a BBN, it is impractical to factor in all variables in the model as the BBN becomes too unwieldy. Instead, the BBN is used to model major system components and linkages. Modellers should acknowledge the existence of other albeit more minor elements that cannot be included. For example, in the ecosystems used in this study, foxes may opportunistically depredate juvenile macropods (Banks *et al.*, 2000) and dingoes seasonally predate on small mammals and reptiles (Paltridge, 2002; Thomson, 1992a). Food preference by predators can change significantly between seasons and years depending on prey availability (Pavey *et al.*, 2008) impacting on interaction strengths between variables captured in the model. Moreover, prey activity was only measured for macropods, rabbits and small vertebrates, although it is recognised by the authors that other alternative, unmeasured prey (such as invertebrates, carrion and birds) are seasonally available to predators.

In addition, data used in the model was only sampled from study sites during one season (summer) and seasonal changes in predator and prey relationships would most likely occur. While the purpose of the model was to show overall trends in predator and prey activity at study sites, patterns in activity, predation and strength of interactions may vary on finer spatial scales due to other environmental variables such as habitat patch suitability (Dell'Arte and Leonardi, 2005), availability of artificial water, landform or geology, elevation, and percentage of vegetation cover (T. Newsome, unpublished data). Finally, the model developed would not be applicable to all arid zone sites due to diversity across the region in species distribution patterns. It is important to recognise the function of a top predator may differ between bioregions (Sergio *et al.*, 2008; Visser *et al.*, 2009), which suggests models should be used to examine ecosystems discretely (Newsome, 2002). Moreover, in other environmental perturbations other than rainfall, such as fire, may play a much more significant role in determining animal abundance and distribution patterns in other regions (C. Pavey pers. comm. September 2011). The advantage of using a BBN is that the model can be easily be adapted and made more representative of trophic dynamics found in other areas or to represent other phases in the "boom-bust" cycles of arid ecosystems, or indeed other bioregions.

Despite its' limitations, the BBN developed was a valuable tool for improving our understanding of how dingo management may affect the function of arid ecosystems. While the results from this study are inherently localised, the results support that in some arid ecosystems dingoes have an important function in trophic regulation (Sergio *et al.*, 2005). Under these circumstances, retaining dingoes in arid ecosystems may be beneficial for the long term conservation of native biodiversity.

Chapter 9: General Discussion: The management of dingoes for biodiversity conservation in the Australian arid zone.

By blending behavioural ecology with population and community ecology, our understanding trophic interactions within ecosystems may be greatly enhanced.

(Schmitz and Booth, 1997).

9.1 Introduction

Hairston *et al.* (1960) introduced the concept of top-down trophic cascades, suggesting that the structure of communities down through the different trophic levels was directly and indirectly influenced by apex predators. Since then, research into the ability of top carnivores to regulate trophic cascades at either the species or community-level has expanded exponentially through both marine and terrestrial ecosystems. In particular, key to their impact on terrestrial ecosystems is the ability of larger predators to regulate, even limit, populations of smaller carnivores through complex interactions (Glen and Dickman, 2005). Through regulating smaller predators, large carnivores influence the abundance and diversity of lower trophic levels, have the ability to determine large-scale biomass distribution patterns and may structure ecosystems on a regional scale (Elmhagen *et al.*, 2010; Letnic *et al.*, 2010). With large carnivores eradicated from many regions worldwide due to human activities (Crooks, 2002; Weber and Rabinowitz, 1996), the 'release' of mesopredator populations from regulation has now become a global issue for biodiversity conservation (Prugh *et al.*, 2009).

Australia provides a unique example of a naturalised medium-sized carnivore, the dingo, an evolutionarily recent addition to the fauna of the continent (~ 4000 yr) that has successfully filled the niche of top predator. Increasingly, evidence reviewed in this thesis suggests that the dingo is capable of determining wide-spread patterns in species distribution and abundance ecosystems at a continental scale (Letnic *et al.*, 2010). Dingoes have previously been found to influence the abundance of native herbivores, including kangaroos and emus (Caughley *et al.*, 1980; Pople *et al.*, 2000), and the activity and distribution of introduced mesocarnivores, including foxes (Johnson and VanDerWal, 2009; Letnic *et al.*, 2010; Newsome *et al.*, 2001), feral cats (Kennedy *et al.*, 2011; Pettigrew, 1993), and mammalian prey species susceptible to mesopredator predation (Johnson *et al.*, 2007; Letnic and Koch, 2010; Letnic *et al.*, 2009b; Wallach *et al.*, 2009a).

In contrast, foxes and feral cats are relatively recent introductions to Australian fauna (~ 200 yr). Both mesopredator species have yet form equilibrium with native prey populations; consequently foxes and feral cats are likely to have a larger impact on prey populations than native predators (Salo *et al.*, 2007; Sinclair *et al.*, 1998). Introduced predators are also most likely to cause extinctions of native species where their abundance is greatly elevated by abundant alternative prey (Harding *et al.*, 2001). As such, the simultaneous introduction of an introduced herbivore (the rabbit) into Australian ecosystems has resulted in increased mesopredator densities, resulting in major perturbations to native faunal communities across a wide variety of Australian ecosystems (Burbidge and Mckenzie, 1989; Burrows *et al.*, 2003; Dickman, 1996a; Johnson and Wroe, 2003). The ecological function of many native taxa is poorly known, and their disappearance may result in major changes in ecological system functioning (Johnson, 2006).

In the case of the dingo, its presence on the continent for > 4000 years means it may now play an integral role in ecosystem function (Daniels and Corbett, 2003). As such the dingo may be so firmly established as to be an important part of the ecosystem for the survival of other species, particularly endemic prey. The results from this thesis support the proposition the dingo is a key component of ecosystem processes in arid areas and that management of dingo population should be based on both its functional value and ecosystem services (Courchamp *et al.*, 1999; Daniels and Corbett, 2003). The following discussion highlights key findings of this research that relate to the role played by the dingo in the regulation of trophic interactions between mesopredators, and between mesopredators and their prey, in arid Australia.

9.2 Predators, prey and trophic regulation

It has previously been theorised that the dingo may play four possible roles in trophic dynamics. Dingoes may be: a) regulators (the community is regulated by top down forces), b) moderators (they limit prey numbers but do not regulate prey dynamics), c) harvesters (they have no impact on prey dynamics) or d) responders (community regulation is through bottom up forces) (Fleming *et al.*, 2001b). Results from this thesis revealed that management which reduces or disrupts dingo populations in arid Australia may affect mesopredator and primary and secondary prey species activity (see Chapter 4). The corollary is that dingoes may play a role in regulating, through top down forces, the activity of these species. These results lend support to the MRH (Mesopredator Release Hypothesis) discussed Chapter 1. More generally, they add to the evidence found by other authors that dingoes have key ecological effects on both mesopredators (Moseby *et al.*, 2012) and their mammalian prey (Letnic *et al.*, 2009b).

The focus of much of the current research on trophic interactions is no longer on whether trophic cascades occur in communities, but on assessment of the temporal variability of interactions, the strength of indirect effects, and the importance of top down versus bottom up forces in relation to external influences such as the environment (Roemer *et al.*, 2009). For example, the fluctuating productivity of arid environments can interact in complex ways with top-down regulation. The impact of variable rainfall patterns in arid and semi-arid Australia greatly favours eruptive prey, particularly the introduced rabbit and both native and introduced rodent species (Newsome, 2002). These sudden increases in the primary introduced prey may lead to hyper-predation (Courchamp *et al.*, 2000), where predator numbers are elevated to artificially high levels by abundant introduced prey, increasing predation pressure on secondary, indigenous prey.

This process of hyper-predation and the numerical and functional response of different predator species to increasing and decreasing primary prey (Sinclair *et al.*, 1998) may lead to the decline or extinction of "buffer" prey species, including native fauna that are less able to sustain high levels of predation (Courchamp *et al.*, 2000; Holt, 1977). As such, these "boom periods", where prey increase exponentially after large rains, may be vitally important for the management of predators (Letnic and Dickman, 2006), and for the conservation of native fauna species which may be secondary prey species for mesopredator populations (Courchamp *et al.*, 1999).

Along this vein, a second key finding of this thesis was the impact of rainfall on predator interactions and the response of prey species. Results from this thesis suggest that top-down regulation of mesopredators by dingoes remains present even when "bottom-up" forces increase productivity post rains (see Chapter 4) and dingo management was found to be a more important overall determinant of mesopredator activity than rainfall (see Chapter 8). However, while increases in primary productivity within arid and semi-arid areas have been found to attenuate top down effects in some ecosystems (Holmgren *et al.*, 2006), the findings of this thesis show that dingoes are able to maintain top-down regulatory effects on foxes even during times of high productivity. As survival rate rather than reproductive rate drives prey increases in booms (Korpimaki *et al.*, 2004), top-down regulation by dingoes may be key to the survival of some native mammals where dingoes persist (Southgate *et al.*, 2007). While dingoes may not determine the presence or reproductive rates of prey species as productivity does, they may assist in the survival rates of species, which is the key to the persistence of many small and medium sized mammals in the boom bust arid areas.

Impacts of predation are particularly important to declining prey populations, reintroduced or vulnerable prey species (Pech, 2002). When drought returns to arid regions, reduced productivity leads to a decline in prey abundance. Predation impacts can then further reduce prey to a point where they become trapped in a "predator pit" and cannot rejuvenate again when conditions improve, leading to an increase in predation pressure on remaining prey (Newsome, 1990). Particularly susceptible to predation under such conditions are taxa whose reproductive rate is too low for population growth rate to exceed the sustained predation rate (Newsome *et al.*, 1989).

Results from this thesis found that where artificially high activity of foxes occurred at Sturt National Park, sustained by the presence of alternative food resources (macropod carcasses and rabbits) and absence of dingoes, small to medium-sized mammalian prey activity was significantly lower, even post rains (see Chapter 4). These results suggest that in areas of higher dingo activity there exists larger baseline small to medium sized prey populations from which prey can respond to increased productivity events. This finding compliments those of Newsome *et al.* (1989), where predation impacts were found to be modulated by environmental influences. However, while this may hold true for general prey-size classes as used in this study, impacts may differ between species, particularly for cyclic and non-cyclic prey, or more commonly in arid Australia, eruptive and non-irruptive species (Salo *et al.*, 2010). The ability of mesopredators to escape regulation in the absence of dingoes and limit prey species is a subject that requires further research.

Top predators have also been found to play an important role in controlling herbivore populations (Nilsen *et al.*, 2007). Perhaps the reason dingoes may work so well as a biological regulator in arid ecosystems is that they exert control over both the invasive eruptive prey (i.e. rabbits) and the introduced mesopredators that depend on them (Courchamp *et al.*, 2000). Complete removal of all predators may lead to an exponential increase in invasive prey, such as rabbits, which may then lead to other negative impacts on native populations through competition and destruction of habitat (Banks *et al.*, 1998). In ecosystems where endangered species are not a staple prey, it may be that mesopredator eradication is not only unfeasible, it may also be unnecessary. Instead a reduction in mesopredator densities that enables successful co-existence may be a more viable management goal (Sinclair *et al.*, 1998). In these circumstances, retaining the dominant predator, the dingo to regulate populations of invasive mesopredators and prey species is most likely to be most beneficial for biodiversity conservation (Baxter *et al.*, 2008).

Predation impacts of native predators not addressed in this study also complicate trophic interactions and must be considered (Lloyd, 2007). Native predators, such as raptors or large varanids, compete with mesopredators and may increase with their reduction or removal, changing impacts on native and introduced prey populations (Lloyd, 2007; Pavey *et al.*, 2008; Sutherland *et al.*, 2011). Interactions between invasive mesopredators are also an important consideration for maintaining the biodiversity of endemic species (Ruscoe *et al.*, 2011). Interactions may include suppression by direct predation (Courchamp *et al.*, 1999) or occur through indirect effects (see review in Chapter 6) and may include a three-tiered response system, with dingoes regulating fox populations but not feral cats, while if dingoes are removed foxes suppress or limit feral cat populations (Molsher, 1998). In Australian ecosystems species cascades may in fact be more common than trophic cascades (Polis *et al.*, 2000; Schmitz *et al.*, 2000). The results of this study (see Chapters 4, 6 and 7) support the proposition that top down trophic regulation appears to be stronger between a canid apex carnivore and canid mesopredator (e.g. the dingo and fox) (Gehrt and Prange, 2007) than between a canid apex carnivore and mesopredators from other families, such as felids (Fedriani *et al.*, 2000). Therefore single species management of any one predator species is likely to induce changes in trophic dynamics which may cause undesirable outcomes for certain native species. The results of this study (see Chapter 8) highlight the importance of understanding these kinds of complex species interactions for informing the effective management of biodiversity (Glen *et al.*, 2007a).

9.3 The influence of behaviour on trophic interactions

Increasing our understanding of trophic webs in the real world requires a blend of population, community and behavioural ecology (Schmitz and Booth, 1997). It is vital to understand the processes and mechanisms behind trophic dynamics in order for management strategies to be successfully implemented (Linnell and Strand, 2000).

Indirect effects have been shown to play a key role in trophic cascades (Berger and Conner, 2008). Results from this study provide field evidence that behavioural mechanisms such as avoidance may be important in driving mesopredator release in arid zone ecosystems of Australia. Dingoes were shown to initiate avoidance competition at shared resources (Chapters 6 and 7), perhaps as Ritchie and Johnson (2009) so eloquently described, instilling "fear and loathing" into mesopredators through dominant, aggressive behaviour. Water, in particular, appears to be a key resource in the arid zone around which behavioural interactions between predators take place (see Chapter 6). Actual avoidance may occur at a local scale (Mitchell and Banks, 2005), however even small scale changes in behaviour may result in significant effects at a population level (Schmitz *et al.*, 2004). Foxes have a low vixen fertility rate as a natural regulatory mechanism, so rely predominantly on immigration to increase population densities (Saunders *et al.*, 1995). If avoidance of dingoes reduces fox immigration to areas, this may be another mechanism by which dingoes are able to regulate fox populations. It is likely that the effects of such local avoidance have large-scale consequences for mesopredator populations, such as reduced survival and reproductive rates in the long term (Brawata and Neeman, 2011; Moseby *et al.*, 2012).

Predation risk has also been shown to structure ecosystems from the top-down (Ripple and Beschta, 2006; Schmitz *et al.*, 2004). Palomares *et al.* (1995) found higher predation rates and lower reproductive rates for prey species when top predators were controlled. One question for future research is to understand how different predator and prey behaviours modulate factors that determine the presence and strength of top down regulatory forces in trophic webs (Power *et al.*, 1992). For example, in addition to modifying mesopredator behaviour, the removal of dingoes from some ecosystems may lead to changes in prey behaviour, with some species better able to adapt than others to increasing fox and/or feral cat predation (Quinn and Cresswell, 2004; Ripple and Beschta, 2004). Future research needs to consider the effects on community structure of differing prey vulnerabilities to exotic and naturalised predators, particularly between native and non-native prey species (Power *et al.*, 1992), and how prey species density and diversity respond to changes in predator guilds (McPeek, 1998). The implications of retaining dingoes in arid ecosystems may be an increase in the vulnerability of some native prey, such as macropods, while dingo removal may decrease baseline densities of prey more vulnerable to mesopredator predation to below minimal viable populations, leading to declines and even extinctions in susceptible populations.

The presence of suitable habitat may be critical for predator avoidance particularly when prey species are at low densities (Pech *et al.*, 1995). Following this, reduction of habitat through climatic disturbance or otherwise may significantly increase vulnerability to predation (Schoener *et al.*, 2001). Ecosystem productivity or other bottom up processes such as habitat change can also determine the strength of top down regulation, and set upper limits on mesopredators even in the absence of top predators (Elmhagen and Rushton, 2007). While habitat preferences by mesopredators were found, habitat use was not found to be a key variable of behavioural change in mesopredators when dingoes were controlled (see Chapter 5). However, when compounded with the effects of a fluctuating environment and the loss of top predator (Ripple and Beschta, 2004), habitat may be an important variable determining the impact of mesopredators on the distribution and abundance of prey. Prey availability may in turn influence trends in some mesopredator populations (e.g. feral cats, see Chapter 4), while other factors such as environmental factors (e.g. site productivity or habitat, see Chapter 5) and the presence of sympatric predators may determine feral cat activity levels *per se*. The effects of habitat change on prey vulnerability under different dingo management strategies in a topic for further research.

The strength of predator/predator and predator/prey interactions are unlikely to be the same in all ecosystems (Miller *et al.*, 2001) or even between sites in the same bioregion. The role of the dingo as an apex predator is likely to be context dependant (Sergio *et al.*, 2008), and may vary temporally within an ecosystem, change seasonally or in response to major perturbations, or differ spatially between different communities and faunal suites (Visser *et al.*, 2009). For example, while top down regulation by dingoes may be common in arid areas, dingoes may not regulate mesopredators in ecosystems with increased habitat complexity (Catling and Burt, 1995). In temperate Australia, the climate is generally moderate and food availability high and rather than seasonal or climatic events, major ecological flux are more determined by wildfires, after which dingo predation may affect prey diversity, abundance and population structure. In the more productive and complex habitats of eastern Australia, the function of dingoes appears to differ, with dingoes likely to be moderators of macropod populations (Robertshaw and Harden, 1985; Robertshaw and Harden, 1986) and to limit, rather than regulate, foxes (Johnson and VanDerWal, 2009). With limited knowledge for many ecosystems, our ability to predict the ecological effects of changes in dingo management regimes in many bioregions remains limited

(Visser *et al.*, 2009). Understanding ecosystem dynamics is fundamental to effective management of predator populations and prey species of conservation concern and to shed light on the possible mechanisms that may drive trophic interactions between dingoes and introduced mesopredators (Glen *et al.*, 2007a).

9.4 Methodological limitations of the study

The results from this thesis need to be considered in light of the limitations that are associated with the methods used, including inaccuracies of sampling procedures and weakness in experimental design. Weakness of design is inherent in all observational studies (Bart *et al.*, 1998), as there is no local control and limited replication. One preference would be to have used a BACI design for sampling, however such a process would not be feasible in the timeframe of a PhD, or suitable at many sites where dingo control regimes are already in place. As such, an observational study was undertaken, with prior assumptions that sites differed due to environmental factors and local dingo management.

Field methods used to collect data were standardised but all contain inherent bias (see Chapter 2). As the methods used in this study provide a measure of animal activity, detection rates may be influenced by season (Edwards *et al.*, 2000), food resources (Marlow, 1992a), the presence of optimal habitat (and shelter) and the presence of competing species (Edwards *et al.*, 2000). In territorial animals such as dingoes, foxes and feral cats, activity levels are also dependant on population density, and as density decreases, individuals may increase in activity (Ables, 1969; Corbett, 1995; Phillips and Catling, 1991). The effect of season on activity indices was somewhat overcome by sampling only during summer, and not the breeding season (Edwards *et al.*, 2000).

Activity of predators, particularly at scent stations, may be influenced by predator behaviour, such as localised avoidance (Mitchell and Banks, 2005) (Chapters 5 and 6). For example, feral cats increased visits to scent stations at Mundowdna-Wilpoorina when foxes were removed by baiting. Feral cat visits to scent stations also decreased at Bollards Lagoon after dingoes were baited and foxes consequently increased. However at the same time, density estimates for feral cats increased on transects (Chapter 4). Similarly, as the presence of foxes and dingoes declined on scent stations at Finniss Springs, feral cat visitations increased. During the study foxes were less wary of approaching scent stations at sites without dingoes (such as at Sturt National Park and Mundowdna-Wilpoorina) than at sites with dingoes present (see Chapter 5). When dingoes were present at Bollards Lagoon during the first sampling season, foxes were detected on transects but not on scent stations (Chapter 4). Such responses may be temporal and localised (see Chapter 5), and the spatial arrangement of individuals may also be important.

The success of the scent station method may also depend on environmental factors such as wind strength and the direction. In addition, during periods of strong winds both scent stations and transect plots became blown out and unreadable. A further limitation of using tracks for indices is the difficulties involved in detecting individual animal tracks, particularly during times of high prey activity. This was evident during 2008 when small mammals were in such high abundance that tracks covered the entire transect, so that counts of other species were difficult. This problem also occurred at water points, mainly on pastoral lease sites where stock moving to and from the water had trampled transects and made them unreadable.

Human activity may also induce bias in activity indices. Predators, in particular dingoes and foxes, may be wary of new objects or scents introduced into their environment and avoid them initially (Allen *et al.*, 1996). When animals are more wary (individuals, or populations), scent stations may be less affective due to avoidance (Engeman *et al.*, 2000). Prior exposure to human activities (for instance leg-hold trapping or shooting) may also affect behaviour of predators at scent stations (Hein and Andelt, 1994). This may be an important consideration in this study due to the differences in predator management between the study sites.

Some discrepancies were also noticed between activity indices obtained from scent stations and transects in this study, although generally both methods showed similar trends in predator activity. Often predator activity increased on both transects and scent stations, however the increase was generally higher on transects. For example, a threefold increase in fox and dingo activity between sampling years at Bollards Lagoon was detected by transects, but only a twofold increase in activity was detected on scent stations (Chapter 4). While scent stations have been previously found to be less effective at estimating predator densities than transects (Allen *et al.*, 1996), but they were beneficial in this study as they provided a second estimate of predator activity and proved to be an appropriate method for behaviour observations (see Chapter 7).

Spotlighting was found to be more effective than transects for estimating activity of rabbits and macropods at most sites (see Chapter 4). For example, increases in the activity of macropods at Sturt National Park and rabbits at Quinyambie Station during sampling years were detected using spotlighting but not transects. For macropods this was probably due to dispersal after rains. The reverse was found at Finniss Springs, where macropods were only detected on transects in the first sampling year. At Mundowdna-Wilpoorina, large differences in macropod activity estimates between transect and spotlighting indices may have been due to two factors. First, on some nights, sampling was conducted in light rain, and macropods are generally less visible under such conditions (S. Litchfield pers comm. 7th March 2006). Second, regular hunting of macropods at Mundowdna-Wilpoorina may affect behavioural response to the motor vehicle, scaring individuals from the spotlighting route. Wind direction and strength during spotlighting are also important, as dust generated by the movement of the motor vehicle reduced visibility on some occasions. Moonlight has also been shown to affect activity and movement (and thus detection) of prey species, with less activity detected on moonlit nights (Dickman, 1992; Gilbert and Boutin, 1991). Finally, large amounts of vegetative growth following rain makes detection of target species (particularly rabbits) using the spotlighting method more difficult. Habitats with dense cover may be preferred by rabbits (see Chapter 5), therefore activity estimates for each site need to be considered in light of the proportion of optimal habitat available.

9.5 Trophic regulation and dingo management in context – the human element.

The presence of large carnivores in an ecosystem can often be an indication of ecological richness and diversity (Estes, 1996; Santiapillai and Jayewardene, 2004), while the removal of top predators can lead to unintended and often undesirable consequences, particularly if that species acts as a keystone species in the community (Rayner *et al.*, 2007). However, conservation of predators is dependent on both the environment and socio-political landscape (Treves and Karanth, 2003), and there remain many practical limitations to the reintroduction of apex carnivores where livestock grazing is the dominant land use. Much dingo research in Australia continues to focus on the control of dingoes as a pest species, rather than as an integral part of ecosystem function and management (Fleming *et al.*, 2006).

The exclusion or eradication of dingoes from ecosystems across Australia is strongly associated with land use factors that are also likely to be of detriment to native mammal populations, such as sheep grazing (Letnic and Koch, 2010). Dingoes persist in relatively intact populations across arid regions north of the DBF, but are heavily controlled in areas south of the DBF where sheep grazing is the primary livestock enterprise (see Chapter 2). While the reintroduction of the dingo may be a cost effective means to restore biological diversity south of the DBF, resistance would most likely be strong within farming communities, and such a process would require extensive community consultation, legislation and the application of innovative and non-lethal means to protect livestock to be at all feasible in the long term (Dickman *et al.*, 2009).

Due to the relationship between agricultural expansion, apex carnivore removal and mesopredator release, one possible solution would be to increase the suitability of some lands in agriculture areas for apex predators (Prugh *et al.*, 2009). By increasing connectivity of landscapes (Soulé *et al.*, 2005) and maintaining buffer zones around susceptible agricultural areas, it may be possible to reintroduce dingoes to selective areas and maintain viable populations. This must also be complemented by changes in regulations and statutes that require and provide incentives for the control of dingo populations in these areas.

Given much of the agricultural landscape is located in the more humid and productive landscapes of eastern and southern Australia, more research is needed into the function of the dingo in these eastern ecosystems, their effect on native species and the quantification of "ecologically effective" dingo populations (Letnic *et al.*, 2012b). The functional cessation of a species can occur even when the species is still present, through reduction in numbers to below a threshold where the species is ecologically effective, or through changes to species behaviour (Soulé *et al.*, 2005). In most cases top predator control should remain below the threshold that maintains dingo populations at a level at which they continue to exert top down effects on mesopredators (Courchamp *et al.*, 1999). However, with little known of ecological interactions between dingoes, prey and mesopredators in many ecosystems, this threshold is largely unknown. It is unlikely that dingo populations will be functionally restored to many regions in Australia in the near future, and their structuring role in these ecosystems may never be fully understood. The long-term implications of this for native species are significant and need to be studied.

Finally, little is known about the impacts of control on the function of dingoes as top predators. Hybridisation with domestic dogs is known to increase when dingo populations are controlled, however the impacts of hybridisation on dingo behaviour and trophic regulation remain in question (Claridge and Hunt, 2008). There is also anecdotal evidence that the behaviour of dingo populations, including social structure, may be a determining factor in the strength or prevalence of interactions with mesopredators and prey. Where dingoes remain in packs with an intact social structure, they may be more effective at suppressing smaller carnivore populations (Wallach *et al.*, 2009b). Similarly, stable, uncontrolled packs of wolves have been found to be less nomadic in their range and from this appear to have more of an impact on resident coyote populations (Carbyn, 1982).

In Australia, an increasing number of fauna have been recently introduced and large behavioural adaptations of many species are yet to be seen. As such, short-term "fix it" management strategies may in the long term cause significant changes in ecosystem structure and function, including loss of biodiversity at all trophic levels (Miller *et al.*, 2001). The recent trend towards conserving ecosystems as intact systems rather than focusing on single species conservation (Estes, 1996) takes into account the importance of community interactions for the effective conservation of species, suites of species or indeed ecosystem function (Linnell and Strand, 2000). There is now sufficient evidence and the urgent need to incorporate understanding of top-order predators in biodiversity management programs. Changing the way we think about ecosystems and trophic interactions that occur within them, may be lead to more effective management and conservation outcomes.

Chapter 10: Conclusion

The aim of this thesis was to investigate the role of the dingo in structuring ecological communities through trophic regulation. Dingoes, as apex predators, have the potential to be of conservation benefit to some native mammals if they are able to suppress or reduce the impacts of introduced mesopredators (foxes and feral cats) on prey populations. Evidence of top-down regulation of mesopredators by dingoes may include avoidance areas of high dingo activity, not exploiting potential food or water sources, or changing activity patterns in areas where dingoes are present.

This research found that the management of the dingo, as the apex predator in arid ecosystems, was a key determining factor of the activity and behaviour, including resource use, of dingoes and the exotic mesopredator, the red fox at the study sites. The impact of dingo management on the activity and behaviour of feral cats was less conclusive. Dingo management also influenced the activity of some prey species. While the findings of this research may be limited to the select study sites used, they add to a growing body of literature that dingoes can and do influence community structure on a regional scale.

Dingo management influenced both the activity of mesopredators, particularly foxes, and select prey species. Where dingoes remained uncontrolled, foxes were significantly less active, as were larger prey such as macropods. At sites where dingoes were selectively controlled (exclusion fencing) fox activity increased dramatically and the activity of medium-sized and smaller mammalian prey declined. These results support both the MRH and the hypotheses outlined in Chapter 1. When dingoes (and non-target foxes) were controlled by baiting, feral cat activity increased. These results suggest that while dingo management influenced fox activity, feral cat activity appeared to be more strongly associated with other influencing variables including fox activity, habitat and prey activity.

A key finding of this thesis was the impact of rainfall events on these interactions. In arid Australia, many prey species are driven by "boom-bust" cycles, increasing in response to rainfall and temporal productivity. This research found that even with increasing prey activity post rains, interactions between predators remained consistent, with top down regulation occurring regardless of prey availability. While the strength of top-down effects may be reduced during times of high productivity, the persistence of interactions indicates the importance of dingoes in maintaining long-term ecological interactions in arid ecosystems.

.A crucial element of this thesis was to examine the role that behavioural change played as a mechanism behind trophic interactions. The influence of dingo management on predator behaviour was explored through examining resource use, including the use of habitat, water and food resources. Management of dingo populations was found to have no determinable effect on the use of habitat by predators. Results did not support the hypothesis that mesopredators would change their use of habitat, for example using more sheltered habitats, at sites where dingoes were uncontrolled. Dingoes showed no preference for habitat, whereas foxes strongly preferred sand dune habitats regardless of dingo management. Similarly, feral cats showed a preference for creek and drainage lines whether dingoes were present or absent. These results suggest that habitat use is more strongly associated with prey presence and suitability to hunting style than the presence of the top predator.

Dingo management did, however, play a key role in determining the activity of foxes and feral cats in proximity to shared water resources at the study sites. Foxes activity was higher closer to water resources where dingoes were controlled through exclusion fencing, while feral cats were found closest to water where dingoes (and non-target foxes) were controlled through 1080 baiting. These results support the MRH for foxes and the hypothesis presented in Chapter 1. Changes in feral cat activity appear to be associated with changes in both dingo and fox activity. The response of feral cats to the removal/reduction of both canids was found to be stronger than the removal of dingoes alone.

Behaviour and visit rates of foxes at shared resources (food and water) were found to be influenced by dingo management. Where dingoes were uncontrolled foxes displayed lower visit rates and spent less time at resources than at sites where dingoes were controlled. Lack of data on feral cats meant that it was difficult to determine the effect of dingo management on feral cat use of resources and results were inconclusive. As such the hypothesis presented in Chapter 1 is supported for foxes, but remains inconclusive for feral cats.

It is clear from these findings that more research is needed into the effect of top down regulation on feral cat populations. It is likely that the control of both dingoes and foxes, or the control of dingo populations in areas where fox populations are suppressed or not present (such as the far north), would result in an increase in feral cat activity and/or abundance and consequently predatory impacts on a wide variety of smaller prey vulnerable to feral cat predation.

From the results of this research, it is clear dingo management strategies or control measures may influence intra-guild interactions and have important implications for biodiversity conservation. If dingoes are found to be able to control mesopredators through top-down forces, then the control and current status of the dingo as a pest species throughout much of Australia may be to the detriment of native prey populations vulnerable to fox and feral cat predation. In particular, where dingoes are removed from ecosystems through exclusion fencing or target poisoning, increased predation by foxes and feral cats may lead to the severe decline even extinction of some native species populations.

Despite increasing evidence of the role dingoes play in the structure of arid Australian ecosystems, the ability to predict changes in dingo management in other bioregions remains limited. Difficulties of assessing the functional role of dingoes in more complex ecosystems, including the increased complexity of human activities (such as livestock enterprises and dingo management protocols associated with this) has restricted the opportunity to conduct large scale studies in the forested and temperate regions of eastern Australia. Never-the-less, much may be gained by further field research in other bioregions, such as the tropical north, semi-arid Queensland and large tracts of Western Australia where intact dingo populations and their ecological effects still remain.

As with most applied ecological research, the final step is the transference of knowledge gained through research activities into practical management strategies. If dingoes are shown to play an important ecological role within ecosystems, there needs to be innovative approaches developed which allow for the conservation of viable and ecologically efficient dingo populations to be retained, ideally on both public and private lands. While this is not always achievable in practice, there is always the hope that small scale achievements in reconciling conflict interests between dingoes and graziers may provide for future scenarios where dingos are retained as apex predators on a national scale, to the benefit of many native species and biodiversity conservation measures in Australia.

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Appendix 1: Published papers

On the following pages are two papers published from the outcomes of a workshop on trophic regulation by the dingo, held in Perth, October 2005. The papers present a review on the general thesis topic; they do not contain information directly obtained from chapters in the thesis. The papers were published under my maiden name of R.L. Visser during my PhD candidature.

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Developing a national framework for Dingo trophic regulation research in Australia: Outcomes of a national workshop. Renee L. Visser, Fenner School for the Environment (The Australian National University, Canberra, ACT 0200, Australia, Tel: +61 2 6125 2623; Email: renee.visser@anu.edu.au); James E. M. Watson, Centre for Applied Environmental Decision Analysis (The Ecology Centre, The University of Queensland, St Lucia, Qld 4072, Australia); Chris R. Dickman, Institute of Wildlife Research (School of Biological Sciences, The University of Sydney, NSW 2006, Australia); Rick Southgate, Envisage Environmental Services (PO Box 305, Kingscote, SA 5223, Australia); David Jenkins, School of Animal and Veterinary Sciences (Charles Sturt University, Locked Bag 588, Wagga Wagga, NSW 2678, Australia); and Christopher N. Johnson (School of Marine and Tropical Biology, James Cook University, Townsville, Qld 4811, Australia).

Key words: *Dingo, workshop, trophic regulation, research framework.*

Introduction

There has been speculation about whether the Dingo (*Canis lupus dingo*) plays an important role in maintaining ecosystem function through top-down trophic regulation. The lack of focused research prompted the organization of a workshop attended by Dingo researchers and managers from across Australia in October 2005 (Dickman *et al.* 2006). Workshop attendees recognized the benefits of improving both the strategic direction and integration of research ideas and results. This led to a second workshop: Towards a National Agenda for Dingo Trophic Regulation Research, held on the 26th November, 2007 in Perth, Western Australia. Attendees sought to develop a framework, based on Visser (2007) and outlined here, for Dingo research in Australia to ensure that future experiments address gaps in our knowledge and minimize repetition among studies.

A possible framework for future Dingo research

Workshop attendees divided the Australian continent into four broad bioclimatic zones following Hobbs and McIntyre (2005) (see Fig. 1) as the trophic roles that the Dingo plays are likely to vary across these zones. This is because: (i) assemblages of native and exotic prey species differ between zones; (ii) an exotic mesopredator possibly affected by the Dingo (the Red Fox *Vulpes vulpes*) occurs in some zones only; and (iii) Dingo management regimes vary widely across the continent. For each bioclimatic zone, a model of interactions was constructed with links within the trophic web (Fig. 1). Workshop attendees discussed past and current research to identify which interactions had been studied, and which required further research. This broad review, which has been submitted for peer review elsewhere, revealed that most hypotheses on Dingo-trophic regulation have not been tested adequately, with research focusing largely on the possible effects of the Dingo on exotic mesopredators and prey. The following is a summary of the key research needs in each of the four bioclimatic zones as discussed at the workshop.

The northern zone

The impacts of the Dingo on cattle in this zone have been explored indirectly through dietary studies (see review in Corbett 1995), but more research into the direct effect of the Dingo on cattle and livestock production is needed (Fig. 1). Current research on the effects of feral Pig (*Sus scrofa*) on rainforest vegetation (Wet Tropics CRC) could be expanded to examine the interaction between the Dingo, feral Pig, cattle and vegetation in both rainforests and savannahs.

Previous research has suggested a positive correlation between the presence of the Dingo and the persistence of small mammal populations (see review in Johnson *et al.* 2007); however, the mechanism driving this pattern is unclear. Limited research has also suggested a negative impact of predation by feral Cat (*Felis catus*) on small mammals, but the overall effect of this predator on biodiversity has yet to be addressed in this bioclimatic zone. Ways to tease out the unstudied interactions (Fig. 1) include: (i) manipulation of Dingo populations by baiting; (ii) manipulation of cattle numbers; (iii) manipulation of fire regimes (whilst monitoring effects on biodiversity); and (iv) manipulation of feral Pig numbers (whilst monitoring cattle attack incidents). To be interpretable, replicated manipulations need to be conducted on cattle stations with and without Dingo. As this zone is subject to changing fire regimes and shifts in rainfall seasonality, experiments should be conducted ideally under varied conditions.

The arid zone

Most current research on Dingo trophic regulation is being carried out in arid central regions, perhaps due to the relative ease of disentangling trophic interactions in these less complex and less productive environments. There are also

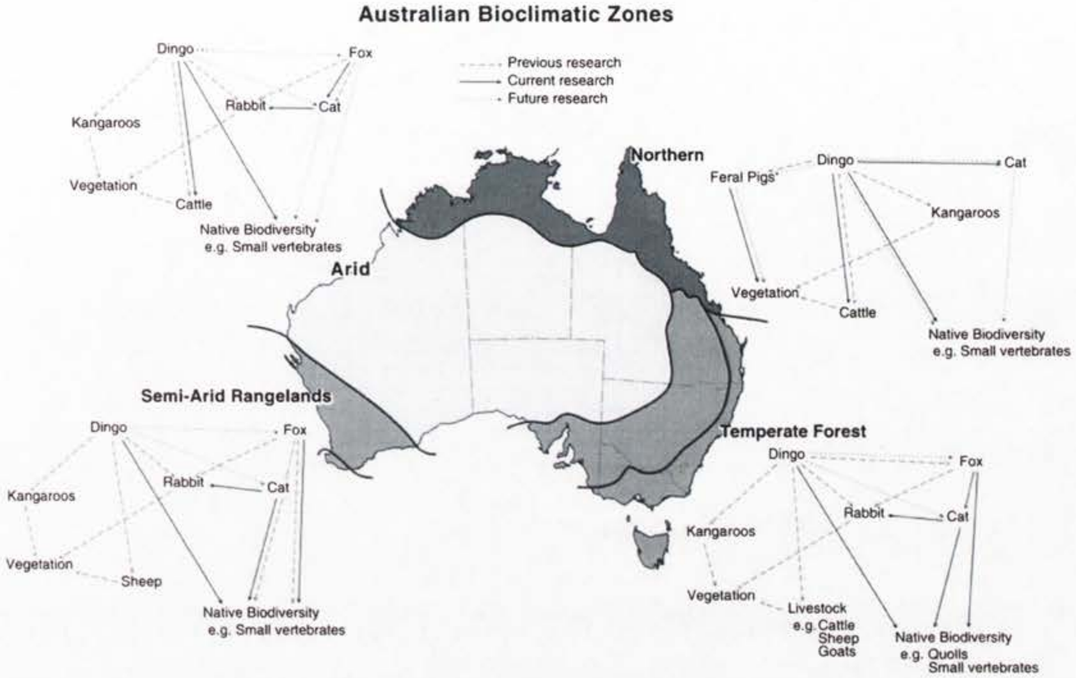

Figure 1. Model of major trophic interactions between the Dingo, mesopredators and prey within each of four bioclimatic zones in Australia. Arrows indicate the status of research on the interactions.

several areas in arid central and north-western Australia where there has been little or no control of the Dingo and there is an extensive reserve system; these factors provide opportunities to study interactions and manipulate populations away from the effects of cattle grazing (Fig. 1).

In parts of this region, the Dingo, feral Cat and Fox occur sympatrically where the Rabbit (*Oryctolagus cuniculus*) is abundant. This situation changes dramatically where the Rabbit is absent and prey scarce. Then, Dingo predation on other predators may provide respite for small and medium-sized native animals such as Bilbies (*Macrotis lagotis*) (Southgate *et al.* 2007) and hopping-mice (Letnic *et al.* 2009). Research has highlighted the effect of the Dingo on large herbivores such as Emu (*Dromaius novaehollandiae*) and macropods by sampling populations either side of the Dingo fence. The Dingo is also a regionally important predator of the (herbivorous) Rabbit, particularly where the Fox and feral Cat occur at lower densities.

As in northern Australia, some work has focused on the effects of Dingo on cattle (Eldridge *et al.* 2002) and on the abundance and behaviour of the Cat and Fox (see Pavey *et al.* 2008).

Possible ways to quantify unstudied interactions within this zone include: broad-scale manipulation of Rabbit populations with calici or myxoma virus; control of water availability; manipulation of fire regimes; and reintroduction of the Dingo into reserves. Importantly, the arid zone represents the northern range limit for two major interactive species, the Fox and Rabbit. The climatic threshold where the Rabbit drops out is likely to have a major influence on interactions within the model. The current limit of the Rabbit's distribution may provide an ideal opportunity to disentangle interactions between these species and predators such as the Dingo and feral Cat, and native herbivores, such as kangaroos and smaller prey species. The reliance on artificial watering points by many species in arid regions means that comparative studies may be needed between wet and dry times. Manipulation of access to water during dry times would also aid in understanding interactions between predators. Alternatively, because vegetation and prey populations respond rapidly to rainfall, manipulations of the Dingo, Foxes or Cat, could take advantage of the state of the environment; the most dramatic results from predator manipulations could be expected a year or more after heavy rain when prey populations were collapsing and predator populations still rising.

The semi-arid rangelands

The Dingo has been reduced to only scattered populations in the semi-arid rangelands due to conflict with sheep grazing (Johnson *et al.* 2007). There is also increased Dingo-feral dog hybridization compared with Dingo populations in the north-west of the continent (Newsome & Corbett 1985). Workshop attendees believed that the only place where higher densities of the Dingo may be found in this bioclimatic zone is on the outside of the New South Wales-Queensland Dingo fence or in Western Australia.

Known interactions in the rangelands include the effects of macropods, Rabbit and sheep on vegetation, Fox and Cat on Rabbit, Dingo on Rabbit and macropods, and Dingo on sheep and cattle (Fig. 1). Possible ways to examine unstudied interactions within this system include: introducing the Dingo to reserves; the use of Dingo surrogates (such as Dingo urine) to test herbivore and mesopredator responses; manipulation of Rabbit populations by poisoning and manipulation of kangaroo numbers (possibly where they are already regularly controlled). If guardian dogs are found to be effective in protecting sheep flocks, controlled reintroductions of the Dingo could be made more broadly into the rangeland environment and the effects studied on small vertebrates, kangaroos, mesopredators and vegetation (Dickman *et al.* 2009).

The temperate forests

In the higher productivity temperate forests and woodlands, vegetation structure replaces water as the major variable influencing Dingo trophic interactions. Dense vegetation may make it easier for the Fox and feral Cat to avoid direct confrontations with the Dingo, but more information is needed on the movement and behaviour of the Dingo in forest habitats.

In more mesic areas, including the rangelands and temperate forests, manipulation of Dingo numbers through baiting is not feasible because of the confounding effect on Fox populations and low Dingo numbers. Due to continuous baiting and other control measures designed to reduce stock losses, populations of Dingo, Dingo hybrids or wild dogs may not be large enough to have trophic or other effects on the Fox or feral Cat, although there is evidence for limitation of the Fox by the Dingo (Johnson & VanDerWal 2009).

Some interactions are similar to those in the semi-arid zone and include the effects of macropods, Rabbit and sheep on vegetation, the effects of the Fox and feral Cat on the Rabbit, and the effect of the Dingo on sheep and macropods (Fig. 1). However, the presence of a mid-sized native carnivore, the Spotted-tailed Quoll (*Dasyurus maculatus*) in this system adds a further dimension to trophic interactions. The interactions between introduced carnivores (feral Cat and Fox) and Spotted-tailed Quoll have been studied to some extent (Glen & Dickman 2005), but little is known about interactions between Spotted-tailed Quoll and Dingo.

Interactions within this system could be explored using isolated but intact Dingo populations; manipulation of fire regimes; and incorporation of research goals into current state programs such as Fox baiting (Fig. 1).

Conclusion

The workshop showed that, despite a substantial amount of literature (e.g. Glen & Dickman 2005; Glen *et al.* 2007; Johnson *et al.* 2007), too little remains known about the trophic interactions of Australia's apex predator. Attendees believed that accurate scientific data must underpin the development of a coherent Dingo conservation policy, and that a coordinated network of researchers able to work within the suggested framework should be established.

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A national framework for research on trophic regulation by the Dingo in Australia

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There is increasing evidence that the Dingo *Canis lupus dingo* plays an important ecological role as a trophic regulator in Australian ecosystems. However, there is sufficient remaining uncertainty about the nature of this role as to hinder the development of effective management policies. This review defines strategic directions for future research on the trophic role of Dingoes by developing a national Dingo research framework. The framework aims to increase our knowledge of the influence that Dingoes have on the maintenance of biodiversity, thereby encouraging Dingo conservation and the refinement of current land-use practices. The framework begins by identifying four major bioclimatic zones across Australia that pose different questions and challenges for Dingo research. For each zone we construct a model that identifies major interactions between Dingoes and key prey or competitor species, and then used the models to identify key research needs, the possible advantages of maintaining Dingo populations within each zone, and ways to tease out unstudied interactions. Important questions identified in the review include the effects of Dingoes on native marsupial populations, vegetation communities, herbivore diets, the use of structural refugia by mesopredators, predator and prey behaviour, and the effect of habitat modification on these interactions. We briefly review legislative constraints and other factors, such as the ongoing hybridization of Dingo populations with domestic dog breeds, that may impede future studies. If research activities follow this framework, we believe that policy and management will be better informed, benefiting both the Dingo and the natural ecosystems and production systems where it occurs.

Key words: Dingo, Australia, ecosystem function, research framework, bioclimatic zone

INTRODUCTION

TOP-order predators have been reintroduced successfully in many parts of the world in attempts both to conserve the species themselves and to restore important ecological interactions. Positive effects on biodiversity have been reported following many of these reintroductions (Hayward and Somers 2009). In consequence, it has been suggested that the Dingo *Canis lupus dingo*, as the largest terrestrial predator on the Australian mainland, may also play a role in maintaining ecosystem function through top-down trophic regulation (Glen *et al.* 2007; Johnson and VanDerWal 2009). A number of hypotheses relating to trophic regulation by Dingoes have been identified, including that Dingoes affect the abundance or activity of mesopredators (medium-sized predators such as the Red Fox *Vulpes vulpes* and Feral Cat *Felis catus*) and herbivores such as the larger species of kangaroos *Macropus* spp., that Dingoes affect ecological relationships between other predators and herbivore species, and whether Dingoes entrain ecological cascades (Dickman *et al.* 2006; Wallach *et al.* 2009). However, considerable uncertainty remains about the ecological role that the Dingo plays in some Australian ecosystems. This lack of understanding, as well as ongoing contention about the impact of the Dingo in production systems, has hindered the development of effective management policy for the species. Some Australian states (e.g., New South Wales, Victoria) currently address the conservation status of the Dingo under their respective threatened species conservation acts, whilst at the same time "wild dogs" (including Dingoes, Feral Dogs *Canis lupus familiaris* and their hybrids) are registered as pests.

Recent research, coupled with an increased awareness of Dingo control as a substantive issue for conservation and management, prompted the organization of workshops on the "Dingo as a trophic regulator". These workshops were attended by Dingo researchers and managers from across Australia in October 2005 (Dickman *et al.* 2006) and November 2007 (Visser *et al.* 2009). The workshops confirmed that progress has been made in research on the trophic and ecological effects of the Dingo over the past decade, and also suggested that there is now sufficient evidence to justify changes in the management of Dingoes in some regions, such as the arid zone. However, attendees of the workshops recognized that not enough is known to predict the outcomes of changing Dingo management in different regional ecosystems, and identified further that benefits would accrue from improving both the strategic direction and level of integration of Dingo research. Furthermore, the workshops highlighted an

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urgent need to develop a framework for guiding such research in Australia. A research framework would ensure that future observations and experiments effectively addressed important questions, with minimal repetition between studies, and that research should be of use for informing decisions about management and policy. The aim of this paper is to provide an overview of past and current research on the trophic interactions of Dingoes, and thus establish an effective framework that will guide the direction of future research.

A FRAMEWORK FOR CONDUCTING POLICY-ORIENTED DINGO RESEARCH

The role that Dingoes play in the Australian environment is likely to vary across different bioclimatic zones. There are several reasons for this. Firstly, assemblages of native and exotic prey species vary between bioclimatic zones, so direct and indirect interactions will differ with location. Secondly, exotic mesopredators that are potentially affected by the presence of Dingoes occur only in some bioclimatic regions and are likely to vary in density even where they are present. Thirdly, Dingo management differs across Australia. As a consequence, different bioclimatic zones raise different questions and challenges for research that is aimed at assessing the trophic role of the Dingo. Following Hobbs and McIntyre (2005), we divided the Australian continent into four broad bioclimatic zones to provide the spatial structure for our framework (Figure 1): northern Australia (>600 mm rainfall per annum; the dominant land use is cattle grazing), the arid zone (low rainfall and very high potential evapo-transpiration, giving rise to low primary productivity; the dominant land use is cattle grazing), the semi-arid rangelands (low rainfall and high potential evapo-transpiration, resulting in moderate primary productivity; the dominant land use is sheep grazing), and the temperate forests and woodlands (high rainfall and primary productivity; dominant land uses include mixed agriculture and pastoral activities).

For each bioclimatic zone, we constructed a model of interactions that identified direct and indirect trophic links between key species and functional groups within the interaction web (Figure 1). We reviewed past and current research in each bioclimatic zone and identified interactions involving the Dingo on which information was available, and also links that require further research to elucidate their importance. The review revealed that most hypotheses generated to date on Dingo-trophic regulation have not been thoroughly tested, with most current research being focused on the effects of Dingoes on the activity of exotic mesopredators and the abundance of prey. As the common Dingo control technique of baiting with 1080 poison kills both Dingoes and Red Foxes, experimental evidence of interactions

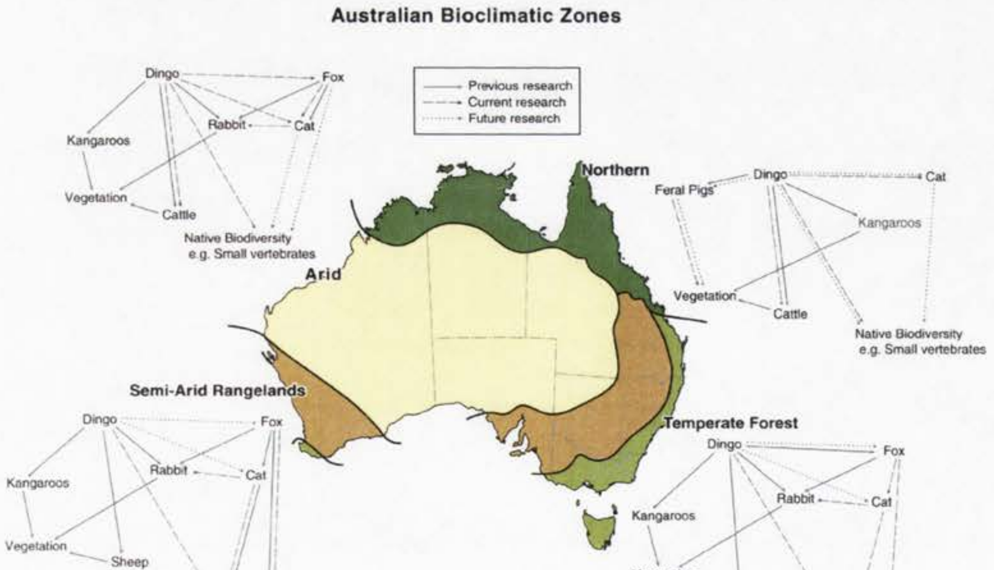

Fig. 1. Key interactions between dingoes and their environment in four broad bioclimatic zones: (a) Northern (>600 mm rainfall per annum), (b) Arid (low rainfall and very high potential evapo-transpiration, low primary productivity; dominated by cattle grazing), (c) Semi-arid rangelands (low rainfall and high potential evapo-transpiration, moderate primary productivity; dominated by sheep grazing) and (d) Temperate forest. (Adapted from Visser *et al.* 2009).

between these species and other mesopredators, such as the Feral Cat, is difficult to obtain.

There has been a substantial amount of research on the diet of Feral Cats, Red Foxes and Dingoes, so that broad patterns of dietary overlap are known for many systems. A few studies have examined the diets of all three predators at one site (May 2000; Paltridge 2002), and limited intra-guild predation of both species of the smaller predators by Dingoes has been recorded (Corbett 1995a; Molsher 1999; Risbey *et al.* 1999). Some research has also been carried out on spatial avoidance of Dingoes by Red Foxes (Mitchell and Banks 2005), but almost no research has focused on the impact of Dingo presence on the behaviour of other species of mesopredators or herbivores. In addition, little research has been conducted in mesic environments, where interactions may vary in type or intensity with habitat complexity (Visser 2007).

In most regions of Australia, climatic variation and environmental perturbations, such as drought and fire, play a role in shaping animal behaviours and population responses; the effects of environmental influences may override those of trophic regulation. It is important that future research within each of the bioclimatic zones incorporates environmental variation into the design of sampling regimes and experimental manipulations.

The following is a breakdown of key research needs in each of the four bioclimatic zones as determined by researchers at the November 2007 workshop (Visser *et al.* 2009).

The northern zone

The predominant land use in the northern Australian climate zone is cattle grazing, with large areas also managed as reserve, defence and indigenous land (Woinarski *et al.* 2007a). Dingoes and Feral Cats are present, but Red Foxes are scarce or absent (Saunders *et al.* 1995; Saunders and McLeod 2007). Feral Pigs *Sus scrofa* are abundant in many areas and are a major pest for livestock enterprises (Choquenot *et al.* 1996). It is hypothesized that the advantages of maintaining Dingoes in this region would include control of populations of Feral Cats, kangaroos *Macropus* spp. and Feral Pigs. Control of the latter two species could provide positive effects on plant biomass and diversity by reducing damage to habitats that might otherwise be caused by over-abundant wild herbivores. Reduction of populations of Feral Pigs and kangaroos could also reduce competitive impacts on livestock and thus provide benefits for livestock production. Control of Feral Cats would benefit populations of small mammals, ground-nesting birds and reptiles.

The impacts of Dingoes on cattle in the northern zone have been explored indirectly through studies on calf predation (e.g., Allen and Gonzalez 1998), but more research into the effect of Dingoes on livestock production is required (Figure 1a). Research has shown that Dingo predation does not necessarily reduce Feral Pig populations, but does act to limit their growth (Corbett 1995b). Current research on the impact of Feral Pigs in rainforest areas (e.g., Wet Tropics Cooperative Research Centre) could be expanded to examine the interaction between Dingoes, Feral Pigs, cattle and vegetation in rainforest and savannah habitats. Further research on the effects of Dingoes on Feral Pigs also could be undertaken profitably in the Kimberley region of north-western Australia, where pig populations are predicted to expand (Cowled *et al.* 2009).

Pattern analyses have suggested a positive correlation between the presence of Dingoes and the persistence of small mammals (Smith and Quin 1996; Johnson *et al.* 2007); however, the mechanism driving this pattern remains unclear. Limited research has found predation by Feral Cats to have a negative impact on small mammal populations in this bioclimatic zone (Cameron 1994), but the overall effect of Feral Cats on biodiversity in this region has yet to be addressed. Possible ways to tease out the unstudied interactions (Figure 1a) include: manipulation of Dingo populations by baiting; manipulation of cattle numbers; manipulation of fire regimes (while monitoring the effects on biodiversity); and manipulation of Feral Pig numbers (while monitoring cattle attack incidents). Replicated manipulations need to be conducted on cattle stations with and without Dingoes. Experimental manipulation of Feral Cat populations also would be desirable, but Feral Cats are currently very difficult to control in large, open areas. In addition, this zone is subject to different environmental states that influence productivity and interactions, such as shifts in rainfall seasonality and fire regimes. Fire is a particularly important regulatory process in the northern bioclimatic zone (Williams *et al.* 2002) and should thus be incorporated into any observations or experiments that seek to uncover mechanisms of trophic regulation.

There is particular urgency for carrying out targeted field research in northern Australia, as populations of Feral Pigs and other introduced herbivores are expanding rapidly in this bioclimatic zone, while populations of native mammals are in decline (Woinarski *et al.* 2001, 2007b).

The arid zone

Most current research on Dingo trophic regulation is being carried out in the arid zone of central Australia (e.g., Corbett and Newsome 1987; Letnic *et al.* 2009a,b; R. Visser, unpublished data). This may be due to the relative ease of teasing out trophic interactions in environments that are structurally less complex and less productive than those in higher rainfall areas. Dingoes, Feral Cats and Red Foxes, as well as a major non-native prey species, the European Rabbit *Oryctolagus cuniculus*, occur throughout most of the region except the northern fringe (Saunders *et al.* 1995; Williams *et al.* 1995; Fleming *et al.* 2001; Robley *et al.* 2004). In arid central and north-western Australia, there is an extensive protected area system in which there has been little or no control of Dingoes. This may provide opportunities to study interactions and manipulate populations away from the otherwise pervasive effects of cattle grazing (Figure 1b).

In the northern parts of the Tanami (and possibly the Great Sandy) Desert, and in arid parts of north-western Australia, there are areas where Red Foxes, European Rabbits and Camels *Camelus dromedarius* are absent or scarce while Dingoes remain abundant (Thomson 1992; Southgate *et al.* 2006). This opens up an opportunity to examine interactions between Dingoes, Feral Cats and prey species. Previous research has revealed that Dingoes, Red Foxes and Feral Cats often occur sympatrically where Rabbits are abundant. This situation changes dramatically where the European Rabbit is absent and alternative prey is scarce. Under such circumstances Dingoes may dominate in more productive habitats, especially those within range of water resources, while Red Foxes (where present) and Feral Cats may become less common and restricted to more unproductive habitats such as sand plains and areas of laterite. In these situations, Dingoes may provide a "rescue" effect for medium-sized native animals such as the Bilby *Macrotis lagotis* (Southgate *et al.* 2007).

Sampling populations either side of the Dingo fence (Caughley *et al.* 1980) has revealed the effect of Dingoes on large herbivores in the arid zone. Populations of Emus *Dromaius novaehollandiae* and macropod species, particularly Red Kangaroos *Macropus rufus*, have been found to be limited, and in some situations regulated, outside the fence by Dingoes (Pople *et al.* 2000). The Dingo is also an important predator of the European Rabbit (Corbett 1995a; Williams *et al.* 1995), particularly in areas where Red Foxes and Feral Cats occur at lower densities, or when Dingoes are young or solitary. A reduction in herbivore populations by Dingo predation may in turn promote vegetation diversity and productivity (Letnic *et al.* 2009a).

As in northern Australia, past research has examined the effect of Dingoes on cattle (Eldridge *et al.* 2002). Interactions between Red Foxes and Feral Cats have also been investigated (e.g., Mahon 1999; Risbey *et al.* 1999). Long-term research into the impacts of foxes and cats on biodiversity in the arid zone is currently underway by scientists at the University of Sydney (Letnic *et al.* 2004, 2005, 2009a,b; Mike Letnic pers. comm.; see also www.bio.usyd.edu.au/dickmanlab/index.htm) and as part of the Arid Recovery project (see www.aridrecovery.org.au), while the effects of Dingoes on the abundance and behaviour of Red Foxes and Feral Cats have been studied to a limited extent (Southgate *et al.* 2006, 2007; Pavey *et al.* 2008). Recent experimental investigations confirm that native rodents increase after the removal of Red Foxes, Feral Cats and European Rabbits (Moseby *et al.* 2009), and perhaps indicate the kind of response that native animals might show if Dingoes are present and have strongly suppressive effects on mesopredators (Letnic *et al.* 2009a,b).

Possible ways to identify unstudied interactions within the arid zone include: broad-scale manipulation of European Rabbit populations with calici or myxoma virus; control of water availability (by changing the accessibility of artificial watering points); manipulation of fire regimes in spinifex grasslands; and the reintroduction of Dingoes into protected areas. Importantly, the arid zone represents the northern range limit for the Red Fox and European Rabbit. This climatic threshold is likely to have a major influence on interactions between these species. The current limit of the European Rabbit's geographical distribution may provide an ideal opportunity to disentangle interactions between Dingoes, Feral Cats, *Macropus* spp. and small prey species. The reliance on artificial watering points by many species in this region means that comparative studies should be conducted in wet and dry times. Manipulation of access to water during dry times would aid in understanding interactions between Dingoes, Red Foxes and Feral Cats. Alternatively, because vegetation and prey populations respond rapidly after rainfall in arid systems (Dickman *et al.* 1999; Pavey *et al.* 2008), manipulations of predators could take advantage of different states of the environment (Letnic *et al.* 2004; Letnic and Dickman 2009). Due to a time lag in the population response of predators, results from such manipulations could be expected when prey populations are declining. Conversely, effects might be reduced during dry periods when both predator and prey populations are sparse and localized (Mahon 1999).

The semi-arid rangelands

Dingoes have been eradicated from much of the semi-arid rangelands by the pastoral industry (Fleming 2000; Johnson *et al.* 2007), and now occur only in scattered populations throughout this vast region. There is also an increased occurrence of Dingo-Feral Dog hybridization in these landscapes compared with Dingo populations in the north-west of the continent (Newsome and Corbett 1985). The effects of reduced Dingo numbers and Dingo-Feral Dog hybridization on trophic interactions are unknown (Claridge and Hunt 2008), although Spencer *et al.* (2009) have shown recently that hybrids are larger than "pure" Dingoes and are potentially capable of hunting very large prey.

Known interactions in the rangelands include the effects of large macropods, European Rabbits and domestic sheep on vegetation (e.g., Tiver and Andrew 1997), the effects of Red Foxes and Feral Cats on European Rabbits (see review in Robley *et al.* 2004), the effects of Dingoes on European Rabbits and macropods (Corbett 1995a) and the effects of Dingoes on sheep and cattle (Allen and Sparkes 2001; Fleming *et al.* 2001) (Figure 1c). Possible methods to examine unstudied interactions within this system include: the introduction of Dingoes to reserves; the use of Dingo surrogates (such as Dingo urine) for testing herbivore and mesopredator responses; manipulation of European Rabbit populations and manipulation of macropod numbers (possibly where these are already controlled on a regular basis). If guardian dogs are found to be effective in protecting sheep flocks, and support is gained from the farming community, localized and controlled reintroductions of Dingoes could be made and the effects on small vertebrates, kangaroos, mesopredators and vegetation studied (Dickman *et al.* 2009).

The temperate forests

In temperate forests and woodlands, vegetation structure replaces water as the variable that most likely influences Dingo trophic interactions. Dense vegetation and rugged topography possibly enable both Red Foxes and Feral Cats to avoid direct confrontations with Dingoes, but more information is needed on the movements and behaviour of all three species in heavy forest. Low Dingo densities, coupled with confounding effects on populations of the Red Fox, make experimental manipulation of Dingo numbers by 1080 baiting unfeasible. Due to continuous 1080 baiting and other control measures designed to reduce stock losses in this bioclimatic zone (Fleming 1996), populations of Dingoes or other wild dogs may seldom be large enough to exert strong effects on other predators or prey species.

Well-known interactions are similar to those in the semi-arid zone, and include the effects of large kangaroos, European Rabbits and sheep on vegetation, the effects of Red Foxes and Feral Cats on European Rabbits (see review in Robley *et al.* 2004), and the effects of Dingoes on sheep (Fleming and Korn 1989; Fleming 2000) and macropods (Newsome *et al.* 1983; Robertshaw and Harden 1985) (Figure 1d). The presence of a native carnivore, the Spotted-tailed Quoll *Dasyurus maculatus*, in forested ecosystems adds a further dimension to trophic interactions. The interactions between exotic carnivores and Spotted-tailed Quolls have been studied (Glen 2005; Glen and Dickman 2005, 2008), but little is known about interactions between any species of quolls *Dasyurus* spp. and Dingoes in this bioclimatic zone.

Possible ways to tease out interactions within forest ecosystems may include the use of isolated Dingo populations (such as those in Kosciuszko National Park or on Fraser Island); manipulation of fire regimes; or incorporating research into current state-based control programmes for the Red Fox, such as the New South Wales Threat Abatement Plan, Southern Ark in East Gippsland, Bounce Back in South Australia, and Western Shield in Western Australia (Figure 1d). Results from these and earlier studies suggest that such programmes may yield valuable insights into predator interactions and impacts (Orell 2004; Olsson *et al.* 2005; Dexter and Murray 2009; Mahon 2009).

CONSTRAINTS AND OTHER IMPORTANT FACTORS IN A NATIONAL DINGO RESEARCH FRAMEWORK

A major hindrance for research on Dingo trophic regulation lies in the fact that the Dingo (as a "wild dog") remains classified as a threatening process and declared pest in most Australian states. This makes restoration of Dingoes into areas containing livestock or threatened prey species impossible and limits the ability of researchers to identify interactions between Dingoes and other species in many areas.

A second important issue particularly relevant to the temperate and semi-arid regions of Australia, is how hybridization may alter Dingo ecology and behaviour, and possibly then the functional role of this canid in these systems (Claridge and Hunt 2008). Feral Dogs and Feral Dog/Dingo hybrids may not have the same ecological effects as Dingoes. For example, it is known that the urine derived from Dingoes and domestic dogs has different effects on the behaviour of macropods (M. Parsons, unpublished data), and hybrids also are often larger than pure Dingoes (Spencer *et al.* 2009). The effects of hybridization on Dingo behaviour are difficult to assess, and likely also to be confounded by the extent of introgression, habitat and other variables such as proximity to human habitation. In addition, the social circumstances will differ for individual animals. For example, a hybrid animal living with mostly purebred Dingoes may behave more like a purebred Dingo than hybrids found in areas dominated by Feral Dogs and hybrids. The location and identification of purebred versus hybrid animals has been approached using microsatellite markers (Wilton *et al.* 1999); however, the identification process can be time consuming and expensive, and there is a need to find new methods that can be used rapidly.

CONCLUSION

This review shows that, despite a substantial literature on the ecological inter-relationships of Dingoes with other species (e.g., Glen and Dickman 2005; Glen *et al.* 2007; Johnson *et al.* 2007; Letnic *et al.* 2009a,b), our ability to predict the outcomes of changed Dingo management remains limited in most regions. There is a clear need to prioritize future research to improve our predictive capabilities. Research gaps identified in this review include the effects of Dingoes on native fauna, vegetation, herbivore diets, the use of structural refugia by mesopredators and prey, and prey behaviour. In addition, the effects of habitat modification and changes to habitat complexity on these interactions are poorly understood.

The first step in the development of a coherent Dingo conservation and management policy is to gain accurate scientific data to advance our understanding of the Dingo's influence on ecosystem function across bioclimatic zones. We believe that, in order to best inform policy and management, a coordinated network of researchers willing to work within the suggested framework needs to be established. Future meetings of the Dingo network are being planned to coincide with conferences, such as the Ecological Society of Australia and the Society for Conservation Biology, where attendees can report research outcomes and progress. This represents an ideal situation for the involvement of students and also promotes future research collaborations.

A second step is to ensure the transfer of scientific knowledge into practical solutions that allow for conservation of viable Dingo populations on both public and private lands. By gaining information and understanding across the broader landscape, researchers should be better able to approach the pastoral community with substantiated information in favour of retaining Dingoes in the ecosystems that they occupy. However, any kind of landscape approach to Dingo conservation will need the engagement, and sometimes education, of all relevant stakeholders, including landholders, researchers and governments.

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Appendix 2: Theoretical background to thermal imaging

Introduction

Thermal infrared imaging devices measure the amount of radiation emitted from the surface of an object in the thermal infrared wavelengths. The biophysical principles that apply to radiation exchange between organisms and their environment are therefore particularly important for understanding how different variables may affect the amount of radiation emitted by an organism and detected by the thermal imaging device. This section explores the theoretical background of radiation exchange and surface temperature measurement as it applies to the use of thermal imaging devices for observing terrestrial mammals.

All natural objects continually conserve or lose heat , maintaining a temperature balance with that of the surrounding environment (Kelly *et al.*, 1954). Heat loss, generated through sustaining this equilibrium, takes place in four main ways - conduction, convection, evaporation and radiation (Best and Fowler, 1981). Thermal infrared imaging technology measures the radiation component of heat loss; therefore this section will focus on radiation theory, environmental variables and physiological attributes of organisms applicable to the use of thermal imaging.

The Radiative Environment of a Terrestrial Organism

Figure A shows radiation received and emitted by a theoretical organism in a terrestrial environment. As shown, the animal is subject to various sources of radiation that differ in spectral composition, intensity and directional properties. Radiation flux forms part of a larger equation of energy transfer between an organism and its environment that is beyond the scope of this document. Of relevance to this study is the interaction of an animal's surface with radiation from ultraviolet, visible and infrared spectral intervals (Gates, 1980).

Solar (or short-wave) radiation is received by the animal either directly from the sun, or as diffuse radiation that is scattered by the atmosphere or reflected off the Earth's surface and other terrestrial objects (McCullough and Porter, 1971; Campbell, 1977). In contrast, long-wave radiation is received by the animal as it is emitted from other natural surfaces. All natural surfaces exchange long-wave radiation continuously with the atmosphere (Monteith and Unsworth, 1990). Long-wave radiation is emitted from all natural objects with a temperature above absolute zero (-273°C) (Croon *et al.*, 1968; Gill *et al.*, 1997), in a broad, continuous band of wavelengths ranging from 0.7 to 1,000μm (Brooks, 1970). Each object differs in the total amount and spectral distribution of emitted radiation (Campbell, 1977). The span of wavelengths within this range in which radiation is emitted from an object will depend on both its molecular structure and its temperature: as the surface temperature of an object decreases, the wavelength at which most radiation is emitted increases (Barber *et al.*, 1991; Croon *et al.*, 1968). The wavelength of maximum emission (l_{max}) is given by Wein's law;

$$l_{max} = 2897/T$$

where T (K) is the surface temperature of an object. Most natural objects on the Earth's surface have surface temperatures less than 200°C (<473.15 K) and therefore have a wavelength of maximum emission between 3-100µm. This range of wavelengths forms the arbitrary limits of the long-wave spectrum (Monteith and Unsworth, 1990).

As radiation reaches the surface of an object, it is either transmitted through the substance, reflected or absorbed (Oke, 1987). The proportions of radiation reflected, transmitted or absorbed define an objects' transmissivity (t), absorptivity (a) and reflectivity (r) at a given wavelength, where $a + t + r = 1$. Objects that absorb all radiation at a given wavelength are termed black bodies or full radiators, and $a = 1$, $r + t = 0$ at that wavelength (Monteith and Unsworth, 1990). The capacity of an object to emanate radiant heat at a given wavelength is referred to as its emissivity(McCullough *et al.*, 1969). At a given wavelength, emissivity of an object equals absorption, as shown by Kirchhoff's Law:

$$a_l = e_l$$

In accordance with this law, the emissivity of a black body =1. This ratio remains constant for all surfaces at the same temperature; that is, if objects are good absorbers, they will also be good emitters at the same wavelength (Gates, 1980). At wavelengths above 3µm, most natural surfaces have emissivities close to 1. This means they act like black bodies in the infrared part of the spectrum. This includes most types of animal coats, which have an absorptivity of 90-100% (Gates, 1980; Monteith and Unsworth, 1990). For instance the emissivity of the grey wolf's coat in both light and dark grey colour morphs has been estimated at 0.99, while the emissivity of the red fox lies between the values of 0.98-1.00, depending on coat hue (Hammel, 1956).

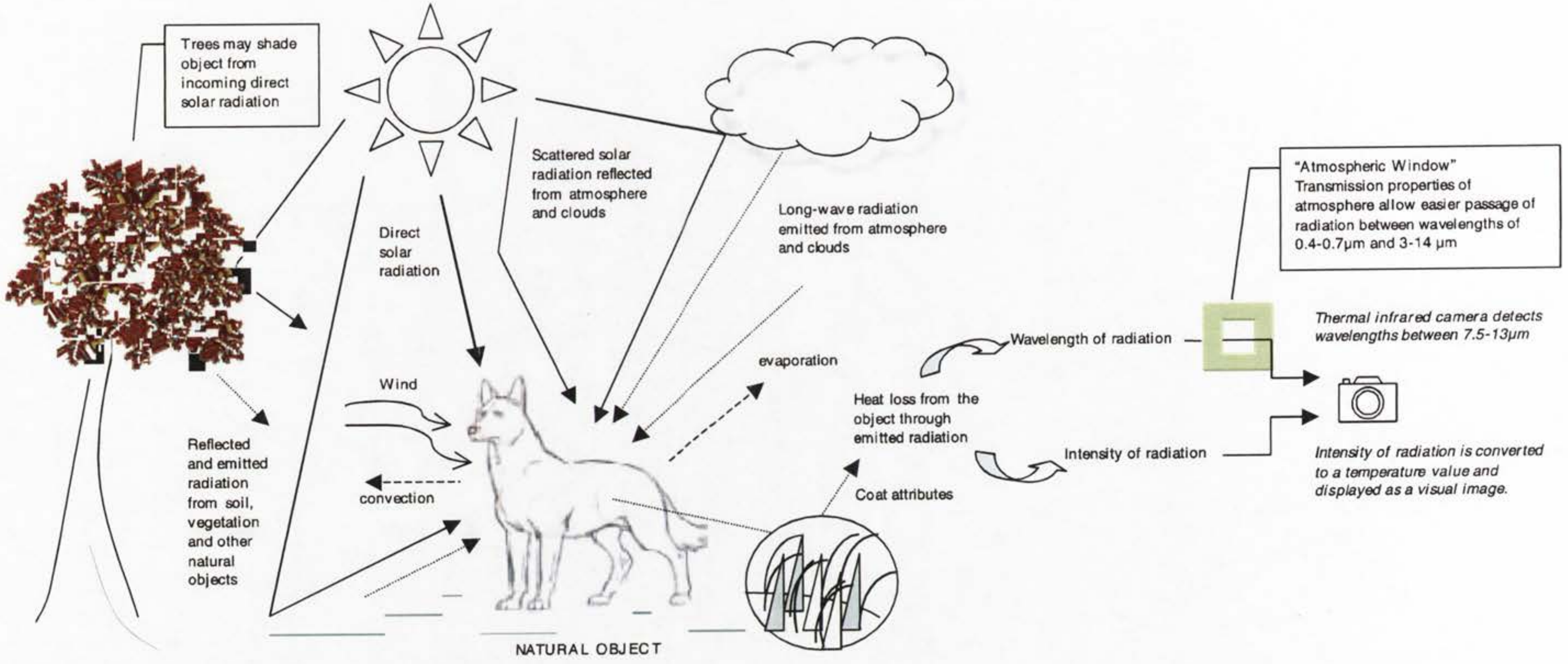

Figure A. A theoretical organism and its radiative environment, showing variables that affect the use of thermal imaging techniques in behavioural studies of terrestrial vertebrates.

Source: Adapted from Porter and Gates (1969).

The emissivity for an object will vary with the spectral wavelength used and surface characteristics (texture and temperature) which affect the objects' ability to absorb, reflect and emit radiation (Bernatas and Nelson, 2004; Croon *et al.*, 1968; Speakman and Ward, 1998). In the case of terrestrial mammals, the surface is typically covered by a coat of hair or fur, and it is the surface temperature of this covering that is of primary interest in thermal imaging. The coat provides an insulative layer over the skin, regulating convective and radiative heat flow, and in doing so forms an adjustable thermal barrier that varies in attributes such as structure and colour (Wolf and Walsberg, 2000; Cena and Clark, 1973). These coat attributes determine how well the coat acts as a thermal resistance mechanism in radiative exchange. A large variation in these attributes occurs between species, between individuals of the same species and across the surface area of each animal (Cena and Clark, 1972). Variation can also occur due to physiological responses to the environment, such as erecting of coat hairs (Cena and Clark, 1973a; Walsberg, 1988; Wolf and Walsberg, 2000) and seasonal changes in insulation.

Coupled with physiological variables, behavioural responses of animals aid in their thermoregulation and may significantly alter radiative heat loads (Wolf and Walsberg, 2000). Most species display an array of particular habits that aid in the conservation or dissipation of heat. Choice of habitat, timing of activity (for example diurnal, nocturnal or seasonal activity patterns) and positioning of the body are some common behavioural mechanisms that may aid to expel or conserve heat (Oke, 1987; Cena and Clark, 1973; Dawson and Brown, 1970). Often these behaviours will determine which parts of the animal are exposed to solar radiation, or they may aim to avoid exposure completely. Exposure to radiation and other environmental factors plays a significant part in an organism's heat balance. Ambient air temperature, wind, humidity, clouds, moisture, vegetation, soil, topography, shade and season are all environmental parameters that act simultaneously upon the animal, with various effects on radiation exchange. These variables are then coupled with physiological and behavioural attributes to produce a combined effect on the amount of radiation emitted from the animal (Porter and Gates, 1969).

An example of this interaction can be shown when the environmental temperature is lower than that of the animal and the environment may act as a significant heat sink. However, if the animal is furred the coat acts as an insulative surface against heat loss and the surface temperature of the coat may be close to the ambient temperature of the environment (Grojean *et al.*, 1981). The amount of radiant energy loss from the animal decreases linearly as the surface of the animal approaches the same temperature as its environment.

The heat loss by radiation from a warm animal to a colder environment depends on the surface temperature of the animal, the ambient temperature of the environment and the emissivity of both (Hammel, 1956) as shown by the Stefan-Boltzmann Law;

$$\text{Energy emitted (radiant flux)} = esT_0^4$$

where e is the emissivity of the surface, s is the Stefan-Boltzmann constant (5.67×10^{-8} W m^{-2} K^{-4}) and T_0 is the temperature of the body (K). To summarise, the amount of radiant heat from an animal in a natural environment will depend on a number of physiological, behavioural and environmental variables to which the organism is exposed.

Measurement of Infrared Radiation using Thermal Imaging

Infrared wavelengths used to measure radiant heat are found within the electromagnetic spectrum from 0.7-14μm (Kastberger and Stachl, 2003). Within this range, three light spectrums are often identified – near-infrared (0.8-1.2 μm), middle infrared (3 -7 μm) and far-infrared (8-14μm) (Barber et al., 1991). The term far-infrared spectrum often collectively encompasses the spectral range from 3-14μm, which is then divided into two wavebands: mid-wave (3-5μm) and long-wave (8-14μm) (Kastberger and Stachl, 2003). Most thermal infrared devices operate in the far-infrared spectrum on the long-wave band.

The choice of wavelength used to measure the surface temperature of an object will, as outlined in section 3.2.1, depend on the temperature of the target object. Objects of low (<200°C) or near ambient temperatures are more suited to long wave systems (Kastberger and Stachl, 2003) and mid-wave systems are more efficient when detecting higher temperatures (Dunn *et al.*, 2002). The choice of using either of the spectral ranges may also be attributed to the historical use of thermal imagery, namely military use, which focused on heat generating objects as targets, a practice also applicable to wildlife surveys (Wyatt *et al.*, 1980). Wildlife studies using thermal imagery technology have been conducted using both long-wave (Naugle *et al.*, 1996; Sabol and Hudson, 1995; Gill *et al.*, 1997; Haroldson *et al.*, 2003) and mid-wave (Boonstra *et al.*, 1994; Havens and Sharp, 1998; Hubbs *et al.*, 2000) systems.

The use of thermal infrared devices operating in the far-infrared spectrum for detection of objects at Earth temperatures (<473.15 K) has also been largely attributed to transmission characteristics of the atmosphere. "Atmospheric windows" are areas within the spectrum through which radiation passes more easily. They are primarily located at the visual, middle infrared and thermal infrared wavelengths (Barber *et al.*, 1991). One such "window" is located between the wavelengths of 8-13 μm, which corresponds to a blackbody emission peak for the earth at 288 K (Campbell, 1977). Due to this atmospheric window, large amounts of long-wave radiation emitted from the Earth are transmitted through the atmosphere between these wavelengths (Campbell, 1977; Dymond *et al.*, 2000). This means objects with Earth temperatures are more easily detected within this spectral range (Boonstra *et al.*, 1994; Graves *et al.*, 1972).

Thermal infrared imaging devices can detect and measure radiated energy with or without the presence of visible light (Sabol and Hudson, 1995). This is done through directing emitted radiation onto detectors and converting this into temperature values via electronic signalling (Kastberger and Stachl, 2003). These temperature values are then displayed as a visual image (Garner *et al.*, 1995). The intensity of the image displayed depends on the temperature of the object (Hill and Clayton, 1985): the image amplifies in intensity as temperature increases.

Emitted radiation is typified by two interacting properties that thermal imaging technology uses for surface temperature calculations: wavelength and intensity (Speakman and Ward, 1998). As infrared sensors rely on contrast between objects and their background, they will detect an object as separate from its surrounding only if its radiated heat contrasts adequately (Adams *et al.*, 1997). The differences in surface temperature needed to detect this contrast will vary depending on the thermal infrared imaging system used. Advances in technology has seen thermal infrared sensors capable of differentiating objects of thermal contrast less than 0.3°C (Garner *et al.*, 1995), and recent studies have demonstrated that objects warmer than adjacent objects by less than 0.1°C can be deciphered at distances up to 500m (Boonstra *et al.*, 1994). Modern systems have increased resolution and sensitivity, consist of smaller, more mobile units and include image processing software that enable easier interpretation of images (Garner *et al.*, 1995). Recent advances have also seen an increase in system stability, reliability, resolution and speed (Kastberger and Stachl, 2003), all of which will contribute to the increased use of thermal infrared technology in the ecological field.

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Appendix 3: An overview of Bayesian analysis

In its simplest form, Bayes's theorem (Bayes, 1763), states that for any given hypothesis (H) and the evidence against which it is to be considered (e):

$$P(H \mid e) = \frac{P(e|H)\,P(H)}{P(e)}$$

where $P(H \mid e)$ is the posterior probability, $P(H)$ is the prior probability and $P(e|H)$ is the likelihood of H given (e). (Howson and Urbach, 1991). This can be rewritten as:

$$P(\theta \mid y) = \frac{P(y \mid \theta)\,P(\theta)}{\int P(y \mid \theta)\,P(\theta)\,d(\theta)}$$

Where $P(\theta \mid y)$ (the probability of a parameter θ, given the data y) is proportional to $P(y \mid \theta)$ (the product of the probability of the data y, given the parameter θ) and to $P(\theta)$ (the probability of the parameter θ, not conditioned upon the data y). The posterior distribution is denoted by $P(\theta \mid y)$. $P(\theta)$ represents the prior distribution, while $P(y \mid \theta)$ is the likelihood function (Smith and Gelfand, 1992; Taylor *et al.*, 1996). The prior distribution is combined with the data to form the likelihood function $P(y \mid \theta)$. This likelihood function (or "Bayes factor") is used to modify initial beliefs (priors) with the data set (Jefferys, 1961). The posterior probability (posterior distribution) ($P(\theta \mid y)$) is the end product of the analysis. Results are presented as the probabilities of events occurring given a set of data values (circumstances) and the size of the effect. The posterior distribution embody all of the conclusions about the values of the unknown parameters presented in the analysis (Ver Hoef, 1996), with the hypothesis with the largest posterior distribution thought most likely to be true (Dennis, 1996).

Prior probabilities ($P(\theta)$) are a quantification of initial beliefs (gained from existing knowledge prior to the data y) about what would occur in a given situation. Prior probabilities (mathematically expressed as prior distributions) are estimated by observing the probability of two events or "states" of parameters occurring in relation to each other. For instance, the probability of a behaviour expressed by a fox at a resource may vary substantially depending on the "state" of other variables, such as rainfall or dingo density. Prior probabilities are specified by the researcher (Iversen, 1984), but the information used may come from many data sources, both subjective (for example hypothetical priors estimated from experience or expert knowledge of underlying processes) (Holthausen *et al.*, 1994) or from empirical data (Wolfson *et al.*, 1996). While some authors advocate the use of expert knowledge to elect priors (Nyberg *et al.*, 2006), others have chosen to use parametric empirical data or hierarchical Bayes methods in order to reduce subjectivity and avoid problems associated with the extrapolation of data or findings from other populations to the one under study (Ver Hoef, 1996). Priors are generally classified as either non-informative (all parameter values thought to be equally likely over the entire range of relevant values) or informative (using results from previous analyses to update our knowledge). So long as the prior distribution assigned to the parameter is not too narrow, both methods work effectively (Iversen, 1984).

The "subjectivity" involved in selecting prior distributions (see Dennis, 1996 for a critique) is moderated by using standard mathematical techniques which are beyond the scope of this thesis to explain. It is worth noting that for larger sample sizes, the posterior distribution is very insensitive to changes in the prior distribution (Howson and Urbach, 1991) so criticisms often directed at the seemingly "subjectivity" of elicitation of priors may be unsubstantiated in many cases (Dennis, 1996). However, the effect of prior distributions on the analysis becomes more important with small sample sizes or limited information (Iversen, 1984), such as in this study. Systematic methods for electing prior distributions are covered in (Berger, 1985; Jefferys, 1961; Winkler, 1967; Wolfson *et al.*, 1996).

It is important to note that there are major differences in terms of the underlying mathematical assumptions between Bayesian and classical statistics. The most prominent is the treatment of parameters. Bayesian statistical inference assumes population parameters θ are random, as we are unsure of their true value, and the data y are treated as fixed, as there is only one data set under consideration (Dixon and Ellison, 1996; Iversen, 1984; Ludwig, 1996). In contrast, frequentist statistics assume that population parameters are fixed constants and data are random values: confidence intervals include all possible sample means derived from the data. In other words, conclusions from Bayesian analysis are derived directly from the mean of the experimental sample and not from the means of possible samples (Howson and Urbach, 1991).

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Appendix 4: Thermal video DVD

A selection of thermal videos is provided on the attached DVD. For a detailed description of video contents, please refer to the DESCRIPTIONS.TXT file on the disc.