What’s That Smell? How Marsupials in Mulligans Flat Respond to Different Predator Odours

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.

Honours in the Fenner School of Environment and Society from 2017 comprises two distinct courses - ENVS4001 (Honours Research Skills) and ENVS4000 (Honours Thesis). Draft versions of chapters 1-3 of this thesis were originally submitted for assessment during the Honours midcourse review, which is part of ENVS4001. These chapters have since been modified extensively and are submitted in final form in this thesis for assessment as part of ENVS4000.

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Abstract

Approximately 10% of native Australian mammals have become extinct in the time since European settlement, with introduced predators being a main contributor to that loss. Predator free reserves act as refuges, or ‘islands’, for vulnerable species and are regularly used for reintroductions. Reintroductions outside of these areas often fail due to prey naïveté, which can include the inability to recognise the odours of predators. Different prey species use landscapes in a variety of ways, and spend more time in areas which they perceive to be less risky as per the ‘landscape of fear’ concept.

I set out to test how resident marsupials and reintroduced marsupials in a reserve free of mammalian predators responded to a range of predator odour cues. I also tested whether odour on its own, or an interaction with vegetation cover, influenced prey animals’ behaviour. I used material treated with body odours of rabbits, foxes, cats, dingoes and thylacine, and placed them in sites characterised by either low or high vegetation cover. Using camera traps, I measured the number of visits by different marsupial species to these sites, the duration of each visit, and the duration of vigilance behaviour compared to control sites with no odour.

I found that vegetation cover played a large role in how marsupial prey responded to odours. Eastern bettongs avoided sites with low vegetation cover and spent less time in the sites with rabbit odour, perhaps to avoid perceived competition. Eastern bettongs also displayed an increase in vigilance behaviour at sites with dingo odour in low and high vegetation cover. Eastern bettongs, eastern grey kangaroos, and brushtail possums all displayed anti-predator behaviour at sites with cat odour in high vegetation cover by displaying increased vigilance. Eastern grey kangaroos and brushtail possums displayed anti-predator behaviour to thylacine odour. Brushtail possums reduced the time spent at sites with fox odour.

My study demonstrates that these marsupials can, to some degree, respond to novel predators after a period of isolation. My results also demonstrate the importance of considering vegetation cover and the ‘landscape of fear’ concept when undertaking olfactory recognition studies. The next step in this research is to understand how marsupial species respond to predators’ odours outside of a predator-free area. This might involve a comparative study that observes species behaviours inside and outside of a fenced reserve. Research to look at volatile chemicals within predator body odour may help explain responses to introduced predators. My research has contributed to the understanding of predator-prey interactions between native marsupials and their potential predators, and has demonstrated all the species studied showed at least some level of naïveté which could be detrimental to them outside Mulligans Flat Woodland Sanctuary. However, further research using an experimental reintroduction to a site with low numbers of predators may allow prey to gain exposure and quickly adapt to the environment.

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List of acronyms and abbreviations

ANU: Australian National University

CWR: Critical Weight Range

GUD: Giving Up Density

IUCN: International Union for Conservation of Nature

MFWS: Mulligans Flat Woodland Sanctuary

Spp.: Species

Glossary and Terms

Biota: The animals, plants, fungi etc., of a region

Browse: vegetation such as twigs and young shoots

Ethogram: a list of quantitative descriptions of an animal’s normal behaviour

Critical Weight Range: The intermediate size group of animals (35g-5.5kg)

Forb: A herbaceous flowering plant other than grass

Giving Up Density: where the amount of food remaining in a food patch after a forager has stopped feeding in the patch is an indicator of cost-benefit behaviour in prey species

Hypogeous: occurring or living below the ground

Integumentary odour: Body odour that comes from the integumentary system such as skin oils and hair

IUCN Red List: The world’s most comprehensive inventory of the global conservation status of threatened animal, fungi and plant species by the International Union for Conservation of Nature

Landscape of fear: the spatial distribution of perceived predation risk as seen by a population or individual

Meso-predator: medium-sized, middle trophic level predator, which also has larger predators

Meso-predator release: Trophic cascade after removal of large top predators, creating a shift in trophic levels, allowing meso-predators to be more abundant

Oestrus: A recurring period of sexual receptivity and fertility in many female mammals

Olfactory recognition: recognition of odour

Prey naïveté hypothesis: prey animals do not recognise introduced and/or isolated predators and therefore do not display appropriate behaviour to avoid predation

Recruitment: The increase in a natural population through births and new members arriving

Reintroduction: putting a species back into a former habitat

Sward: the grassy surface of land

Translocation: The capture, transport and release or introduction of species from one location to another

Trophic level: Each of several hierarchical levels in an ecosystem, consisting of organisms sharing the same function in the food chain

Volatile: easily evaporated at normal temperatures

Chapter 1: Introduction

The fear of being eaten greatly influences prey behaviour, often having significant physiological, foraging and fitness costs (McArthur *et al.*, 2014). To survive amongst predators in their environment, prey species have adapted to use several senses for predator recognition and avoidance. Predators use stealth and surprise, so many prey species assess predation risk using predator odours in the landscape, produced from urine, faeces and body odour (Kats and Dill, 1998; Parsons *et al.*, 2017). If prey recognise their predators' odours, they can evaluate predation risk and modify their behaviour. Whether a scent is left by accident, or as a signal, it can be used by prey to decide how to avoid the predator (Russell and Banks, 2007; Wyatt, 2010).

Since 1788 - when Europeans settled in Australia - approximately 10% of mammal species have become extinct (see Appendix 1, Johnson, 2006; Woinarski *et al.*, 2015). The decline in the last 200 years means Australia has the highest mammal extinction rate in the world (Short, 1998; Woinarski *et al.*, 2015). Contributing factors include changed fire regimes, disease, hunting, habitat destruction and introduced predators (Robley *et al.*, 2002; Woinarski *et al.*, 2015; Legge *et al.*, 2017). Introduced predators put strong selective pressure on native prey and can restructure ecosystems, pushing many species to extinction (Letnic *et al.*, 2012).

The decline of many native fauna species coincided with the introduction of the fox (*Vulpes vulpes*) and cat (*Felis catus*) to the Australian landscape (Russell and Banks, 2005; Moseby *et al.*, 2011). Body size is believed to be linked to extinction, because most extinct and threatened Australian mammals include rodents and small marsupials weighing between 35g to 5.5kg – known as the 'Critical Weight Range' (CWR) (Burbidge and McKenzie, 1989). Animals in the CWR are disproportionately impacted by introduced predators because they are so small (Chisolm and Taylor, 2010).

The prey naïveté hypothesis (Cox and Lima, 2006) states that prey that have co-evolved with predator species will have adapted ways to avoid predation. However, introduced predators present in the landscape for a short period may not be recognisable. Consequently, Australian animals may be unable to use odours to avoid introduced predators. Australia's wildlife is thought to be so susceptible to introduced predators because many animals are naïve (Banks and Dickman, 2007; Anson and Dickman, 2013).

For foraging herbivores, predation risk varies across the landscape, as does the quality of food patches. High quality food patches should be favoured over low quality ones, and safer areas should be favoured over risky areas (McArthur *et al.*, 2014). Vegetation can provide shelter to prey from some predators, while increasing the risk from others, depending on their hunting strategies. Therefore, an animal's spatial and temporal use of the landscape is driven by fear (Laundré *et al.*, 2001). This 'landscape of fear' is a "landscape where peaks and valleys are defined by the predation risk related to differences in habitat as they affect the level of predation risk” (Laundré *et al.,* 2001). Consequently, vegetation paired with a predator odour may have more of an effect on prey behaviour compared to odour on its own.

The chance of survival for vulnerable species increases on offshore islands where they are isolated from introduced predators (Woinarski *et al.*, 2015). There are several fenced nature reserves found within Australia which act as island sanctuaries, protecting animals from introduced predators through isolation. These sites are used for conservation management and research involving reintroductions of locally extinct species (Moseby *et al.,* 2011; Shorthouse *et al.,* 2012). Reintroductions outside fenced reserves often fail because of exotic predators (Moseby *et al.,* 2011). Mulligans Flat Woodland Sanctuary (MFWS) is a nature reserve in the north of the Australian Capital Territory where animals have been isolated from exotic predators since 2009, when a predator-proof fence was closed and foxes and cats were removed (Manning *et al.,* 2011). Marsupials found within MFWS include brushtail possums (*Trichosurus vulpecula*), eastern grey kangaroos (*Macropus giganteus*), swamp wallabies (*Wallabia bicolor*) and red-necked wallabies (*M. rufogriseus*). In addition, two locally extinct marsupials have been reintroduced: the eastern quoll *(Dasyurus viverrinus)* and eastern bettong *(Bettongia gaimardi).* Once widespread throughout south-eastern Australia, these are two small, nocturnal, native marsupials which, until their reintroductions, were locally extinct on mainland Australia (Stannard *et al.*, 2013; Portas *et al.,* 2016). The eastern quoll was first reintroduced from Tasmania to Mt Rothwell, Victoria, in 2002, and then MFWS in 2016 (Adrian Manning, pers. comm). The eastern bettong was reintroduced to MFWS and Tidbinbilla Nature Reserve from Tasmania in 2011-2012 (Batson *et al.,* 2016).

1.1 Research Questions

Considering the ‘landscape of fear’ concept, the prey naïveté hypothesis, and that these marsupials are isolated from mammalian predators, I developed the following research questions:

(i) After a period of isolation since 2009, do marsupial species including brushtail possums, eastern grey kangaroos, swamp wallabies and red-necked wallabies respond to historical and novel predator odours?

(ii) Do the eastern quoll and eastern bettong, reintroduced to Mulligans Flat Woodland Sanctuary, display anti-predator behaviour to historical and novel predator odours?

(iii) Does vegetation cover influence prey responses to predator odours?

I was also interested in assessing whether quolls (that prey on rabbits – Peacock and Abbott, 2013) seek out rabbit odour, and evaluating the behavioural responses of native herbivores to the threat of competition from introduced rabbits. The reintroduced eastern quolls may have experienced rabbit odour, being fed rabbits in Mt Rothwell and Tasmanian derived quolls may have encountered rabbits in the wild.

Answering these questions could help assess how the innate behaviour of resident and reintroduced prey species within a predator-free environment facilitates the detection and avoidance of introduced (foxes and cats), native (dingo (*Canis lupus dingo*)) and extinct (thylacine (*Thylacinus cynocephalus*) predators based on their odour cues and position in the landscape. The results could then help anticipate the relative vulnerability of each prey species to predation if they were exposed to an environment containing those predators.

1.2 Hypotheses

Based on my research questions, I developed the following hypotheses:

(i) *Resident marsupials within Mulligans Flat would display anti-predator behaviour towards native predator (dingo and thylacine) odours but not to novel predator (fox and cat) odours.* This hypothesis is based on the theory that prey species evolved innate responses to native predators that will be maintained across many generations once removed.

(ii) *Reintroduced marsupials are naïve and so would not respond to dingo, fox or cat odour, but would respond to thylacine odour.* This is because they came from Tasmania where there are no dingoes, and foxes and cats are relatively new predators.

(iii) *Visitation rates to sites holding odours would be higher and duration of visits longer in high vegetation cover.* This hypothesis is based on the 'landscape of fear' concept, suggesting that prey perceive an area with more coverage to be less risky.

(iv) *Smaller marsupials would respond to predator odours more than larger marsupials.* This is because medium sized predators are more of a threat to smaller prey.

Low visitation rates, short site visits and displays of high vigilance at predator odour sites would indicate these marsupials use anti-predator behaviours in response to predator odour. No response would demonstrate there was some level of naïveté. My research will contribute to the understanding of predator-prey interactions between native marsupials and their potential predators. Discovering how eastern bettongs and eastern quolls respond to predator odours could help researchers understand whether they are capable of predator avoidance, giving them a chance to establish self-sustaining populations on the mainland. It may then be possible to use odours to maximise reintroduction success. Discovering how other marsupials respond can indicate whether evolutionary behavioural responses are retained, or if predator avoidance capabilities are lost over time.

The following chapter is a literature review of predator-prey interactions between Australian mammalian fauna and their predators, both historical and introduced. The third chapter describes the methodology and contains the methods I used for my research. Chapter Four includes results from these methodologies, as well as statistical analyses. The fifth chapter is a discussion of the results and is followed by a concluding chapter.

Chapter 2: Literature Review

This chapter examines interactions between Australia’s mammalian fauna and their predators, both historical and introduced. I focus on three themes: predator recognition, odour cues and the theory that vegetation cover affects prey marsupial responses to predator odours. I conclude that more research on olfactory recognition in Australian marsupial species is required to properly understand how they respond to predator odours, and suggest that species should be examined individually, because results vary among species. Further, variations in habitat structure should be considered in future olfactory recognition studies, because responses may not be due to naïveté, but to differences in landscapes and how vulnerable the animal is feeling in a given location.

2.1 Australia’s Mammal Extinctions

Australia's isolation has led to its extraordinarily distinct biodiversity. However, this isolation means the biota is incredibly vulnerable to novel threats (Burbidge and McKenzie, 1989; Woinarski *et al.*, 2015). In the 200 years since European settlement, over 10% of 273 endemic land mammals have become extinct (Woinarski *et al.*, 2015). Although there are several contributing factors, the loss of Australian land mammals, particularly those in the CWR, is mainly driven by predation by introduced foxes and cats (Abbott, 2002; Kovacs *et al.*, 2012). Some species that have been lost from mainland Australia are still found on islands off the continent, where populations can persist (Short and Smith, 1994; Burbidge *et al.*, 1997; Woinarski *et al.*, 2015).

2.2 The Arrival of Novel Predators and Herbivores

At the time of European settlement (1788-1800s), many of the now extinct and threatened mammal species occurred in high numbers, with extensive ranges across multiple habitats (Peacock and Abbott, 2013). By the mid to late 19th century and early 20th century, foxes were found over most of the southern half of Australia (Marlow *et al.*, 2015). Cats were introduced to Australia in the early 1800s and are now found in all terrestrial habitats across >99.8% of Australia's land area (Abbott, 2002; Marlow *et al.*, 2015; Legge *et al.*, 2017). As well as direct predation, introduced predators can impact native species through competition for shared resources such as food and territories. Hollow logs, burrows and rock crevices used by small mammals are often used by foxes and cats (Glen and Dickman 2006b, 2008). The European rabbit arrived in Australia with the First Fleet and were established in their current range in the early 1900s (Eldridge and Simpson, 2002). Rabbits are known to compete with many ground dwelling mammals for resources (Bird *et al.*, 2012).

2.2.1 Foxes

The European red fox (family Canidae) is a carnivorous mammal that survives in urban, alpine, woodland and arid environments (Stokes *et al.,* 2004; Saunders *et al.,* 2010). Foxes are mostly nocturnal, sleeping in dens and logs during the day (Glen and Dickman 2006b, 2008). They are solitary hunters but can survive in small home ranges allowing high population densities. Foxes feed on small mammals and insects, scavenging opportunistically (Short *et al.,* 2002). Both males and females reach sexual maturity after one year with litters averaging four cubs (Short *et al.,* 2002). Compared to larger canids, they stalk and ambush rather than chase prey (Short *et al.,* 2002). Foxes prey on young eastern grey kangaroos, significantly affecting their population growth (Banks *et al.,* 2000). Foxes have been found to be attracted to novel prey odours, actively seeking them out (Bytheway *et al.,* 2016; Andrewatha, 2017).

2.2.2 Feral Cats

Feral cats (family Felidae) are the same species as domestic cats but they live in the wild. Their distribution covers nearly all of mainland Australia including forests, woodlands, grasslands, wetlands and arid habitats (Legge *et al.,* 2017). Feral cats are solitary and are mostly nocturnal. During the day, they shelter in burrows, rocks or log piles (Glen and Dickman 2006b, 2008). Feral cats eat a variety of animals including small mammals, reptiles, and amphibians, and are known to consume 28 International Union for Conservation of Nature (IUCN) Red List species (Doherty *et al.,* 2015). Feral cats can travel long distances, up to 30 km outside of their home ranges in Northern Australia after high intensity burns, taking advantage of the increased exposure of prey (McGregor *et al.,* 2016). Subsequently, even when in low densities, feral cats can have a large negative impact on fauna.

2.2.3 European Rabbits

The European rabbit came to Australia with the First Fleet and was well established by the early 1900s (Eldridge and Simpson, 2002). Introduced herbivores are known to compete with native herbivorous marsupials for resources and they damage native plant communities because they favour native plants over exotics (Parker *et al.,* 2006; Bird *et al.,* 2012). Overgrazing leads to an increase in exotic plant abundance in plant communities (Bird *et al.,* 2012). Their impact increases during drought and after a fire, when resources are limited (Morton, 1990; Robley *et al.,* 2002). Feral rabbits are believed to have contributed to the extinction of several CWR ground-dwelling mammals of Australia’s arid regions, and the decline of many native plants (Robley *et al.,* 2002). Rabbits support populations of foxes and cats, and so contribute to the suppression of native prey (Glen and Dickman, 2005).

2.3 Australian predators

Before foxes and cats arrived in Australia, there were many native mammal predators, which shared a long history with, and preyed upon smaller mammals. These included top predators like the dingo, thylacine, Tasmanian devil (*Sarchophilus harrisii*) and quoll species (*Dasyurus* spp.) (Corbett, 1995; Peacock and Abbott, 2013; Hunter *et al.*, 2015). Dingoes are considered native in this study because they arrived in Australia ~4000 years ago (Corbett, 1995), and so share a co-existence history with many native marsupials. Top predators can constrain populations of mid-level predators, such as foxes and cats, protecting prey from excessive predation (Johnson *et al.*, 2007). Many of Australia's predator species disappeared after European settlement, causing an increase in mid-level predators. Removing top predators leads to uncontrolled numbers of mid-level predators, known as meso-predator release (Glen and Dickman, 2005; Ehrich *et al.,* 2016). An example of meso-predator release is the increase in cat numbers in areas of Tasmania where Tasmanian devil populations have declined due to devil facial tumour disease (Hollings *et al.*, 2014). Impacts flow through the trophic levels from top predator down to primary producers (Glen *et al.,* 2007). The next two paragraphs will give a brief overview of the two native predators involved in this research.

2.3.1 Dingoes

The dingo is a large mammal (average weight 15kg) from the family Canidae (Short *et al.*, 2002). Introduced to Australia ~4000 years ago by Asian seafarers, their arrival is believed to have contributed to the extinction of the thylacine and Tasmanian devil on mainland Australia (Corbett, 1995; Johnson, 2006; Glen *et al.,* 2007). Females reach sexual maturity at two years old, having an average of five pups in a litter, with one oestrus a year (Corbett, 1995). Dingo social packs have a strict social hierarchy where the dominant pair are often the only successful breeders (Short *et al.,* 2002). Dingoes have flexible hunting strategies, capturing a diverse range of prey, hunting for larger prey in packs (Short *et al.,* 2002). When hunting juvenile kangaroos, dingoes run alongside them biting the chest and neck (Corbett, 1995). Males disperse greater distances than females, travelling up to 250 km (Short *et al.,* 2002). The dingo is often considered to be an agricultural pest that preys on livestock. Human persecution has seen its decline in large parts of south-eastern Australia (Glen *et al.,* 2007). Like top predators in other parts of the world (e.g. the grey wolf (*Canis lupus*) in North America) there are conflicting goals of protecting livestock, while maintaining top-down ecosystem regulation (Glen *et al.,* 2007). Most of the species in MFWS share an evolutionary history with dingoes, however the eastern quolls and eastern bettongs translocated from Tasmania do not. Although once common on the mainland, dingoes never made it to Tasmania because the flooding of the Bass Strait created the island at the end of the last glaciation, separating it from the mainland (Corbett, 1995).

2.3.2 Thylacines

The thylacine was the last extant member of the family Thylacinidae, which constituted the carnivorous marsupial superfamily, Dasyuroidea (Jones and Stoddart, 1998). The thylacine faced persecution for allegedly hunting farmers' sheep which led to its extinction before its ecology was documented (Jones and Stoddart, 1998) and so available literature is limited. Before the dingo arrived in Australia, the thylacine was widely distributed on the mainland and persisted in Tasmania until the arrival of Europeans (Jones and Stoddart, 1998; Letnic *et al.*, 2012). The thylacine became extinct on mainland Australia at least 3000 years ago and extinct in Tasmania in 1936 (Corbett, 1995; Johnson 2006; Glen *et al.*, 2007).

The thylacine's body form resembled that of large canids with a long snout, straight forelimbs and non-retractable claws for running (Jones and Stoddart, 1998). Thylacines are believed to have been pounce and pursuit predators like the Tasmanian devil rather than ambush predators, suggesting they hunted in open habitats, including open forest, which is consistent with their former distribution and sighting records (Jones and Stoddart, 1998). Jones and Stoddart's (1998) study observing morphological features of thylacine remains suggested that thylacine killed medium sized prey, with a crushing bite like quolls and smaller canids. They are thought to have hunted co-operatively for larger species and are known to have fed on red-necked wallabies and forester kangaroos (*M.giganteus tasmaniensis*) (Prowse *et al.*, 2013).

2.4 Anti-predator Behaviour

It is widely accepted that prey behaviour is influenced by predation risk and prey species will often use anti-predator behaviours to avoid predation (Lima and Dill, 1990; Russell and Banks, 2007). Anti-predator behaviours include escape and avoidance responses and vigilance (Kats and Dill, 1998; Apfelbach *et al.*, 2005; Anson and Dickman, 2013). Apfelbach *et al.*, 2005 defined vigilance as “species-typical behaviours with a focus on detection, localisation, and identification of a predator, in which species may selectively utilise particular sensory modalities” There are several ways animals may identify the risk of predation, including sight, sound and odour (olfactory recognition) (Parsons *et al.*, 2017). In the next section, I will review key literature on the latter.

2.5 Olfactory Recognition

Both predator and prey species have an interest in gaining information about the presence and activities of each other (Glen and Dickman, 2005). Many marsupial species evolved to be nocturnal to avoid the heat and day time predation. Predator odours can be used by these species as reliable cues to assess predation risk (Anson and Dickman, 2013). Little is known about the chemical composition and stability of messages contained within odours (Parsons and Blumstein, 2010b). Odours are made of compounds that differ in volatility. The non-volatile compounds (which include proteins and lipids) can slow down the rate at which the volatile compounds might evaporate (Parsons *et al.*, 2017). Some odours contain chemicals which are related to metabolism, while others evolved to function as signals (Parsons *et al.*, 2017). Over time, prey species have learnt to use odour signals left by predator species as a sign of where they are in the landscape (Atkins *et al.*, 2016). Recognition of predator odour cues often leads to anti-predator behaviours such as vigilance and subsequent fleeing (Blumstein, 2002). The source of an odour cue is important because prey may respond in different ways to scents produced from urine, faeces, saliva or fur (Kats and Dill, 1998; Parsons *et al.*, 2017). Previous studies on the topic of olfactory recognition in marsupials have mainly used faecal matter or urine as odour cues to elicit behavioural responses from prey species (Russell and Banks, 2005, 2007; Anson and Dickman, 2013; Tortosa *et al.*, 2015). Integumentary odour comes from an animal's skin, fur and body oils (which contain lipids), and is thought to represent a den site or predator resting place, indicating an animal is close by (Carthey and Banks, 2016). Studies (Apfelbach *et al.*, 2005; Carthey and Banks, 2016) have found integumentary odour incites the greatest behavioural responses from prey species. These results informed my decision to use integumentary odour cues in my research which will be covered more in Chapter 3. Prey may display weak anti-predator responses as odours age – perceiving predation risk as low, or because they do not recognise the threat associated with the odour (Dickman and Doncaster, 1984, Parsons *et al.*, 2017).

2.6 Prey Naïveté to Predator Odours

The prey naïveté hypothesis states that prey animals will display anti-predator behaviour towards coevolved predators, but they would not have adapted to the presence of introduced predators (Cox and Lima, 2006). The implication is that because they do not share a co-existence history, prey species are unable to use olfactory recognition as a strategy to avoid predation by foxes and cats (Apfelbach *et al.*, 2005; Atkins *et al.,* 2016; Carthey and Banks, 2016). Consequently, we would expect native fauna to be naïve to exotic predator odour cues. Naïveté can also be due to long-term isolation from co-evolved predators, often occurring in species found in fenced reserves, predator free islands or bred in captivity (Sih *et al.,* 2010; West *et al.,* 2017). Fenced nature reserves act as island sanctuaries, isolating animals from introduced predators. These reserves (e.g. Arid Recovery in Roxby Downs, South Australia) are used for reintroductions of locally extinct species. Reintroduction failures are often attributed to predation by exotic predators (Moseby *et al.,* 2011).

2.6.1 Levels of Prey Naïveté

Banks and Dickman (2007) proposed that when it comes to novel predators there are three levels of naïveté in prey species. Level (1) naïveté is when prey have no recognition of the predator and therefore see no risk of predation. Prey that demonstrate Level (2) naïveté are those that can recognise the predator as dangerous but use an unsuccessful anti-predator response. An example of Level (2) naïveté is how bush-stone curlews (*Burhinus grallarius*) use cryptic poses, making them blend into their environment as a defence. This behaviour is beneficial in response to predators that rely on vision for hunting but proves to be largely unsuccessful with foxes that hunt using scent to locate their prey (Banks and Dickman, 2007). Level (3) naïveté occurs when prey recognise a predator to be dangerous, and demonstrate appropriate anti-predator behaviour, but are overwhelmed by the skills of the novel predator. For example, in response to the presence of foxes, eastern grey kangaroos foraged closer to cover in larger groups, however fox predation still limited population recruitment (Banks *et al.,* 2000; Banks and Dickman, 2007).

2.7 Landscape of Fear Theory

While the introduction of foxes and cats to Australia has caused a decline in many small and medium sized mammals, when dingoes arrived there was a considerably smaller impact (Banks and Dickman, 2007). European settlers cleared large amounts of habitat for agriculture which was then maintained by domestic stock (Banks and Dickman, 2007; Legge *et al.,* 2017). This led to a reduction in understorey complexity, removing shelter for many animals. Consequently, even if prey could detect predators, habitat destruction and changed fire regimes have created more open areas and increased hunting opportunities for feral cats and foxes (Banks and Dickman, 2007; Legge *et al.,* 2017). Predator cues can help prey evaluate the risk over a landscape, and decide on where to forage most efficiently (Mella *et al.,* 2014a). Predator cues can either be direct, like odours, or indirect, like different landscape features. Habitat cues are linked with the likelihood of a predator encounter (Apfelbach *et al.,* 2005; Mella *et al.,* 2014a).

Visibility and suitable coverage for prey species changes with varying vegetation cover (Parsons *et al.,* 2017). To avoid predation, potential prey may sacrifice foraging opportunities, but to access resources they might have to sacrifice their safety, increasing vulnerability (McArthur *et al.,* 2014). Predation risk determines where prey forage and how long they stay at a feeding patch, which can have sub lethal behavioural impacts on the success of a population (Mella *et al.,* 2014a). When animals need to feed in areas of risk they alter their behaviour to manage threats by reducing time allocation, increasing vigilance and group foraging (Lima and Dill, 1990). The landscape of fear can help explain how an animal uses an area whilst trying to reduce its vulnerability to predation (Laundré *et al.,* 2010).

An animal should leave a patch when the costs of potential predation outweigh the fitness gains from feeding (Brown and Kotler, 2004). A common method used in research is the ‘Giving up Density’ (GUD) – where the amount of food remaining after a forager stops feeding is an indicator of cost-benefit behaviour in prey species (Searle *et al.*, 2008; Mella *et al.,* 2014a). The GUD of a forager should be higher (i.e. there should be more food left over) in a riskier environment compared to a low risk environment. Searle *et al.* (2008) found that when making foraging decisions, northern brown bandicoots (*Isoodon macrourus*) responded to possible predation risk, trading food for safety. They left feeding stations at a higher GUD as the distance from high vegetation cover increased.

A longitudinal study on mule deer (*Odocoileus hemionus*) and pumas (*Puma concolor*) demonstrated pumas had more success when hunting deer along forest edges compared to open areas (Laundré and Hernandez, 2003). This was due to the hunting strategy of the puma as it requires cover to attack prey (Hornocker, 1970; Laundré *et al.,* 2010). Hernández and Laundré (2005) found elk made a significant shift toward the forest edges within five years of reintroducing wolves into Yellowstone National Park. Creel and Winnie (2005) also demonstrated that edge areas were used more frequently by elk in response to predation by wolves. The shifts in habitat use by the elk resulted in a loss of foraging opportunities with a noticeable decline in diet quality. Studies demonstrate that in varying habitats, prey realise risks, adjusting their behaviour accordingly (Laundré *et al.,* 2010). The examples above indicate that behavioural shifts by prey depend on the prey and predator species.

Most wild studies have focused on direct or indirect cues on their own. However, wild animals encounter both types of predation cues at the same time, so it is important to understand how they use these cues in the landscape. Differences in responses to predator odour cues may not necessarily be due to naïveté, but to variations in vegetation cover. In my study, vegetation is taken into consideration as a variable which may affect behavioural responses of prey species. I predicted that variation in vegetation between camera sites would affect visitation rates of animals to different odours. This will be explained in Chapter 3.

2.8 Rapid Adaptations

Studies have suggested that to deal with new predators, prey species that occur in large densities may rapidly evolve anti-predator adaptations (Kovacs *et al.*, 2012; Mella *et al.*, 2014a; Carthey and Banks, 2016). For example, Anson and Dickman (2013) stated selection pressure from the fox had been enough for ringtail possums (*Pseudocheirus peregrinus*) to develop anti-predator behaviours over the few generations since foxes became established. They found that over large areas, the presence of foxes did not affect ringtail possum density and they had clearly survived early impacts. Although possums do feed on the ground at times (Pickett et al., 2005), the presence of foxes may not have a large impact on ringtail possums because they are mainly arboreal, and so have an advantage against foxes and cats compared to many threatened ground dwelling marsupials that were once common.

In the United States, wolves and brown bears (*Ursus arctos)* were eliminated for approximately 100 years from most of their range. The reintroduction of these predators meant that moose (*Alces alces*) had no experience with them for 50-100 years prior and so were naïve and highly vulnerable (Berger *et al.,* 2001). Weak responses to predators occur if the prey is young or otherwise inexperienced (Kovacs *et al.,* 2012). However, after many offspring were lost to predation, behavioural adjustments developed within a single generation (Berger *et al.,* 2001).

Where the young are mainly targeted, learning may come from mothers or conspecifics in a social group (Berger *et al.,* 2001). For example, a reintroduction of eastern bettongs in 2016 into an unfenced area of intense fox control (but with regular fox incursions) to the Lower Cotter Catchment in the ACT has been very successful despite the presence of foxes. During this trial, several bettongs survived over a year post-release during time they would have inevitably encountered foxes and cats. It is likely the reintroduced eastern bettongs have learnt to detect and avoid these predators after witnessing conspecifics being attacked, or they themselves have had close encounters (Will Batson, pers. comm). Increased experience through learning and/or evolution should lead to improvement in recognition and anti-predator defence (Banks and Dickman, 2007; Carthey and Banks, 2015).

A recent study at the Arid Recovery Reserve compared burrowing bettongs (*Bettongia lesueur*) in an area without predators to a population of bettongs that had been exposed to cats within the reserve. West *et al.* (2017) found that in a period of 18 months after reintroduction, bettongs exposed to cats had greater flight distances, and approached feeding trays slower compared to the control bettongs, demonstrating that in a short period, exposure to predators can change behaviour in prey animals.

2.9 Responses to Odours of Absent Predators

Innate response or 'species memory' is when prey species can recognise odours of predators that have been absent for a long period of time and respond to an odour on their first encounter. (Parsons *et al.,* 2017). Black tailed deer (*Odocoileus hemionus columbianus*) could discriminate between the odours of wolves (that they had not encountered after being absent for 100 years) and black bear (*Ursus Americanos*) that were present (Chamaille-Jammes *et al.*, 2014; Parsons *et al.,* 2017). Studies like this indicate that evolutionary knowledge of predators may persist for a long time. Behavioural responses to predators may continue regardless of the extinction of a certain predator (Blumstein, 2006). This informed my decision to include thylacine odour in my study to test whether I could detect an evolutionary response in marsupials to a long-lost predator.

2.10 Studies on Marsupials and Predator Odour

The literature on marsupial recognition of odour cues is limited. Past research indicates, in Australian mammals, predator recognition is variable: some species display clear discrimination of predator odours (e.g. Mella *et al.,* 2014b), while others either have no recognition or recognition at some places and times only (Banks 1998; Russell and Banks, 2007; McEvoy *et al.*, 2008; Anson and Dickman, 2013).

Deciding whether marsupials respond to predator odour is difficult when different behaviours are recorded across studies. Some studies only considered 'avoidance' as an anti-predator behaviour (e.g. Russell and Banks, 2005). However, other behaviours should be measured, such as fleeing, vigilance, and those that demonstrate investigation, for example, approaching slowly and sniffing odours (Jones, 1998b; Atkins *et al.,* 2016). Although ethograms (tables of recordable behaviours) have been used in other types of predator recognition studies (e.g. Atkins *et al.,* 2016), I could only find two studies that used ethograms observing different behavioural responses to odours (Mella *et al.,* 2014b; Andrewatha, 2017).

Many studies have used methods involving traps lined with predator faecal matter and measured trap success as a way of recording behavioural responses to odour cues (Dickman and Doncaster, 1984; Apfelbach *et al.,* 2005; Anson and Dickman, 2013). Some animals may flee into traps in response to predator odour cues to be safe and so results from these studies may not reflect how animals would behave naturally in the wild (Carthey and Banks, 2016). My literature review suggests that the number of studies that look at marsupials recognising predator odours as well as variations in the landscape or the 'landscape of fear' is minimal. Due to the inconsistencies found on whether native marsupial species respond to predator odours, studies should focus on individual species rather than claiming marsupials as a group recognise odours when studying one or two species. This is the approach that I have taken, and there are six marsupial species that are found within the MFWS that I was interested in studying. None of which have had previous experience with mammalian predators in their lifetimes.

2.11 Species of Interest

2.11.1 Eastern Quolls

The eastern quoll is a small, solitary, carnivorous marsupial of open habitats, from the family Dasyuridae (Jones, 1998a). The species is listed as endangered on the IUCN Red List (Burbidge and Woinarski, 2016). They are nocturnal, nesting in dens during the day within fallen logs or rocky areas. They have a varied diet of small reptiles, worms, small mammals, insects and berries (Blackhall, 1980). The eastern quoll had been extinct on mainland Australia since the 1960s but was reintroduced in 2016 to MFWS from a wild Tasmanian population, and from a breeding program population at Mount Rothwell in Victoria (Adrian Manning, pers. comm). The introduction of foxes and cats contributed to their extinction on the mainland (Peacock and Abbott, 2013; Fancourt, 2016). As eastern quolls are predators, it is possible they may be attracted to both the rabbit and predator odours. Without recognising foxes, dingoes and thylacines as larger carnivores, they may perceive the odour to be an opportunity instead of a threat. Carnivorous species often seek out competitors when they smell odour cues to gain information about their enemies (Banks *et al.*, 2016).

2.11.2 Eastern Bettongs

Eastern bettongs are small, herbivorous marsupials within the family Potoroidae, a subgroup of the kangaroo superfamily. Eastern bettongs occupy open, dry forest with a grassy or heath understorey (Short, 1998; Batson *et al.*, 2016). They nest during the day in a thickly woven nest of dry grass and bark, typically under a fallen limb or among tussock grass (Short, 1998). Eastern bettongs are strictly nocturnal, and feed on hypogeous fungi, seeds, roots and bulbs. The species is listed as Near Threatened on the IUCN Red List (Burbidge *et al.,* 2016). Within the genus *Bettongia*, the eastern bettong has the largest remaining population, still present in Tasmania after disappearing from mainland Australia in the early 1900s (Taylor, 1993). They were reintroduced in 2012 to MFWS with a population translocated from Tasmania, and from a breeding program at Tidbinbilla Nature Reserve in the ACT (Adrian Manning, pers. comm). A major contributor to their local extinction was predation by introduced foxes (Short, 1998).

2.11.3 Brushtail Possums

The common brushtail possum is a large (up to 3 kg) non-gliding arboreal marsupial from the family Phalangeridae. Brushtail possums are nocturnal omnivores with a diet including foliage, flowers, fruit, bird eggs and nestlings (Lindenmayer *et al.,* 2017). The brushtail possum depends on tree hollows for nesting during the day and male and female pairs or small groups have overlapping ranges (Lindenmayer *et al.,* 2017). Brushtail possum responses to predator odour cues vary. Direct cues from predator odours produced weak, or no response in free-ranging possums (Russell and Banks, 2005; Parsons and Blumstein, 2010b). Studies have also indicated that there are varied results due to habitat differences (McDonald-Madden *et al.,* 2000; Pickett *et al.,* 2005). Mella *et al.* (2014a) found that brushtail possums did not respond to odour predator cues from dog (*Canis lupus familiaris)* and powerful owl (*Ninox strenua*) faeces. However, they discovered brushtail possums distinguished between feeders that were on ground (considered as risky) and feeders that were above ground (considered safe), where above ground were preferred. Possums spent more time foraging and there was a lower GUD at the feeders that were above the ground. This suggests possums had more fear on the ground, where the trade-off between foraging and evading predators was higher (Mella *et al.,* 2014a). In MFWS, with mammalian predators absent since 2009, brushtail possums have been observed frequently travelling slowly along the ground, with low levels of vigilance (Adrian Manning, pers. comm). It is believed that possums manage their risk of predation during foraging by varying time allocation, rather than adjusting vigilant behaviour (Mella *et al.,* 2014a).

2.11.4 Eastern Grey Kangaroos

The eastern grey kangaroo is one of the largest macropod species (family Macropodidae). They are sexually dimorphic with males growing up to 70kg in weight, over 2m tall and females reaching half their size (Miller *et al.,* 2010; Descovich *et al.,* 2016). They maintain social hierarchies with large groups dividing into smaller units and vice versa depending on the activity and the season (Miller *et al.,* 2010; Descovich *et al.,* 2016). This behaviour is believed to be an adaptive response to increased exposure to predation (Descovich *et al.,* 2016). Eastern grey kangaroos like woodland habitats with sparse understorey, lots of grass and open clearings for grazing (Howland *et al.,* 2014). Their behaviour depends on weather conditions and when conditions are hot and dry they feed mainly at night (Descovich *et al.,* 2016). Kangaroos are commonly preyed on by dingoes and dependent young and juveniles are more vulnerable to attacks. The thylacine probably hunted eastern grey kangaroos, as they were known to feed on other large macropods such as forester kangaroos and red-necked wallabies (Prowse *et al.,* 2013).

2.11.5 Red-necked Wallabies

Red-necked wallabies are found on mainland Australia and in Tasmania. They belong to the Macropodidae family and are found in habitats with open grazing areas and shelter in patches of dense cover (Garnick *et al.*, 2016). They are grazers that have a mixed diet made up of grass, forbs and browse (Garnick *et al.*, 2016).

A study on eastern grey kangaroos and red-necked wallabies (Cox *et al.*, 2015) tested dingo odour from individuals that consumed eastern grey kangaroos. The result indicated that there was increased defensive and fleeing behaviour in response to dingo odour. Red-necked wallabies also displayed more vigilant behaviour (Cox *et al.*, 2015). This suggests that recognition of predators may involve the odours of deceased conspecifics. Red-necked wallabies are known to have been prey to thylacine (Prowse *et al.*, 2013).

2.11.6 Swamp Wallabies

Swamp wallabies are large macropods (family Macropodidae) that regularly use dense vegetation including for foraging (Garnick *et al.*, 2016). They have browser dentition and feed on forbs and shrubs (Fitzsimons, 2017). They are opportunists, taking advantage of high-quality food resources when available, such as fruiting bodies of hypogeous fungi (Fitzsimons, 2017). Robertshaw and Harden (1986) found that swamp wallaby made up a large proportion of dingo diet in Northern New South Wales where areas were thickly vegetated and rugged. Predation by dingoes caused disruptions in swamp wallaby breeding cycles and reduced recruitment.

To my knowledge, no studies have looked at the effect of predator odour cues or the ‘landscape of fear’ in the eastern bettong, swamp wallaby or eastern quoll. While there have been previous studies on these topics concentrating on the eastern grey kangaroo, red-necked wallaby and brushtail possum, research is yet to be conducted on wild, isolated populations. The next section describes the methodology and the methods I used for my research.

Chapter 3: Methods

This study was conducted in two parts. Experiment 1 studied marsupial responses to odours of dingo, cat and rabbit. Experiment 2 studied marsupial responses to odours of thylacine and fox.

3.1 Ethics Statement

This research was conducted with ethics approval from the Animal Experimentation Ethics Committee of the Australian National University under protocol number A2017/04. Ethics approval was also granted by the University of Melbourne for obtaining odour from a captive cat colony there at the National Vision Research Institute, Australian College of Optometry under approved research project #1413312.

3.2 Study Site

My study was conducted in the Mulligans Flat Woodland Sanctuary (MFWS) (-35.166325, 149.164484), in the district of Gungahlin, in the north of the Australian Capital Territory (Figure 3.1). The Sanctuary is co-managed by the ACT Government and the Woodlands and Wetlands Trust. It is also the site of the ‘Mulligans Flat-Goorooyaroo Woodland Experiment’, a long-term ecological restoration study of the critically endangered Box-Gum Grassy Woodland ecological community (Manning *et al.,* 2011). The MFWS is a reserve free of exotic predators. A predator-proof fence was erected in 2009 with the subsequent eradication of foxes and cats (Shorthouse *et al.,* 2012). The total fenced area is 485 hectares and the area is dominated by Blakely’s Red Gum (*Eucalyptus blakelyi*) and Yellow Box (*E. melliodora*) grassy woodland. The lower slopes contain areas of grassland and forests of Red Stringybark (*E. macrorhyncha*). Scribbly Gum (*E. rossi*) and Brittle Gum (*E. mannifera*) cover the upper sloped areas (Shorthouse *et al.,* 2012). Field work for Experiment 1 occurred between 4/06/2017 and 21/06/2017. Experiment 2 occurred between 27/07/2017 and 10/08/2017.

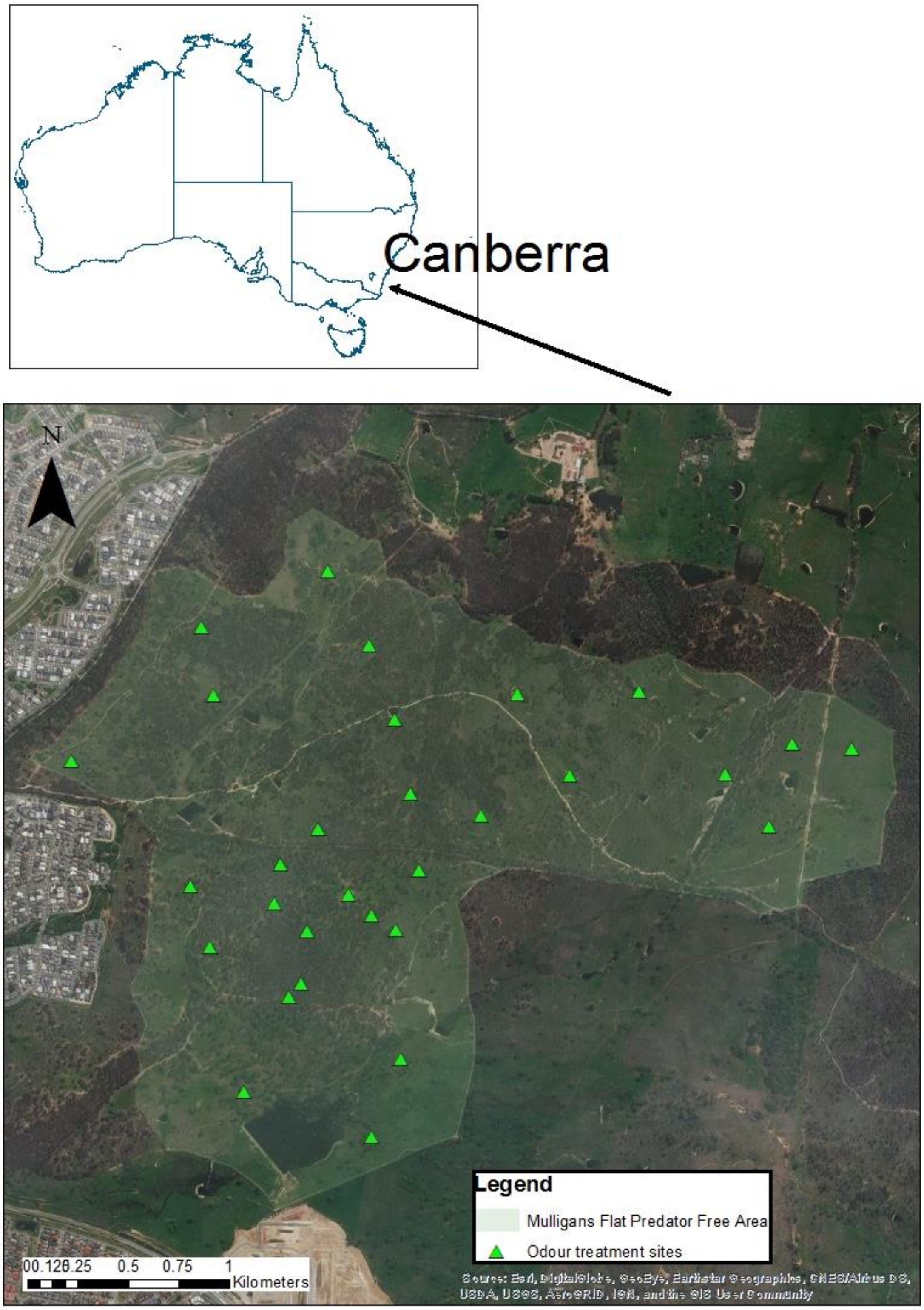

Figure 3.1: Map of MFWS (485 hectares) with reserve boundaries and odour treatment sites (n=30) within the predator proof fence. Created using ArcMap 10.4.1.

3.3 Odour Collection

Body odours were collected from foxes, cats, dingoes and rabbits, as well as odour from a thylacine museum specimen. Odours were chosen to represent both novel and co-evolved predator species in the landscape. As rabbit is known to be a prey item of foxes and cats, rabbit odour was chosen as a treatment to determine if quolls as carnivores were attracted to the odour. Thylacine represents an evolutionary predator of all marsupials found within MFWS.

I used polar fleece material to collect cat, dingo, rabbit and thylacine odours and for unscented controls. I used towelling for the fox odour treatment, because foxes tore up any polar fleece material placed in their enclosures. To prepare the material for odour transfer, I submerged it in boiling water for 30 minutes, air dried it outside in the sun and then sealed it in three zip lock bags to prevent any contamination from outside odours (Andrewatha, 2017). The material for the control was prepared in the same way. Bagged material was sent to volunteers who held captive populations of fox, cat, dingo, and rabbit. Volunteers placed clean material in contact with each target species in housing aviaries for a period of two weeks (Bytheway *et al.*, 2013; Andrewatha, 2017). The diet of foxes, cats and dingoes consisted mainly of meat, and rabbits were fed commercial pellets. The diet of thylacine would have been of wild prey in Tasmania. This odour collection method is an appropriate and viable alternative to collecting odours from wild animals which would likely be more stressed by exposure to novel items in resting areas.

After odour collection, volunteers placed material in three zip lock bags using sterilised metal tongs whilst wearing powder free latex gloves (Andrewatha, 2017). Treated material was sent to me at the Australian National University (ANU) by express post. Upon receiving, I placed all the material, including the control samples, in a -20 ^{O}C freezer to prevent odour degradation until material was needed for fieldwork (Bytheway *et al.*, 2013; Banks *et al.*, 2016; Andrewatha, 2017). Thylacine odour material was kept in a glass container in the freezer. Dingo odours were collected from a private property in Michelago, New South Wales. Rabbit odours were supplied by the Biochemical Radiochemistry Department of Applied Mathematics Research School of Physics animal lab at the ANU. Cat odour was collected by the National Vision Research Institute (NVRI), Australian College of Optometry (ACO) at the University of Melbourne. Fox odour was supplied by Jirrahlinga Koala and Wildlife Sanctuary, Barwon Heads in Victoria. Thylacine odour was collected from a museum specimen in the Tasmanian Museum and Art Gallery and was collected by rolling the polar fleece in contact with an untanned thylacine skin for a two-week period.

Before commencing field work, I removed the odour material from the freezer, cut material into patches (7cm^2) with sterilised scissors whilst wearing gloves, and placed the patches into three zip lock bags. Odours were kept separated and gloves and scissors were changed each time. I cut each piece of treated material over a fresh lining of cling wrap plastic which was then disposed of and changed for each odour cutting.

3.4 Site Selection and Characteristics

There was an existing camera trap network set up in MFWS before I commenced my field work which included 59 camera traps. I identified each camera location using GPS coordinates supplied by the MFWS rangers in the ARCGIS app ‘Collector’. Considering the ‘landscape of fear’ concept (see Introduction. Laundré *et al.,* 2001, 2010), I measured vegetation characteristics at each of the 59 cameras before choosing my sites. Some of the species of interest (eastern bettongs and eastern quolls) are small, ground dwelling marsupials that nest in grasses or dens (Short, 1998; Glen and Dickman 2006b, 2008), therefore, vegetation characteristics could strongly influence their visitation to the sites. To test and control for this, I recorded vegetation characteristics at each camera site. I measured vegetation by laying out a 10m tape and estimating the percentage of sward (grasses and forbs) within the ten-metre radius of each camera. From these data, I categorised sites as ‘low vegetation’ (n=15) and ‘high vegetation’ (n=15). A site considered to have ‘high vegetation’ is a camera site which had a grass, small shrub or forb understorey cover of 50% or more. A site considered to have ‘low vegetation’ is a camera site which had less than 50% cover. I selected thirty cameras from the 59, with a minimum distance of 75 metres between cameras. This separation distance was chosen to maximise independence of odour stations.

3.5 Field Methods and Data Collection

I used spherical, metal tea strainers which had latches to hold odour material (Figure 3.2). Tea strainers were used to allow air to flow through the material (Andrewatha, 2017). I attached them to one metre wooden posts that I hammered into the soil, where the tea strainers were hanging approximately 80 centimetres from the ground surface, three metres in front of each camera trap (Figure 3.3). This height allowed smaller marsupials such as eastern quolls, eastern bettongs and brushtail possums to reach if they were interested in sniffing the tea strainer. I placed the wooden posts out in the reserve approximately five weeks prior to starting data collection to minimise animals’ attraction to a novel object in the environment. In low vegetation sites, cameras were often attached to posts. In high vegetation sites, they were mostly attached to tree trunks. Most of the cameras I used were in place for at least 18 months prior to the study because they were being used as part of an existing monitoring regime at MFWS. Motion sensor/thermal cameras (Ltl Acorn brand – Model Ltl-5310A) were set to be active from 5pm until 7am (Figure 3.4). As this study was conducted over winter, these times were considered appropriate to capture the behaviour of nocturnal animals including my target species. Video length was set to the maximum 60 seconds, with intervals between camera retriggers removed. I moved four of the cameras to new sites to ensure an even number of ‘high vegetation’ and ‘low vegetation’ sites.

Figure 3.2: An odour station at a “low vegetation” field site. A low vegetation site was one where in a ten-metre radius there was less than 50% sward cover (Images: Author’s own)

Figure 3.3: Site set up at a low vegetation site containing the odour post with tea strainer holding the odour and a camera (3 metre distance) (Image: Author’s own)

Figure 3.4: A motion sensor/thermal camera (Ltl Acorn brand – Model Ltl-5310A) (Image: Author's own)

Data collection for Experiment 1 ran for a period of 16 days. It focused on dingo (a historical, placental predator to all except eastern bettongs and eastern quolls), cat (a novel, placental predator) and rabbit (an introduced herbivore) odours. A temporal control ran for four days at each camera, followed by three rotations over the 30 cameras of dingo, cat and rabbit odours. Odours were rotated at each camera every four days, differing from the odour it replaced. For example, a camera might have had cat odour for four days, then rabbit odour for the next four, followed by dingo odour (see Appendix 2). This was to account for variation due to site and camera – i.e. some sites might have more animal trappings than others due to their locations.

Data collection for Experiment 2 ran for 12 days and contained three rotations of four days each using all 30 cameras (see Appendix 3). In Experiment 2, I tested thylacine (a historical, marsupial predator) and fox (a novel, placental predator) odours but also included controls where no odour was placed at the sites in the rotation. The controls differed from Experiment 1 because I was concerned about temporal changes affecting the results.

For both experiments, each of the treatments (and controls for Experiment 2) were present at five camera sites in 'low vegetation' and five 'high vegetation' sites (n=30) to remove any habitat or spatial bias (Table 3.1). Each camera site would always hold a different odour to neighbouring cameras. Odour rotation involved cleaning the tea strainers with ethanol and cotton wool whilst wearing latex gloves. Tea strainers were kept matched to the original species odour and moved between sites to prevent any odour contamination whilst handling materials (Andrewatha, 2017). Camera batteries and labelled memory cards were changed after each odour rotation.

Table 3.1: Division of odours across different vegetation levels

Experiment 1					
Low vegetation n=15			**High vegetation n=15**		
Rabbit n=5	Cat n=5	Dingo n=5	Rabbit n=5	Cat n=5	Dingo n=5
Experiment 2					
Low vegetation n=15			**High vegetation n=15**		
Control n=5	Thylacine n=5	Fox n=5	Control n=5	Thylacine n=5	Fox n=5

3.6 Behavioural Analysis

Prior to commencing field work, I studied ethograms (behaviour tables) from published literature to determine what should qualify as vigilance (an anti-predator behaviour) before creating my own ethogram (Table 3.2) (Mella *et al.*, 2014b; Atkins *et al.*, 2016; Andrewatha, 2017). For this study, I considered vigilant behaviour to be a head lift, followed by visual scanning of the environment. I also considered investigative behaviour, such as sniffing the odour station which held the predator odour treatments and sniffing the air as vigilance. I recorded which species were present in each video, the duration of each visit and duration of each behaviour. I used Microsoft Excel to record video data. I watched videos without knowing the site's odour type or whether it was a control. This was to prevent any biases on behavioural responses to odours.

Table 3.2: Ethogram used to classify marsupial responses to odour cues. Only behaviours classed as vigilance counted towards duration of vigilance

Behaviour	Classification
Sniffing odour station/climbing odour station/trying to fight odour station	Vigilance
Head raised scanning/sniffing air/listening	Vigilance
Jumping away upon smelling odour (fright response)	Vigilance
Slow approach to odour station	Other behaviour
Sniffing ground/foraging	Other behaviour
Interacting with conspecifics/ other species	Other behaviour
Self-grooming	Other behaviour
Hopping/walking/running out of view	Other behaviour
Hopping/walking/running past	Other behaviour
Fast approach: Hopping directly towards odour station	Other behaviour
Sniffing camera	Other behaviour
On camera with behaviour obscured	Other behaviour

3.7 Data Analysis

I analysed data from Experiment 1 and Experiment 2 separately (Table 3.3). This was because the design of the controls differed between experiments and they ran at different times with different odours. For Experiment 1, three species (eastern bettong, eastern grey kangaroo and brushtail possum) were observed on camera enough times to provide sufficient data to analyse in a statistical modelling framework. For each species, I ran sets of models for three response variables: counts of visits, duration of visit (on camera) and duration of exhibited vigilant behaviour. The count of visits response variable was to test the amount of times the animal was seen at the site of the odour treatment, and included sites where no visits occurred. The duration of visit and duration of vigilance response variables build on the first response variable and test the behaviour once the marsupial was seen on camera (i.e. non-visits were not included).

I used generalised linear mixed models (GLMM) to determine the effect of treatment on visitation count data. For Experiment 1, I tested for the effects of the odour treatments (rabbit, cat, dingo), whilst considering the effect of the control. I also tested for an interaction of these treatments with vegetation cover (high versus low) to determine whether it influenced behaviour around odours. In all models, to account for the repeated measures at the site (or camera) level, I treated camera as a random effect. Testing whether odour, vegetation and their interaction influenced the number of visits, I assumed a poisson distribution, or, if the model demonstrated overdispersion, a negative binomial distribution. I checked the fit of each model by examining its histogram of residuals.

I used linear mixed models (LMM) to test the effects of the treatments (rabbit, cat, dingo) compared to the controls on the duration of visitation and duration of vigilance behaviour for each species (eastern bettong, eastern grey kangaroo and brushtail possum). I also tested an interaction of these treatments with vegetation cover (high versus low) and, as with the visit counts models, treated camera (or site) as a random effect. To ensure that the response variables met the assumption of normality, I fitted models using the raw and log transformed response variable. I then checked both models' histograms of residuals, residual vs fitted plots and qq residual plots. In all cases, log transformation was required for the assumption of normality to be met.

For Experiment 2, I followed the same methods as above, but instead tested for the effects of the Experiment 2 treatments (thylacine and fox). On the three response variables testing for whether odour and odour with vegetation influenced the number of visits, I assumed a poisson distribution unless the model displayed oversdispersion, in which case I used a negative binomial distribution. I checked for overdispersion and used a histogram of residuals to ensure a good fit of the model. As with the models for Experiment 1, log transformation of the duration of visit and duration of vigilance response variables was required to satisfy the assumption of normality. I present the effect sizes of treatment relative to the controls, with a 95% confidence interval.

Analyses were performed using the ‘lme4’ (Bates *et al.,* 2016), ‘glmmTMB’ (Magnusson *et al.,* 2017), ‘lmerTest’ (Kuznetsova *et al.,* 2016) and the MuMIn (Barton, 2016) packages in R (R Core Team, 2016). I used R Studio (Rstudio Team, 2016) as a shell and interface for R. For marsupials that I did not have sufficient camera data for modelling, I plotted the counts of visits using bar charts to determine the differences between the controls and odour treatments considering differences in vegetation (Figures 4.3 and 4.14). Statistical modelling was not done for these species as their visits were not in high numbers.

Table 3.3: Model types and distribution used for testing odour and vegetation on the response variables

	Response Variable	Fixed Effects	Random Effects	Distribution	Transformation	Model Type
Exp 1	Visits count	Odour/ odour: vegetation	Camera	poisson/ negative binomial	na	GLMM
	Duration of visit	Odour/ odour: vegetation	Camera	normal	log	LMM
	Duration of vigilance	Odour/ odour: vegetation	Camera	normal	log	LMM
Exp 2	Visits count	Odour/ odour: vegetation	Camera	poisson	na	GLMM
	Duration of visit	Odour/ odour: vegetation	Camera	normal	log	LMM
	Duration of vigilance	Odour/ odour: vegetation	Camera	normal	log	LMM

Chapter 4: Results

A total of 810 videos in Experiment 1, and 491 videos in Experiment 2 contained footage of marsupials (Tables 4.1 and 4.20). Videos of unidentifiable or non-target species were not included. I did not count any visible pouch young as separate individuals because their behaviour was dependant on the mother. Statistical modelling was done for the three most abundant species, being eastern bettong, brushtail possum and eastern grey kangaroo. The results of each experiment are set out below with the visit counts, the duration of visit and the duration of vigilance for each species. Visit count data for eastern quoll, red-necked wallaby and swamp wallaby are displayed in bar graphs because there were not enough data for statistical modelling. Appendices 4 and 5 show the distribution of each species over each Experiment.

Within the model summary tables, for visits, a minus (-) symbol means there was a negative effect, or less visits compared to the control and a plus (+) symbol means more visits. For duration of visit a – symbol means there was a negative effect, or less time was spent in those sites compared to the control and a + means there was more time spent there. For duration of vigilance, a – symbol means there was a negative effect, or less time was spent being vigilant in those sites compared to the control and a + means there was more time spent being vigilant.

4.1 Experiment 1 – Effects of Cat, Dingo, Rabbit odours

Table 4.1: Abundance of species caught on camera in low and high vegetation in Experiment 1

	Eastern Bettong	Eastern Quoll	Eastern Grey Kangaroo	Brushtail possum	Swamp Wallaby	Red-necked Wallaby	Total
Total	367	4	166	165	68	40	810
Low Veg	193	2	75	96	38	23	427
High Veg	174	2	91	69	30	17	383

4.1.1 Visit Counts

4.1.1.1 Eastern Bettong

The number of visits by eastern bettongs was affected by an interaction between odour treatment and vegetation. There was a significant negative effect of rabbit treatment in low vegetation on the number of visits compared to the control (p=0.016*, Table 4.2, Figure 4.1). In Experiment 1, there were no significant effects of odour treatment on its own on the number of visits (Table 4.3).

Table 4.2: Model summary of interaction effect on eastern bettong visits in Experiment 1 (*p<0.05, **p<0.01, ***p<0.001)

Eastern Bettong Model: response ~ Vegetation * Odour + random(camera)								
Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|z|)
1	Visits	poisson	na	0.075	(Intercept)	0.497	0.319	0.119
					VegetationLow	0.377	0.440	0.393
					Rabbit odour	0.223	0.209	0.285
					Dingo odour	-0.025	0.222	0.909
					Cat Odour	0.223	0.209	0.285
					VegetationLow: Rabbit Odour	-0.722	0.299	0.016*
					VegetationLow: Dingo odour	-0.135	0.295	0.647
					VegetationLow: Cat odour	-0.089	0.276	0.748

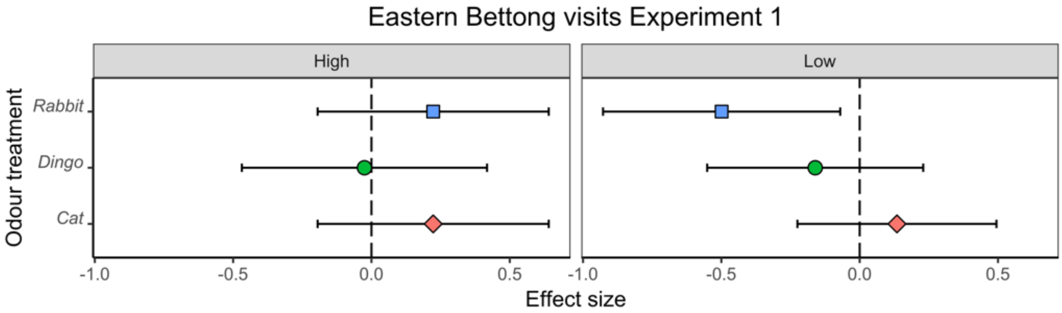

Figure 4.1: Effect size of an interaction between cat, rabbit and dingo odour in high and low vegetation on eastern bettong visits in Experiment 1. Where the effect size line does not overlap with the dashed line that sits on 0.0 there is a significant effect

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Table 4.3: Model summary of odour effect on eastern bettong visits in Experiment 1

Eastern Bettong Model: response~odour+random(camera)								
Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|z|)
1	Visits	poisson	na	0.126	(Intercept)	0.698	0.223	<0.001
					Rabbit odour	-0.134	0.147	0.364
					Dingo odour	-0.103	0.146	0.484
					Cat odour	-0.173	0.136	0.204

4.1.1.2 Brushtail Possum

In Experiment 1, odour with vegetation had no significant effects (Table 4.4, Figure 4.2) on the number of visits. There were no significant results for the effects of odour on the number of visits in Experiment 1 (Table 4.5).

Table 4.4: Model summary of interaction effect on brushtail possum visits in Experiment 1

Brushtail possum Model: response ~ Vegetation * Odour + random(camera)								
Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|z|)
1	Visits	poisson	na	0.609	(Intercept)	-0.256	0.331	0.439
					VegetationLow	0.708	0.429	0.099
					Rabbit odour	-0.061	0.340	0.858
					Dingo odour	-0.061	0.340	0.858
					Cat Odour	0.211	0.318	0.507
					VegetationLow: Rabbit Odour	-0.238	0.434	0.583
					VegetationLow: Dingo odour	-0.236	0.439	0.591
					VegetationLow: Cat odour	-0.686	0.422	0.105

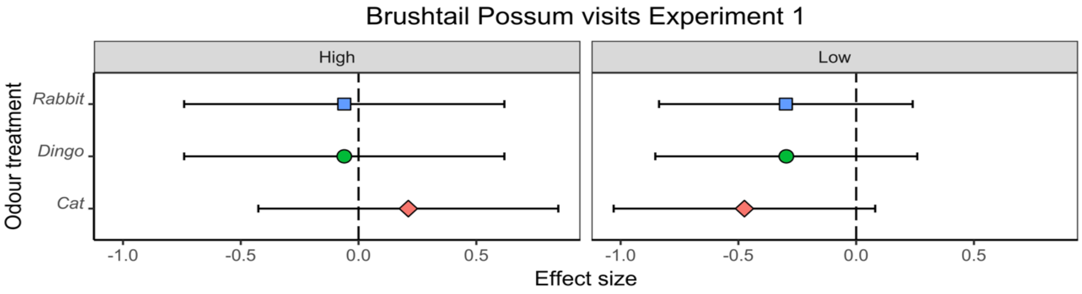

Figure 4.2: Effect size of an interaction between cat, rabbit and dingo odour in high and low vegetation on brushtail possum visits in Experiment 1

Table 4.5: Model summary of odour on brushtail possum visits in Experiment 1

Brushtail possum Model: response~odour+random(camera)								
Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|z|)
1	Visits	poisson	na	0.721	(Intercept)	0.135	0.217	0.534
					Rabbit odour	-0.208	0.211	0.324
					Dingo odour	-0.211	0.214	0.325
					Cat odour	-0.180	0.207	0.383

4.1.1.3 Eastern Grey Kangaroo

Odour and vegetation cover had no significant effects on the number of eastern grey visits in Experiment 1 (Table 4.6) and there were no significant effects caused by odour to the number of visits (Table 4.7).

Table 4.6: Model summary of interaction effect on eastern grey kangaroo visits in Experiment 1

Eastern Grey Kangaroo

Model: response ~ Vegetation * Odour + random(camera)

Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|z|)
1	Visits	Negative binomial	na	0.255	(Intercept)	0.384	0.409	0.348
					VegetationLow	-0.750	0.618	0.225
					Rabbit odour	0.375	0.465	0.420
					Dingo odour	-0.767	0.533	0.150
					Cat Odour	-0.893	0.554	0.107
					VegetationLow: Rabbit Odour	0.036	0.730	0.960
					VegetationLow: Dingo odour	0.882	0.786	0.262
					VegetationLow: Cat odour	-0.686	0.422	0.105

Table 4.7: Model summary of odour effect on eastern grey kangaroo visits in Experiment 1

Eastern Grey Kangaroos

Model: response~odour+random(camera)

Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|z|)
1	Visits	Negative binomial	na	0.181	(Intercept)	0.067	0.318	0.833
					Rabbit odour	0.367	0.366	0.316
					Dingo odour	-0.382	0.405	0.346
					Cat odour	-0.298	-0.750	0.453

4.1.1.4 Other species

For the species where there were not enough data for analyses, visitation rates were recorded using a bar graph looking at an interaction effect between odour and vegetation cover (Figure 4.3) I did not look at the duration of the visit and the duration of vigilance.

There were not enough data from eastern quolls visits because they were only caught at rabbit odour sites twice, and once each for cat and dingo. For eastern quolls, the odour most visited was rabbit with one each in low and high vegetation. There was only one visit to both cat (low vegetation) and dingo (high vegetation) and there were zero visits to control sites.

Red-necked wallabies appeared to be present the most at rabbit odour sites. For red-necked wallabies, rabbit was visited 13 times with only three visits in high vegetation. There were nine visits (three in high vegetation) to cat odour sites, and eight visits to dingo sights with an even number in high and low vegetation. There were 10 visits to the control sites with 7 of those in high vegetation.

Swamp wallabies were seen most at the dingo odour sites. For swamp wallabies, rabbit odour sites were visited 14 times with 5 in high vegetation. Cat odour was visited 15 times with 6 in high vegetation and dingo was visited 21 times with 11 visits in high vegetation. The control odour sites received 18 visits, with 8 in high vegetation.

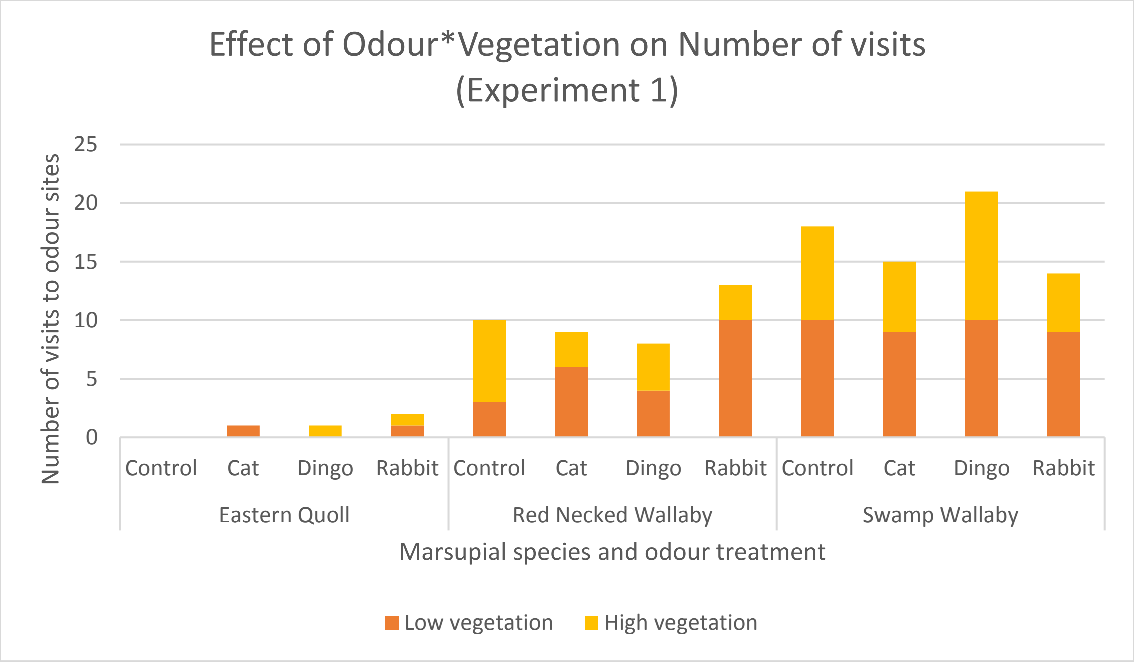

Figure 4.3: Effect of odour (grouped by vegetation type) on the number of other species visits in Experiment 1

4.1.2 Duration of visit

4.1.2.1 Eastern Bettong

In Experiment 1, there were no significant effects on the duration of visit when considering an interaction with vegetation (Table 4.8, Figure 4.4). However, rabbit treatment had a significant negative effect (p=0.025*, Table 4.9, Figure 4.5) on the duration of visits by eastern bettongs. This is the only significant value found for odour effect on its own.

Table 4.8: Model summary of interaction effect on eastern bettong duration of visit in Experiment 1 (*p<0.05, **p<0.01, ***p<0.001)

Eastern Bettong

Model: log(response) ~ Vegetation * Odour + (1|Camera)

Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|t|)
1	Duration of Visit	normal	log	0.045*	(Intercept)	3.318	0.426	<0.001
					VegetationLow	0.229	0.585	0.697
					Rabbit odour	-0.099	0.475	0.836
					Dingo odour	-0.436	0.435	0.320
					Cat Odour	-0.526	0.438	0.235
					VegetationLow : Rabbit Odour	-1.114	0.621	0.077
					VegetationLow : Dingo odour	0.693	0.626	0.273
					VegetationLow : Cat odour	0.331	0.598	0.583

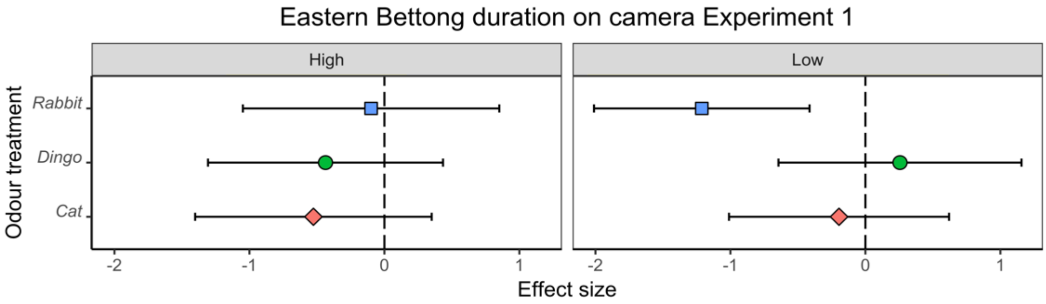

Figure 4.4: Effect size of an interaction between cat, rabbit and dingo odour in high and low vegetation on eastern bettong duration of visit in Experiment 1

Table 4.9: Model summary of cat, rabbit and dingo odour effect on eastern bettong duration of visit in Experiment 1 (*p<0.05, **p<0.01, ***p<0.001)

Eastern Bettong

Model: log(response)~odour+random(camera)

Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|t|)
1	Duration of Visit	normal	log	0.142	(Intercept)	3.474	0.302	<0.001
					Rabbit odour	-0.751	0.327	0.025*
					Dingo odour	-0.213	0.332	0.523
					Cat Odour	-0.358	0.320	0.268

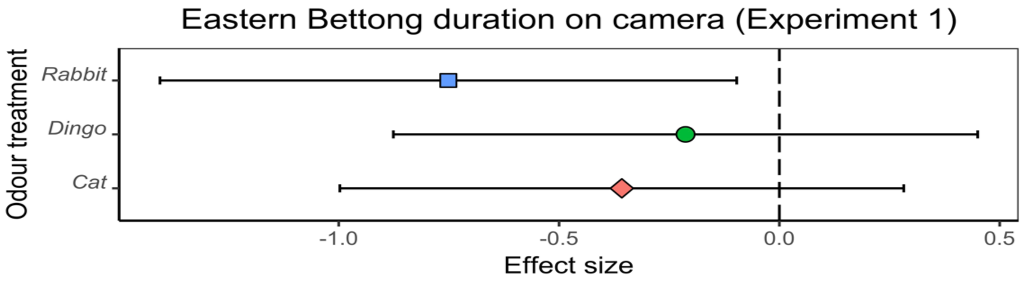

Figure 4.5: Effect size of cat, rabbit and dingo odour on eastern bettong duration of visit in Experiment 1. Where the effect size line does not overlap with the dashed line that sits on 0.0 there is a significant effect

4.1.2.2 Brushtail Possum

There are no significant effects of odour with vegetation (Table 4.10, Figure 4.6) or with odour on its own on the duration of visit by brushtail possums (Table 4.11).

Table 4.10: Model summary of the effect of an interaction between cat, rabbit and dingo odour in high and low vegetation on brushtail possum duration of visit in Experiment 1

Brushtail Possum

Model: log(response) ~ Vegetation * Odour + (1|Camera)

Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|t|)
1	Duration of Visit	normal	log	0.383	(Intercept)	2.750	0.394	<0.001
					VegetationLow	0.599	0.520	0.254
					Rabbit odour	0.726	0.491	0.145
					Dingo odour	0.694	0.491	0.163
					Cat Odour	0.459	0.473	0.337
					VegetationLow: Rabbit Odour	-0.477	0.675	0.483
					VegetationLow: Dingo odour	-0.765	0.727	0.297
					VegetationLow: Cat odour	-1.138	0.621	0.073

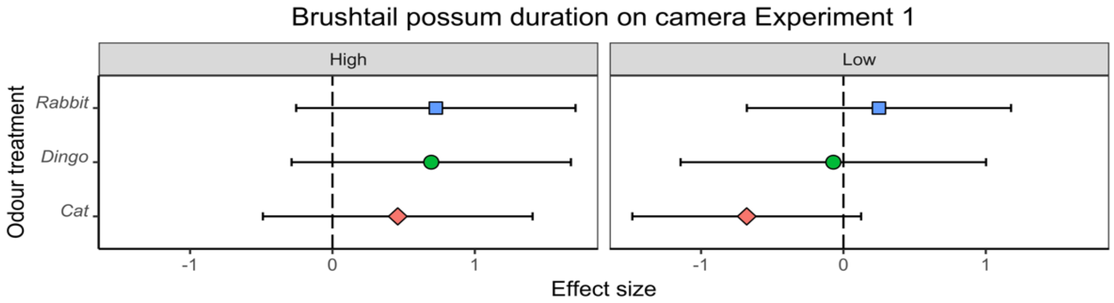

Figure 4.6: Effect size of an interaction between cat, rabbit and dingo odour in high and low vegetation on brushtail possum duration of visit in Experiment 1

Table 4.11: Model summary of cat, rabbit and dingo odour effect on brushtail possum duration of visit in Experiment 1

Brushtail Possum

Model: log(response)~odour+random(camera)

Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|t|)
1	Duration of Visit	normal	log	0.258	(Intercept)	3.100	0.263	<0.001
					Rabbit odour	0.442	0.374	0.208
					Dingo odour	0.278	0.367	0.452
					Cat Odour	-0.204	0.316	0.522

4.1.2.3 Eastern Grey Kangaroo

The duration of visit was affected by an interaction between odour and vegetation cover (Table 4.12, Figure 4.7). In Experiment 1, cat odour had a significant negative effect (p=0.016*) on the duration of visit compared to the control in high vegetation. There was a significant positive effect (p=0.008**) in low vegetation. Dingo odour had a significant positive effect in low vegetation sites (p=0.033*). Odour treatments on their own did not have a significant effect on the duration of visit (Table 4.13).

Table 4.12: Model summary of the effect of an interaction between cat, rabbit and dingo odour in high and low vegetation on eastern grey kangaroo duration of visit in Experiment 1 (*p<0.05, **p<0.01, ***p<0.001)

Eastern Grey Kangaroo

Model: log(response) ~ Vegetation * Odour + (1|Camera)

Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|t|)
1	Duration of Visit	normal	log	0.018*	(Intercept)	4.614	0.503	<0.001
					VegetationLow	-2.020	0.698	0.006 **
					Rabbit odour	-0.030	0.475	0.950
					Dingo odour	-0.255	0.674	0.707
					Cat Odour	-1.449	0.581	0.016 *
					VegetationLow: Rabbit Odour	0.671	0.676	0.328
					VegetationLow: Dingo odour	2.053	0.925	0.033 *
					VegetationLow: Cat odour	2.168	0.773	0.008**

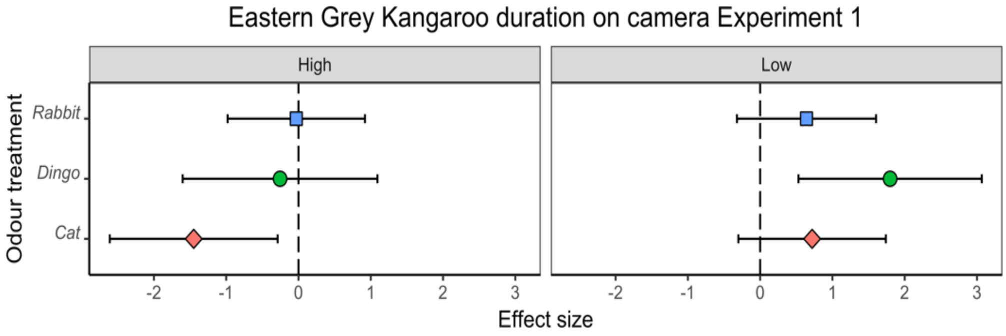

Figure 4.7: Effect size of an interaction between cat, rabbit and dingo odour in high and low vegetation on eastern grey kangaroo duration of visit in Experiment 1. Where the effect size line does not overlap with the dashed line that sits on 0.0 there is a significant effect

Table 4.13: Model summary of cat, rabbit and dingo odour effect on eastern grey kangaroo duration of visit in Experiment 1

Eastern Grey Kangaroo

Model: log(response) ~ Odour + (1 | Camera)

Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|t|)
1	Duration of Visit	normal	log	0.156	(Intercept)	3.502	0.381	<0.001
					Rabbit odour	0.348	0.374	0.358
					Dingo odour	0.909	0.510	0.083
					Cat Odour	-0.179	0.423	0.675

4.1.3 Duration of Vigilance

4.1.3.1 Eastern Bettong

The duration of vigilance in Experiment 1 was affected by an interaction between odour treatment and vegetation (Table 4.14, Figure 4.8). Cat odour treatment had a significant positive effect (p=0.012*) on the duration of vigilance in high vegetation. In low vegetation dingo odour had a significant positive effect (p=0.010**) on the duration of vigilance and on its own, dingo odour had a significant positive effect (p=0.044*) (Table 4.15, Figure 4.9).

Table 4.14: Model summary of the effect of an interaction between cat, rabbit and dingo odour in high and low vegetation on eastern bettong duration of vigilance in Experiment 1 (*p<0.05, **p<0.01, ***p<0.001)

Eastern Bettong

Model: log(response) ~ Vegetation * Odour + (1|Camera)

Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|t|)
1	Duration of Vigilance	normal	log	0.006*	(Intercept)	1.298	0.302	<0.001
					VegetationLow	0.061	0.418	0.884
					Rabbit odour	0.311	0.385	0.425
					Dingo odour	0.205	0.412	0.623
					Cat Odour	1.155	0.432	0.012 *
					VegetationLow: Rabbit Odour	-0.802	0.561	0.162
					VegetationLow: Dingo odour	1.611	0.582	0.010 **
					VegetationLow: Cat odour	-0.680	0.565	0.239

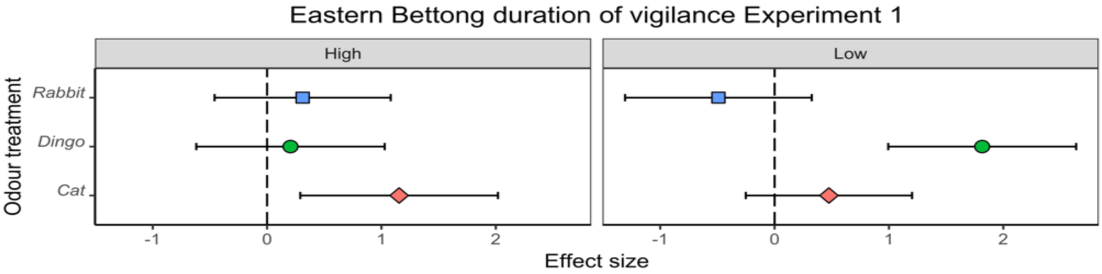

Figure 4.8: Effect size of an interaction between cat, rabbit and dingo odour in high and low vegetation on eastern bettong duration of vigilance through Experiment 1. Where the effect size line does not overlap with the dashed line that sits on 0.0 there is a significant effect

Table 4.15: Model summary of cat, rabbit and dingo odour effect on eastern bettong duration of vigilance in Experiment 1 (*p<0.05, **p<0.01, ***p<0.001)

Eastern Bettong Model: log(response)~odour + random(camera)								
Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|t|)
1	Duration of Vigilance	normal	log	0.045*	(Intercept)	1.413	0.226	<0.001
					Rabbit odour	-0.156	0.356	0.663
					Dingo odour	0.792	0.379	0.044*
					Cat Odour	0.718	0.366	0.058

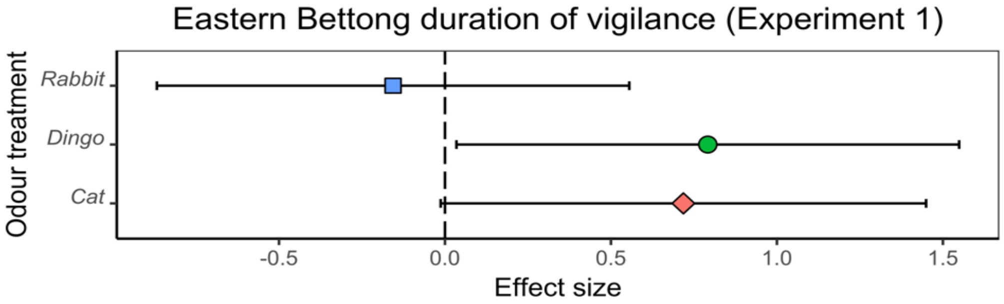

Figure 4.9: Effect size of cat, rabbit and dingo odour on eastern bettong duration of vigilance in Experiment 1. Where the effect size line does not overlap with the dashed line that sits on 0.0 there is a significant effect

4.1.3.2 Brushtail Possum

In Experiment 1, cat treatment had a significant positive effect (p=0.045*) on the duration of vigilance in brushtail possums whilst in high vegetation (Table 4.16, Figure 4.10) which was the same effect for the eastern bettong. There was no significant effect of odour on duration of vigilance in Experiment 1 (Table 4.17).

Table 4.16: Model summary of the effect of an interaction between cat, rabbit and dingo odour in high and low vegetation on brushtail possum duration of vigilance in Experiment 1 (*p<0.05, **p<0.01, ***p<0.001)

Brushtail Possum

Model: log(response) ~ Vegetation * Odour + (1|Camera)

Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|t|)
1	Duration of Vigilance	normal	log	0.220	(Intercept)	2.0157	0.3923	<0.001
					VegetationLow	-0.017	0.483	0.972
					Rabbit odour	0.507	0.469	0.284
					Dingo odour	0.783	0.476	0.111
					Cat Odour	1.091	0.518	0.045 *
					VegetationLow: Rabbit Odour	0.106	0.606	0.863
					VegetationLow: Dingo odour	-0.888	0.766	0.255
					VegetationLow: Cat odour	-1.029	0.675	0.138

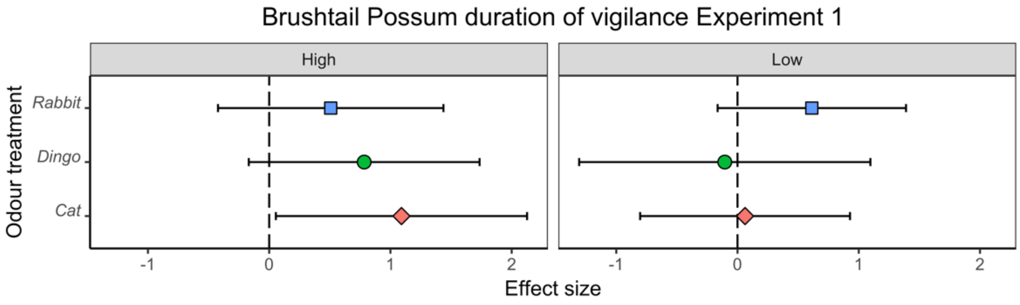

Figure 4.10: Effect size of an interaction between cat, rabbit and dingo odour in high and low vegetation on brushtail possum duration of vigilance in Experiment 1. Where the effect size line does not overlap with the dashed line that sits on 0.0 there is a significant effect

Table 4.17: Model summary of cat, rabbit and dingo odour effect on brushtail possum duration of vigilance through Experiment 1

Brushtail Possum Model: log(response)~odour + random(camera)								
Experiment	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|t|)
1	Duration of Vigilance	normal	log	0.273	(Intercept)	2.001	0.244	<0.001
					Rabbit odour	0.569	0.318	0.082
					Dingo odour	0.554	0.371	0.144
					Cat Odour	0.545	0.357	0.135

4.1.3.3 Eastern Grey Kangaroo

Eastern grey kangaroos responded differently to eastern bettongs and brushtail possums. Cat odour in low vegetation had a significant positive effect (p=0.018*, Table 4.18, Figure 4.11) on the duration of vigilance. In high vegetation, there was a near significant (p=0.058) negative effect by cat odour. Odour on its own had no significant effect (Table 4.19).

Table 4.18: Model summary of the effect of an interaction between cat, rabbit and dingo odour in high and low vegetation on eastern grey kangaroo duration of vigilance in Experiment 1 (*p<0.05, **p<0.01, ***p<0.001)

Eastern Grey Kangaroo Model: log(response) ~ Vegetation * Odour + (1|Camera)								
Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|t|)
1	Duration of Vigilance	normal	log	0.013*	(Intercept)	4.481	0.423	<0.001
					VegetationLow	-1.973	0.628	0.003 **
					Rabbit odour	-0.277	0.560	0.624
					Dingo odour	-0.838	0.669	0.217
					Cat Odour	-1.300	0.669	0.058
					VegetationLow: Rabbit Odour	0.342	0.805	0.673
					VegetationLow: Dingo odour	1.359	0.965	0.166
					VegetationLow: Cat odour	2.243	0.918	0.018*

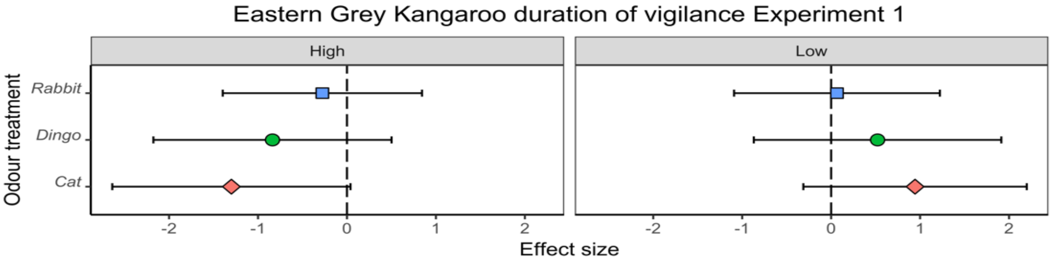

Figure 4.11: Effect size of an interaction between cat, rabbit and dingo odour in high and low vegetation on eastern grey kangaroo duration of vigilance in Experiment 1

Table 4.19: Model summary of cat, rabbit and dingo odour effect on eastern grey kangaroo duration of vigilance in Experiment 1

Eastern Grey Kangaroo Model: log(response)~odour + random(camera)								
Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|t|)
1	Duration of Vigilance	normal	log	0.957	(Intercept)	3.584	0.378	<0.001
					Rabbit odour	-0.243	0.485	0.618
					Dingo odour	-0.247	0.582	0.673
					Cat Odour	-0.241	0.548	0.662

4.2 Experiment 2 – Effects of thylacine and fox odours

Table 4.20: Abundance of species caught on camera in low and high vegetation in Experiment 2

	Eastern Bettong	**Eastern Quoll**	**Eastern Grey Kangaroo**	**Brushtail possum**	**Swamp Wallaby**	**Red-necked Wallaby**	**Total**
Total	230	8	125	57	39	32	491
Low Veg	83	2	58	30	18	24	215
High Veg	147	6	67	27	21	8	276

4.2.1 Visit Counts

4.2.1.1 Eastern Bettong

An interaction between odour treatment and vegetation (Table 4.21, Figure 4.12) had no significant effects on eastern bettongs number of visits and there were no significant effects of odour on its own (Table 4.22).

Table 4.21: Model summary of the effect of an interaction between fox and thylacine odour in high and low vegetation on eastern bettong visits in Experiment 2

Eastern Bettong								
Model: response~Vegetation*Odour+random(camera)								
Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|z|)
2	Visits	poisson	na	0.923	(Intercept)	0.435	0.352	0.217
					VegetationLow	-0.252	0.498	0.612
					Fox odour	0.078	0.195	0.687
					Thylacine odour	-0.085	0.203	0.675
					VegetationLow: Fox odour	-0.078	0.332	0.813
					VegetationLow: Thylacine odour	0.261	0.328	0.427

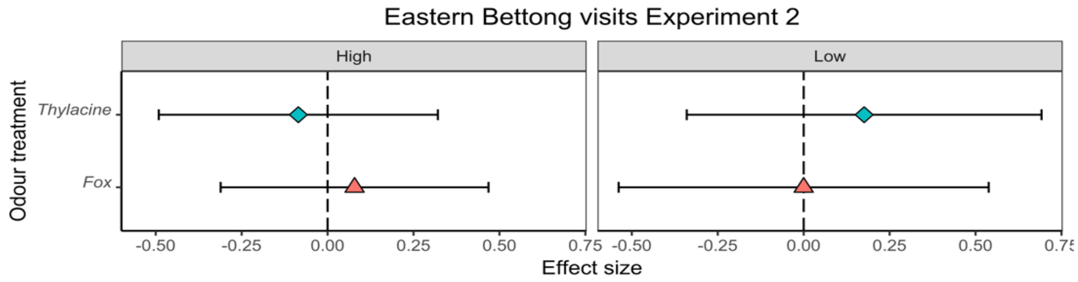

Figure 4.12: Effect size of an interaction between fox and thylacine odour in high and low vegetation on eastern bettong visits in Experiment 2

Table 4.22 : Model summary of fox and thylacine odour effect on eastern bettong visits in Experiment 2

Eastern Bettong								
Model: response~odour+random(camera)								
Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|z|)
2	Visits	poisson	na	0.945	(Intercept)	0.312	0.255	0.220
					Fox odour	0.052	0.158	0.742
					Thylacine odour	0.013	0.159	0.934

4.2.1.2 Brushtail Possum

In Experiment 2, fox odour had a significant negative effect (p=0.048*) on the number of visits of brushtail possums in high vegetation (Table 4.23, Figure 4.13). There are no significant effects of odour treatment of the number of visits (Table 4.24).

Table 4.23: Model summary of the effect of an interaction between fox and thylacine odour in high and low vegetation on brushtail possum visits in Experiment 2 (*p<0.05, **p<0.01, ***p<0.001)

Brushtail Possum

Model: response~Vegetation*Odour+random(camera)

Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|z|)
2	Visits	poisson	na	0.288	(Intercept)	-1.311	0.677	0.053
					VegetationLow	-0.132	0.821	0.873
					Fox odour	-1.030	0.521	0.048*
					Thylacine odour	-0.560	0.443	0.207
					VegetationLow: Fox odour	1.135	0.695	0.102
					VegetationLow: Thylacine odour	0.760	0.631	0.228

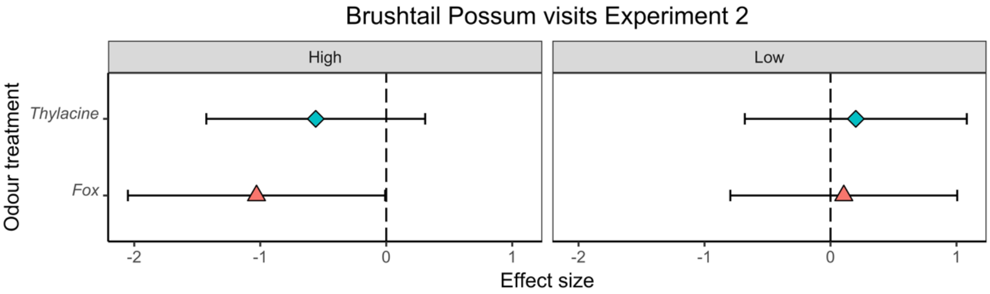

Figure 4.13: Effect size of an interaction between fox and thylacine odour in high and low vegetation on brushtail possum visits in Experiment 2. Where the effect size line does not overlap with the dashed line that sits on 0.0 there is a significant effect

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Table 4.24: Model summary of fox and thylacine odour on brushtail possum visits in Experiment 2 (*p<0.05, **p<0.01, ***p<0.001)

Brushtail Possum Model: response~odour+random(camera)								
Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|z|)
2	Visits	poisson	na	0.428	(Intercept)	-1.341	0.506	0.008 **
					Fox odour	-0.427	0.332	0.198
					Thylacine odour	-0.191	0.310	0.538

4.2.1.3 Eastern Grey Kangaroo

There was no significant effect of an interaction of odour and vegetation level for the number of visits (Table 4.25). Odour on its own had no effect on the number of eastern grey kangaroo visits (Table 4.26).

Table 4.25: Model summary of the effect of an interaction between fox and thylacine odour in high and low vegetation on eastern grey kangaroo visits in Experiment 2

Eastern Grey Kangaroo Model: response~Vegetation*Odour+random(camera)								
Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|z|)
2	Visits	poisson	na	0.778	(Intercept)	-0.169	0.367	0.655
					VegetationLow	-0.074	0.510	0.885
					Fox odour	-0.154	0.321	0.631
					Thylacine odour	0.288	0.289	0.319
					VegetationLow: Fox odour	0.103	0.454	0.821
					VegetationLow: Thylacine odour	-0.339	0.431	0.432

Table 4.26: Model summary of fox and thylacine odour effect on eastern grey kangaroo visits through Experiment 2

Eastern Grey Kangaroo Model: response~odour+random(camera)								
Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|z|)
2	Visits	poisson	na	0.546	(Intercept)	-0.203	0.268	0.447
					Fox odour	-0.103	0.227	0.651
					Thylacine odour	0.137	0.214	0.523

4.2.1.4 Other Species

For the species where there were not enough data for analyses, their visitation rates were recorded using bar graphs looking at the effect of an interaction effect between odour and vegetation cover (Figure 4.14). For eastern quolls, there were two visits to fox odour sites (one in each vegetation type). There were three visits to thylacine odour sites where two were in high vegetation and there were three visits to control sites, which were all in high vegetation. For red-necked wallabies, there were 14 visits to the fox odour sites, where only one was in high vegetation. In thylacine odour sites, there was an even split of five visits to each high and low vegetation and at control sites there were eight (three in high vegetation). For swamp wallabies, there were 17 visits to sites holding fox odour (seven in high vegetation), and 14 visits to thylacine odour (eight in high vegetation). The control sites had eight visits with six in high vegetation.

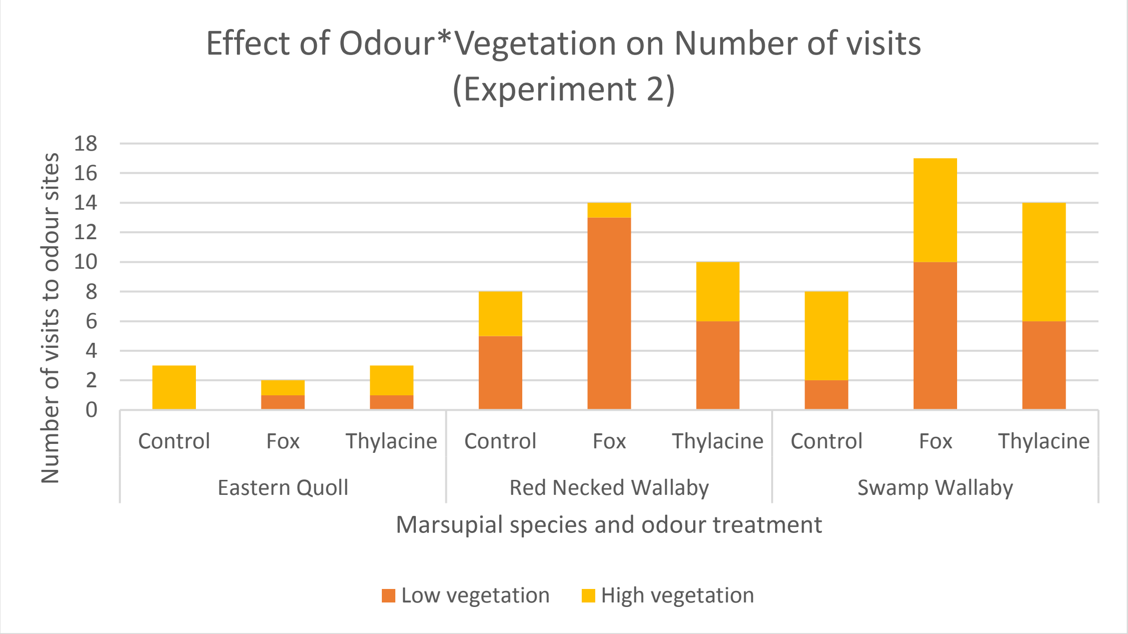

Figure 4.14: Effect of odour with vegetation on the number of visits by eastern quolls, red-necked wallabies and swamp wallabies in Experiment 2

4.2.2 Duration of visit

4.2.2.1 Eastern Bettong

There was a significant positive effect (p=0.014*) by fox treatment on the duration of visit in low vegetation (Table 4.27, Figure 4.15). Odour treatment on its own did not have a significant effect (Table 4.28, Figure 4.16) on the duration of visit.

Table 4.27: Model summary of the effect of an interaction between fox and thylacine odour in high and low vegetation on eastern bettong duration of visit in Experiment 2 (*p<0.05, **p<0.01, ***p<0.001)

Eastern Bettong

Model: log(response) ~ Vegetation * Odour + (1 \| Camera)

Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|t|)
2	Duration of visit	normal	log	0.099	(Intercept)	3.818	0.457	<0.001
					VegetationLow	-1.681	0.627	0.010 *
					Fox odour	-0.642	0.431	0.145
					Thylacine odour	-0.345	0.441	0.439
					VegetationLow: Fox odour	1.580	0.609	0.014*
					VegetationLow: Thylacine odour	1.011	0.601	0.102

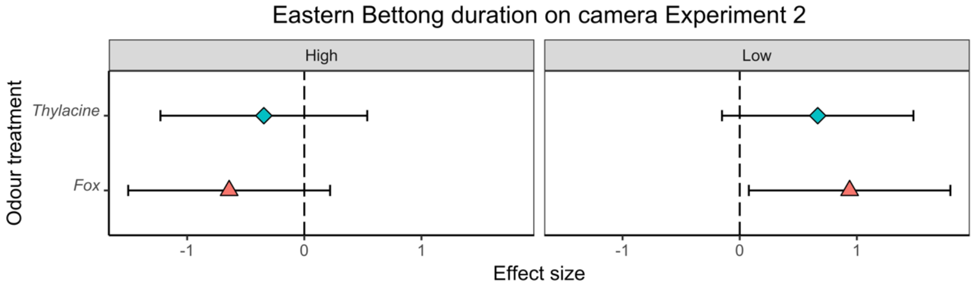

Figure 4.15: Effect size of an interaction between fox and thylacine odour in high and low vegetation on eastern bettong duration of visit in Experiment 2. Where the effect size line does not overlap with the dashed line that sits on 0.0 there is a significant effect

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Table 4.28: Model summary of fox and thylacine odour effect on eastern bettong duration of visit in Experiment 2

Eastern Bettong Model: log(response)~odour + random(camera)								
Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|t|)
2	Duration of visit	normal	log	0.823	(Intercept)	2.924	0.338	<0.001
					Fox odour	0.171	0.328	0.605
					Thylacine odour	0.172	0.323	0.597

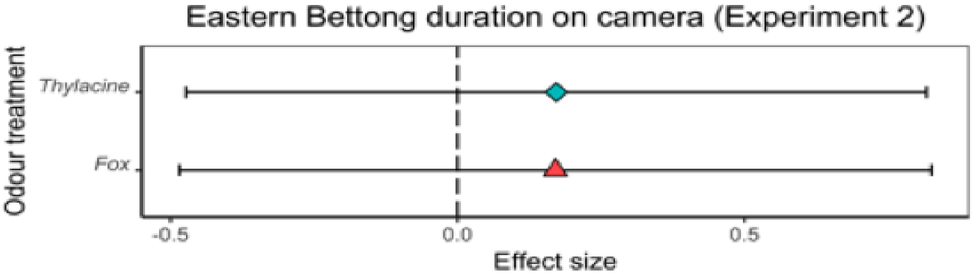

Figure 4.16: Effect size of fox and thylacine odour on eastern bettong duration of visit in Experiment 2

4.2.2.2 Brushtail Possum

The duration of visit was affected by an interaction between odour treatment and vegetation. Fox odour treatment had a near significant ($p = 0.050$) negative effect in high vegetation (Table 4.29, Figure 4.17). There were significant positive effects from both thylacine ($p=0.010$*) and fox ($p=0.007$**) treatments in low vegetation. There were no significant effects of thylacine or fox odour on their own on the duration of visit (Table 4.30).

Table 4.29: Model summary of the effect of an interaction between fox and thylacine odour in high and low vegetation on brushtail possum duration of visit in Experiment 2 (*p<0.05, **p<0.01, ***p<0.001)

Brushtail Possum

Model: log(response) ~ Vegetation * Odour + (1 | Camera)

Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|t|)
2	Duration of visit	normal	log	0.065	(Intercept)	3.569	0.421	<0.001
					VegetationLow	-1.020	0.545	0.073
					Fox odour	-1.075	0.511	0.050
					Thylacine odour	-0.868	0.511	0.107
					VegetationLow: Fox odour	2.133	0.710	0.007 **
					VegetationLow: Thylacine odour	1.939	16.908	0.010 *

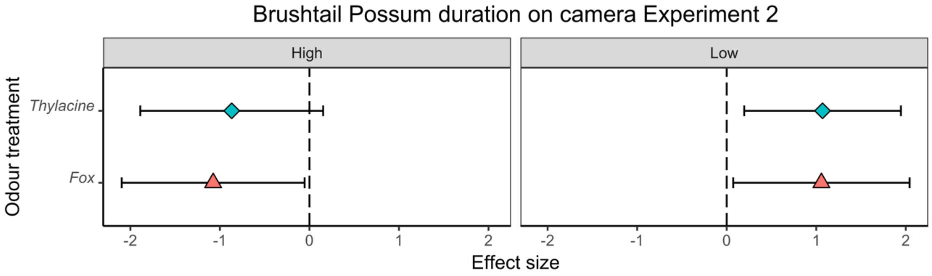

Figure 4.17: Effect size of an interaction between fox and thylacine odour in high and low vegetation on brushtail possum duration of visit in Experiment 2. Where the effect size line does not overlap with the dashed line that sits on 0.0 there is a significant effect

Table 4.30: Model summary of fox and thylacine odour effect on brushtail possum duration of visit in Experiment 2

Brushtail Possum

Model: log(response)~odour + random(camera)

Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|t|)
2	Duration of visit	normal	log	0.829	(Intercept)	2.968	0.322	<0.001
					Fox odour	0.048	0.425	0.911
					Thylacine odour	0.236	0.400	0.562

4.2.2.3 Eastern Grey Kangaroo

There was a significant positive effect (p=0.007**) by thylacine odour treatment on the duration of visit in high vegetation. In low vegetation thylacine had a significant negative effect (p=0.013*) (Table 4.31, Figure 4.18). Odour treatments on their own did not have a significant effect on the duration of visit (Table 4.32).

Table 4.31: Model summary of the effect of an interaction between fox and thylacine odour in high and low vegetation on eastern grey kangaroo duration of visit in Experiment 2 (*p<0.05, **p<0.01, ***p<0.001)

Eastern Grey Kangaroo

Model: log(response) ~ Vegetation * Odour + (1 | Camera)

Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|t|)
2	Duration of visit	normal	log	0.070	(Intercept)	3.462	0.400	<0.001
					VegetationLow	0.262	0.615	0.672
					Fox odour	0.673	0.623	0.288
					Thylacine odour	1.612	0.563	0.007 **
					VegetationLow: Fox odour	-0.766	0.874	0.387
					VegetationLow: Thylacine odour	-2.238	0.846	0.013 *

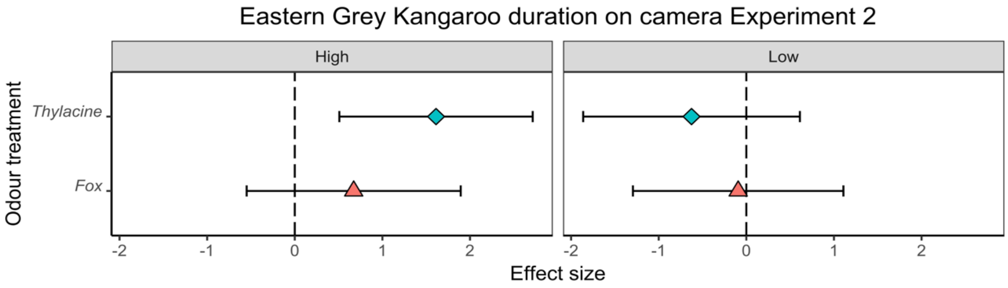

Figure 4.18: Effect size of an interaction between fox and thylacine odour in high and low vegetation on eastern grey kangaroo duration of visit in Experiment 2. Where the effect size line does not overlap with the dashed line that sits on 0.0 there is a significant effect

Table 4.32: Model summary of fox and thylacine odour effect on eastern grey kangaroo duration of visit in Experiment 2

Eastern Grey Kangaroo Model: log(response)~odour + random(camera)								
Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|t|)
2	Duration of visit	normal	log	0.448	(Intercept)	3.556	0.332	<0.001
					Fox odour	0.250	0.471	0.599
					Thylacine odour	0.584	0.457	0.211

4.2.3 Duration of vigilance

4.2.3.1 Eastern Bettong

There are no significant effects caused by odour treatment and vegetation on the duration of vigilance (Table 4.33, Figure 4.19). Both thylacine and fox odours on their own did not significantly affect the duration of vigilance (Table 4.34, Figure 4.20).

Table 4.33: Model summary of the effect of an interaction between fox and thylacine odour in high and low vegetation on eastern bettong duration of vigilance in Experiment 2

Eastern Bettong Model: log(response) ~ Vegetation * Odour + (1 | Camera)								
Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|t|)
2	Duration of vigilance	normal	log	0.866	(Intercept)	2.075	0.380	<0.001
					VegetationLow	-0.256	0.760	0.739
					Fox odour	-0.598	0.518	0.258
					Thylacine odour	-0.100	0.601	0.870
					VegetationLow: Fox odour	0.303	0.920	0.744
					VegetationLow: Thylacine odour	-0.036	1.005	0.972

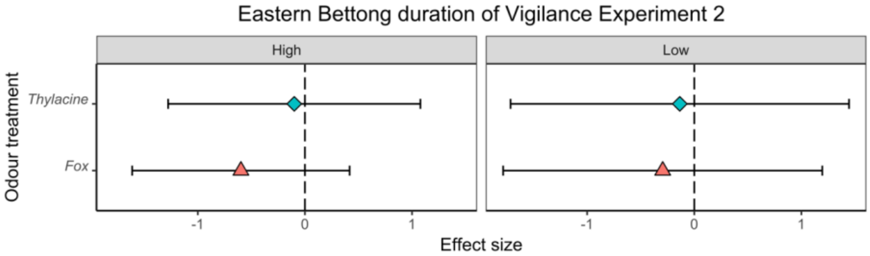

Figure 4.19: Effect size of an interaction between fox and thylacine odour in high and low vegetation on eastern bettong duration of vigilance in Experiment 2

Table 4.34: Model summary of fox and thylacine odour effect on eastern bettong duration of vigilance in Experiment 2

Eastern Bettong Model: log(response)~odour + random(camera)								
Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|t|)
2	Duration of vigilance	normal	log	0.458	(Intercept)	2.011	0.331	<0.001
					Fox odour	-0.512	0.421	0.233
					Thylacine odour	-0.182	0.468	0.701

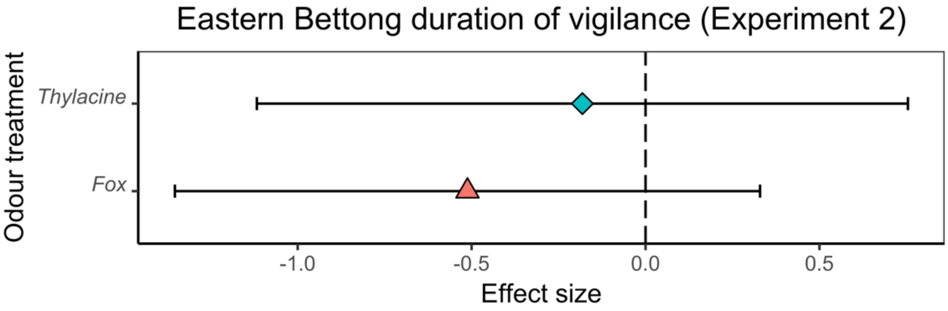

Figure 4.20: Effect size of fox and thylacine odour on eastern bettong duration of vigilance in Experiment 2

4.2.3.2 Brushtail Possum

There were no significant results when considering odour with vegetation (Table 4.35, Figure 4.21) and there were no significant effects from odour treatments on their own (Table 4.36).

Table 4.35: Model summary of the effect of an interaction between fox and thylacine odour in high and low vegetation on brushtail possum duration of vigilance in Experiment 2

Brushtail Possum

Model: log(response) ~ Vegetation * Odour + (1 | Camera)

Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|t|)
2	Duration of vigilance	normal	log	0.575	(Intercept)	1.859	0.449	0.001 ***
					VegetationLow	0.669	0.682	0.339
					Fox odour	-0.488	0.566	0.414
					Thylacine odour	0.530	0.602	0.410
					VegetationLow: Fox odour	-0.200	0.986	0.842
					VegetationLow: Thylacine odour	-0.746	0.853	0.405

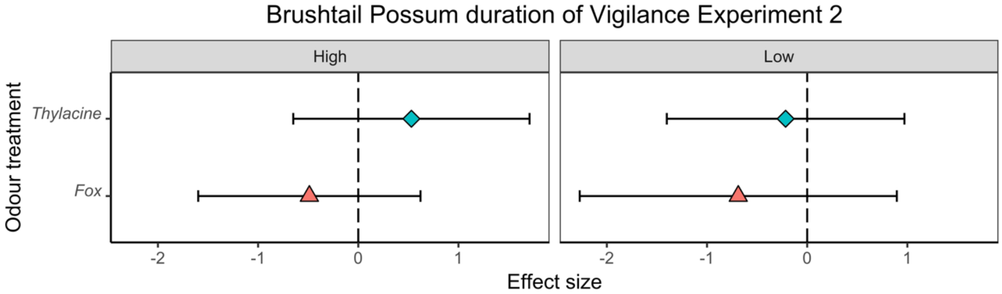

Figure 4.21: Effect size of an interaction between fox and thylacine odour in high and low vegetation on brushtail possum duration of vigilance in Experiment 2

Table 4.36: Model summary of fox and thylacine odour effect on brushtail possum duration of vigilance in Experiment 2

Brushtail Possum Model: log(response)~odour + random(camera)								
Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|t|)
2	Duration of vigilance	normal	log	0.287	(Intercept)	2.155	0.347	<0.001
					Fox odour	-0.604	0.477	0.224
					Thylacine odour	0.193	0.432	0.663

4.2.3.3 Eastern Grey Kangaroo

There were no significant effects caused by an interaction between odour and vegetation (Table 4.37, Figure 4.22) and odour on its own had no significant effect on duration of vigilance (Table 4.38).

Table 4.37: Model summary of the effect of an interaction between fox and thylacine odour in high and low vegetation on eastern grey kangaroo duration of vigilance in Experiment 2

Eastern Grey Kangaroo Model: log(response) ~ Vegetation * Odour + (1 | Camera)								
Exp	Response	Distribution	Transformation	Chisq p	Predictor variable	Estimate	Std. error	Pr(>|t|)
2	Duration of vigilance	normal	log	0.626	(Intercept)	3.390	0.462	<0.001
					VegetationLow	-0.476	0.654	0.471
					Fox odour	-0.265	0.654	0.687
					Thylacine odour	0.134	0.630	0.833
					VegetationLow: Fox odour	0.981	0.925	0.296
					VegetationLow: Thylacine odour	-0.440	0.908	0.631

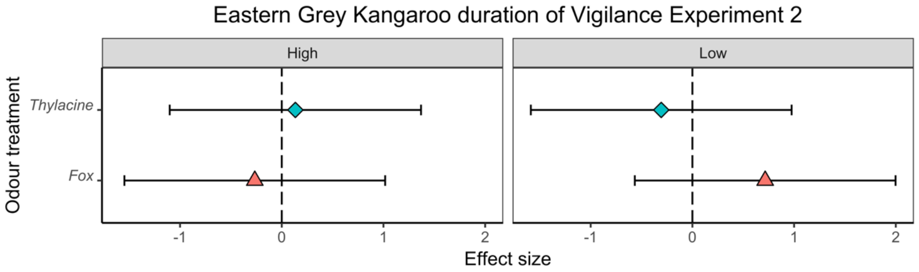

Figure 4.22: Effect size of an interaction between fox and thylacine odour in high and low vegetation on eastern grey kangaroo duration of vigilance in Experiment 2

Table 4.38: Model summary of fox and thylacine odour effect on eastern grey kangaroo duration of vigilance in Experiment 2

<table>
<tr><td colspan="9">Eastern Grey Kangaroo
Model: log(response)~odour + random(camera)</td></tr>
<tr><td>Exp</td><td>Response</td><td>Distribution</td><td>Transformation</td><td>Chisq p</td><td>Predictor variable</td><td>Estimate</td><td>Std. error</td><td>Pr(>|t|)</td></tr>
<tr><td>2</td><td>Duration of vigilance</td><td>normal</td><td>log</td><td>0.828</td><td>(Intercept)</td><td>3.152</td><td>0.341</td><td><0.001</td></tr>
<tr><td></td><td></td><td></td><td></td><td></td><td>Fox odour</td><td>0.225</td><td>0.482</td><td>0.643</td></tr>
<tr><td></td><td></td><td></td><td></td><td></td><td>Thylacine odour</td><td>-0.051</td><td>0.473</td><td>0.914</td></tr>
</table>

Below is a summary table (Table 4.39) of all results across both experiments with odour and odour with vegetation. Bold font indicates significant effects. For visits, a - symbol means there was a negative effect, or less visits compared to the control and a + symbol means more visits. For duration of visit a – symbol means there was a negative effect, or less time was spent in those sites compared to the control and a + means there was more time spent there. For duration of vigilance, a – symbol means there was a negative effect, or less time was spent being vigilant in those sites compared to the control and a + means there was more time spent being vigilant.

Table 4.39: Results of odour and vegetation effect on eastern bettongs, brushtail possums and eastern grey kangaroos (Effect/-or +/veg). Bolded red font indicates a significant effect

Visits	**Rabbit**	**Cat**	**Dingo**	**Fox**	**Thylacine**
Eastern Bettong	**Y/-/L**	N	N	N	N
Brushtail Possum	N	N	N	**Y/-/H**	N
Eastern Grey Kangaroo	N	N	N	N	N
Duration visits	**Rabbit**	**Cat**	**Dingo**	**Fox**	**Thylacine**
Eastern Bettong	**Y/-/NA**	N	N	**Y/+/L**	N
Brushtail Possum	N	N	N	**Y/+/L,** Y/-/H	**Y/+/L**
Eastern Grey Kangaroo	N	**Y/-/H, Y/+/L**	**Y/+/L**	N	**Y/+/H, Y/-/L**
Duration vigilance	**Rabbit**	**Cat**	**Dingo**	**Fox**	**Thylacine**
Eastern Bettong	N	**Y/+/H**	**Y/+/L, Y/+/NA**	N	N
Brushtail Possum	N	**Y/+/H**	N	N	N
Eastern Grey Kangaroo	N	**Y/+/L,** Y/+/H	N	N	N

Chapter 5: Discussion

In this study, I set out to test whether predator odour on its own, or an interaction of odour with vegetation cover influenced the behaviour of different marsupials. I measured three kinds of responses to the odours: i) the number of visits to odour sites, (ii) the duration the marsupial was at that site and (iii) the duration of vigilance the marsupial displayed when at an odour site.

Considering the 'landscape of fear' concept (Laundré *et al.*, 2001), the prey naïveté hypothesis (Cox and Lima, 2006), and isolation from mammalian predators, I developed the following research questions:

(i) After a period of isolation since 2009, do marsupial species including brushtail possums, eastern grey kangaroos, swamp wallabies and red-necked wallabies respond to historical and novel predator odours?

(ii) Do the eastern quoll and eastern bettong, reintroduced to MFWS, display anti-predator behaviour to a range of historical and novel predator odour cues?

(iii) Does vegetation cover influence the prey species responses to predator odour cues?

I was also interested in assessing how quolls and other resident species respond to recently eradicated rabbit odour.

Based on my research questions, I developed the following hypotheses:

(i) *Resident marsupials within Mulligans Flat would display anti-predator behaviour towards native predator (dingo and thylacine) odours but not to novel predator (fox and cat) odours.* This hypothesis is based on the theory that prey species evolved innate responses to native predators that will be maintained across many generations once removed.

(ii) *Reintroduced marsupials are naïve and so would not respond to dingo, fox or cat odour, but would respond to thylacine odour.* This is because they came from Tasmania where there are no dingoes, and foxes and cats are relatively new predators.

(iii) *Visitation rates to sites holding odours would be higher and duration of visits longer in high vegetation cover.* This hypothesis is based on the 'landscape of fear' concept, suggesting that prey perceive an area with more coverage to be less risky.

(iv) *Smaller marsupials would respond to predator odours more than larger marsupials.* This is because medium sized predators are more of a threat to smaller prey.

Below, I discuss and interpret my findings on the effect of each odour on each marsupial species and discuss some of the limitations I faced through my study, outlining some areas for future research.

5.1 Key Findings

My key findings from this study (see Table 4.39) were that visitations by eastern bettongs and brushtail possums were affected by an interaction with odour and level of vegetation cover. Interestingly these responses by the CWR marsupials were both to introduced species. The results for duration of visit were varied, with odour and low vegetation mainly influencing species spending more time in those sites. This demonstrated that my third hypothesis stating visits would be longer in high vegetation was incorrect. However, vigilance increased in high vegetation with odours. So, whilst they spent more time in low vegetation, they did not increase vigilance. The results for duration of vigilance demonstrate that in high vegetation, cat odour made eastern bettongs and brushtail possums more vigilant. Eastern grey kangaroos were more vigilant in response to cat odour in low vegetation and eastern bettongs were more vigilant in response to dingo in low vegetation. These results contradict my first two hypotheses because novel odours were responded to. This demonstrates that there was at least some level of naïveté in each species analysed because response rate was not consistent across all odours. Nearly all responses were from an interaction between odour and vegetation cover, suggesting that how animals perceived the threat of predator odours cues was dependent on vegetation. This suggests the landscape of fear influenced how these marsupials responded in the presence of odour. My fourth hypothesis stated that responses would be greater in smaller marsupials, however, size of the prey animals had no effect on response, with eastern grey kangaroos also responding to predators smaller than them.

5.2 Eastern Bettongs

5.2.1 Rabbit odour

Sites in low vegetation with rabbit odour were visited less by eastern bettongs compared to the controls. Although fruiting bodies of hypogeous fungi (truffles) make up most their diet, the eastern bettong also forages for seeds, roots and bulbs (Johnson, 1994; Adrian Manning, pers. comm), and so patches where rabbits are present may limit the amount of food available. Consequently, bettongs may instead be visiting patches where there is greater access to resources to avoid competition. Introduced herbivores are known to compete with native herbivorous marsupials for resources (Bird *et al.,* 2012). These results suggest that in the short time they co-existed (2012-2016) in MFWS, eastern bettongs learnt to recognise rabbit odour and avoid them. In 2016 rabbits were eradicated from MFWS (Will Batson, pers. comm).

The effect of rabbit odour alone (i.e. not considering vegetation cover) on the duration of visits was also clear. There was a negative effect indicating bettongs spent less time at a rabbit odour site compared to the control. This suggests that eastern bettongs were avoiding competition, or the danger of being in a risky, open area where they may be required to spend more time looking for limited resources. For example, Searle *et al.,* (2008) found northern brown bandicoots traded food for safety, leaving feeding stations at a higher GUD as the distance from high vegetation cover increased. The rabbit eradication process in MFWS involved shooting rabbits. It may be possible eastern bettongs associated rabbit odour with disturbance associated with the culling operation.

As a herbivorous competitor, rabbit odour appeared to have no effect on the duration of vigilance. It is known that carnivorous competitors are highly vigilant when encountering their competitor odours (Glen and Dickman, 2005; Andrewatha, 2017). Environmental change related to rabbits could help explain variation in the presence of Australian ground dwelling mammals, with population decreases often correlated with higher rabbit densities (Johnson *et al.,* 2007). My results on eastern bettong responses to rabbits demonstrate that introduced herbivores can be detrimental to species with reduced ranges. It is harder to avoid a competitor as they become more established, creating fewer available patches. This can then create competition within a species (Glen and Dickman, 2005).

5.2.2 Cat odour

Cat odour appeared to have no effect on the number of visits or the duration of visits for eastern bettongs. However, eastern bettongs increased vigilance in response to cat odour in high vegetation. A decrease in visit numbers and the duration of visits would demonstrate predator odour recognition, so the response indicated eastern bettongs have some level of naïveté towards cats as a novel predator.

There were examples of investigation where the individual approached the odour station, sniffing the tea strainer holding the odour. In some situations, this happened more than once in a visit so I believe that “predator investigation” was involved. Predator investigation is when upon first sensing a predator, or its odour, some prey respond by first approaching a potentially fearful scent rather than fleeing, freezing, or hiding (Parsons *et al.,* 2017). As investigation was also counted as vigilant behaviour in this study, part of the ‘duration of vigilance’ was investigation of the odour, rather than just scanning surroundings.

Cats are stealthy and rely on coverage to stalk their prey (Hornocker, 1970; Laundré *et al.,* 2010). Being more vigilant in an area of high vegetation in response to predators is an appropriate response, particularly if the prey species is uncertain of who the odour belongs to. None of the MFWS animals have experienced cats, and so the odour does not indicate the size and the hunting strategies of these predators. Eastern bettongs may not fully recognise cat odour. Therefore, being in an area of low visibility may mean there is a greater requirement to keep watch in the absence of prior experience. West *et al.* (2017) found that between a population of cat exposed and a population of non-exposed burrowing bettongs, those not exposed where more naïve and the exposed bettongs adjusted their behaviours, displaying anti-predator behaviours in a short time.

5.2.3 Dingo odour

Dingo odour had no effect on the number of visits or the duration of visits in eastern bettongs. Eastern bettongs only responded to dingo odour by increasing vigilance in low vegetation and to dingo odour on its own. The eastern bettongs in MFWS had no experience with dingoes as they were translocated from Tasmania where there are no dingoes (Corbett, 1995). Dingo odour to an eastern bettong is therefore novel. The eastern bettongs had some level of prey naïveté. Whilst there are wild dogs in Tasmania, that are likely to have similar diets, eastern bettongs may not fully recognise the smell of the predator and so are extra vigilant. Vigilance may be increased in low vegetation because there are fewer grasses for hiding in case of predator interaction. I was unable to find literature on the differences in odours emitted by dingoes and dogs. However, odour may be influenced by whether the dingoes are purebred (like the ones used in this study) or wild crossbred (*Canis familiaris dingo)* by individuals in the wild. For example, a study found that foraging beavers (*Castor fiber*) responded to wolf odour cues, but not to dog odour, and western grey kangaroos (*Macropus fuliginosus*) could differentiate between coyote and dingo odour (Parsons and Blumstein, 2010a). Consequently, experience with wild dogs may not result in recognition of dingoes. Carthey and Banks in their 2016 study predicted that prior experience with dingoes would result in bush rats (*Rattus fuscipes*) responding to dogs and found that they increased GUD, increased vigilance and decreased foraging. However, Banks *et al.* (2003) found there was no response to dog faeces by bush rats. Again, this demonstrates the large variability between studies. A response to two novel predator odours suggests the bettongs recognise or are interested in something within the odour. It is possible that carnivore predators produce odours that contain similar volatile compounds. This will need further research.

5.2.4 Thylacine odour

Eastern bettongs appeared to be completely naïve to thylacine odour because there were no effects on the number of visits, how long they visited for, or how long they were vigilant. This may mean the odour was too weak for a response from eastern bettongs, or the separation period between species from when thylacine became extinct has led to a loss of their innate anti-predator responses to their key historical predator (Blumstein *et al.*, 2006). Whilst the odour was derived from a deceased specimen, it was treated in the same manner as those from living specimens. It be may the case that over time, the volatile chemicals have changed to be unrecognisable, though brushtail possums and eastern grey kangaroos did respond.

5.2.5 Fox odour

Although fox had no effect on the number of visits, or the duration of vigilance, eastern bettongs increased their duration of visit in response to fox odour in low vegetation cover. The responses to foxes (a novel predator) by bettongs suggest that there was some level of naïveté because they increased their duration at the low vegetation sites. Without a threat associated with the odour, eastern bettongs could spend time feeding in open areas. If the reasoning for increased duration of visit was predator investigation, there should also be an effect on duration of vigilance. My results suggest that outside of a fenced reserve eastern bettongs would not recognise the threat of predation, and would need to learn through either close encounters or by seeing conspecifics being attacked. Upon release, it is possible that a number of eastern bettongs would die due to the lack of experience and history with foxes.

5.3 Brushtail Possums

5.3.1 Rabbit odour

There were no effects of rabbit odour with vegetation or on its own on brushtail possum behaviour. Brushtail possums and rabbits had co-existed in the Sanctuary up until 2016 when rabbits were eradicated. No response to the odour does not necessarily mean it was not recognised. As possums are a mainly arboreal species they do not face the same level of competition from rabbits as ground dwelling marsupials such as the eastern bettong.

5.3.2 Cat odour

Cat odour in high vegetation sites had a positive effect on the duration of vigilance in brushtail possums. Odour influenced both eastern bettongs and brushtail possums (both within the CWR) to be more vigilant when in sites of high vegetation. Cats stalk their prey, so whilst high vegetation may mean more hiding spots for prey animals, it also means there is less visibility which may be detrimental when considering some predator hunting techniques such as stalking and pouncing (Laundré *et al.,* 2010). On its own, cat odour had a near significant positive effect on the duration of vigilance, suggesting there was some recognition of the odour, which again, may be associated with chemical composition of the odour because the brushtail possums have not been exposed to cats since 2009.

5.3.3 Dingo odour

There were no effects for dingo odour on the behaviour of brushtail possums. This suggests that they are naïve to dingoes. Although dingoes have been on mainland Australia for ~4000 years (Corbett, 1995) they have not been common in the ACT for some time, particularly with rapid urbanisation and agricultural use of the north of the ACT. This absence of separation may have led to a loss of innate responses to dingo odour. The dingo odour used came from purebred dingoes to ensure it represented a historical predator. These results contrast with a previous study on Tasmanian brushtail possums which showed brushtail possums showed flight and vigilance when encountering dingo odour outside an enclosure (Parsons and Blumstein, 2010b). Dingoes are absent from Tasmania so this odour cue was novel.

5.3.4 Fox odour

Foxes and brushtail possums co-existed for a short period of time before eradication of foxes in 2009. Fox odour had a negative effect on the number of visits in high vegetation and a near significant negative effect on how long brushtail possums were present in high vegetation.

In high vegetation there is less visibility and so it is a riskier environment if predators use pouncing techniques. Possums are mainly arboreal so if they decided to stay in the trees upon smelling fox odour, it may have affected visit numbers. For those possums that did visit the sites, there were no effects of fox odour on its own or with vegetation on the duration of vigilance. My results suggest there was a level of naïveté in MFWS brushtail possums towards fox odour. It also seems that possums perceived risk before approaching an area, which is why the number of visits were affected negatively. Brushtail possums feed mainly on eucalypt leaves however, ground vegetation makes up ~25% of their diet (Kerle, 1984; Dearing and Cork, 1999; Pickett et al, 2005). Ground feeding can offer a higher-quality diet but can come with a higher predation risk (Mella *et al.,* 2014a). Possums are susceptible to fox predation when they come to the ground to feed or travel between trees and the presence of foxes may reduce the distance on the ground that possums travel in one night (MacLennan, 1984; Pickett et al., 2005).

It is thought possums manage predation risk whilst foraging by varying time allocation, rather than adjusting vigilant behaviour (Mella *et al.,* 2014a). Being away from mammalian predators may have resulted in a shift in behaviour, because in MFWS possums are observed frequently travelling slowly along the ground, with low levels of vigilance (Adrian Manning, pers. comm). No effect on vigilance whilst on the ground may suggest they are naïve. However, in a study by McDonald-Madden *et al.* (2000), brushtail possums feeding on the ground, from the safety of trees did not increase vigilance. When possums perceived the risk of predation as high they left the feeding patch. This is supported by my results showing a near significant effect of fox odour with high vegetation on the duration of visit.

5.3.5 Thylacine odour

There was a positive effect of thylacine treatments on duration of visit in low vegetation. I do not believe this is due to predator investigation, because investigative behaviour such as odour sniffing was counted as vigilance, so duration of vigilance should also have been affected.

Thylacine odour did not influence the number of visits, or how long brushtail possums were vigilant. It could be possible they have lost their instinctive anti-predator behaviour in response to the thylacine, or that perhaps the odour was too weak for the brushtail possum. Weak anti-predator responses may be shown as odours age, with the risk of predation perceived to be low, or because they do not recognise the threat attached to the odour (Dickman and Doncaster, 1984, Parsons *et al.,* 2017). My interpretation is that once there was some recognition and the possums discovered there was no threat, they felt the risk disappeared and so could spend more time in the area. Assessing predation risk would be easier in low vegetation cover compared to high vegetation because there is more visibility in low vegetation sites.

5.4 Eastern Grey Kangaroo

5.4.1 Rabbit odour

There were no effects on eastern grey kangaroo behaviour by rabbit odour. This is an interesting result as they are both grazers and therefore competitors. However, eastern grey kangaroos are generally social feeders (Miller *et al.,* 2010; Descovich *et al.,* 2016). Their individual size and their group size may mean they do not consider rabbits as competition. Interesting observations contradicting that idea is juvenile male kangaroos sniffing the odour station, scanning their surroundings, sniffing the odour station again then attempting to fight the odour station, holding it and kicking it. This behaviour was captured in more than one video, only in sites holding rabbit odour. Perhaps, being herbivores, they have similar odours as kangaroos and so the young males wanted to play fight. Perhaps rabbit odour was associated with disturbance linked with the rabbit culling operation and so seen as threatening.

5.4.2 Cat Odour

Although there was no effect on the number of visits to cat odour sites, eastern grey kangaroos spent less time in high vegetation sites holding cat odour. Cats are not really a threat to large macropods, however in high vegetation their young may be at risk. Feral cats have been known to predate on smaller wallabies (Hardman *et al.,* 2016). While these results on duration of behaviour are like those of the smaller marsupials, there was also a positive effect from cat odour in low vegetation on duration of visit (they were there longer) and duration of vigilance (increased vigilance). This may be due to predator investigation, where having the visibility from an open area makes them less vulnerable and more confident to investigate. I counted investigative behaviours (i.e. sniffing the tea strainer and sniffing the air towards the odour pole) as vigilance. Kangaroos spent more time in low vegetation sites with cat odour because they needed more time to investigate what the odour was and the increased visibility allowed them to do so.

5.4.3 Dingo odour

There were no effects of dingo odour on its own or with vegetation on the number of visits to odour sites. For duration of visit, kangaroos spent more time in low vegetation. Whilst this result contradicts my hypothesis of showing anti-predator behaviour in response to coevolved predators, the response in low vegetation might indicate that with increased visibility, the fast realisation that there is no threat allowed eastern grey kangaroos to forage without fear. There were no effects on the duration of vigilance in eastern grey kangaroos. This suggests there was some level of naïveté to dingo odour because in the wild, dingoes are known to influence large macropod behaviour (Short *et al.,* 2002).

5.4.4 Thylacine odour

In low vegetation, thylacine reduced the duration of visit in eastern grey kangaroos showing a possible innate response. Thylacines were believed to be pounce and pursuit predators that hunted in open areas (Jones and Stoddart, 1998). This response contrasts with responses to other predator (cat and dingo) odours in low vegetation where eastern grey kangaroos spent more time. Thylacine odour influenced eastern grey kangaroos to spend more time in high vegetation sites. There were no effects on duration of vigilance so I do not think the increased duration at sites was from investigation. This differs from my other results which showed duration of visit to be shorter in high vegetation. Eastern grey kangaroos may recognise the odour of thylacine as threatening. This demonstrates in some species their innate responses to absent predators can be retained. My results support those of Chamaille-Jammes *et al.* (2014) where black tailed deer could discriminate between the odours of wolves and black bear, when they had no experience with the wolves after they had been absent 100 years.

5.4.5 Fox odour

Fox odour on its own and with vegetation had no effect on eastern grey kangaroo behaviour. This suggests that eastern grey kangaroos are naïve to the odour of foxes, as novel predators. This is an interesting result because there was no investigation but they did have some responses to cat odour (another novel predator). Foxes and dingoes are both from the family Canidae, and eastern grey kangaroos showed very little response to both. Although kangaroos and wallabies are rare in the diet of foxes, studies in montane areas of Australia have suggested that foxes may prey on young eastern grey kangaroos, affecting their population growth (Banks *et al.*, 2000). The lack of response to fox odour suggests outside of MFWS young kangaroos would be vulnerable to fox predation.

5.5 Landscape of fear theory

My hypothesis was that visitation rates to sites holding odours would be higher, and duration of visits would be longer in high vegetation cover because there was more coverage from predators. However, most of the effects on duration of visit involved low vegetation. Spending extended periods in the open increases vulnerability but gives an animal more visibility and so may reduce fear.

How fear and habitat variation influences animal behaviour of course depends on the prey species. In bandicoots, they seem to use areas of high vegetation more for foraging, perceiving it as less risky (Searle *et al.*, 2008). For mule deer open areas were perceived to be less risky (Laundré and Hernandez, 2003). For duration of visit, my results mainly demonstrated that when an animal visited, it spent more time at odour sites in low vegetation, however it was in high vegetation they were more vigilant. With eastern bettongs, brushtail possums and eastern grey kangaroos, when there was an effect on the duration of vigilance to cat odour, it was an interaction effect with high vegetation cover. High vegetation gives prey species more places to hide from predation. When considering vegetation cover and a novel predator odour, prey are required to estimate predation risk so more cover may be safer for them to assess the situation. Behavioural shifts depend on the prey and predator species involved (Laundré *et al.,* 2010). Prey realise risk and adjust their behaviour appropriately. Over time, in the presence of predators, prey may change from spending more time in low vegetation and increasing vigilance in high vegetation once their predators and their hunting strategies are recognised. My results suggest that generally, high vegetation sites were perceived to be riskier.

Figure 4.17 shows some interesting results, with brushtail possums responding the same way to thylacine and fox, spending less time in areas of high vegetation and more time in low vegetation. Whilst not significant, there is a similar pattern when looking at bettong responses to these two odours (Figure 4.15). With thylacine gone, foxes may be occupying the same niche in terms of odour. It is interesting that bettongs and possums responded to these odours in the same way when they coexisted with thylacine but weren't negatively affected until foxes arrived. This is probably due to land clearing that came with European settlement, opening more areas for foxes to roam and hunt more effectively. The mixed responses suggest these animals are likely experiencing Level 3 naïveté (Banks and Dickman, 2007), where prey recognise a predator to be dangerous, and demonstrate the appropriate anti-predator behaviour, but the attack strategies are more successful than the prey's anti-predator response. The combination of naïveté and the landscape of fear could explain why so many animals have fallen victim to novel predators.

5.6 Predator inspection

When first detecting an odour, some prey responded by approaching a scent rather than fleeing, freezing, or hiding (Parsons *et al.,* 2017). Approaching an odour can indicate that an animal needs to examine it more closely to get more information about the true predation risk (Parsons *et al.,* 2017). Many of the animals approached the odour stations slowly, followed by sniffing the tea strainer. This was commonly seen with eastern grey kangaroos, red-necked wallabies and bettongs. They would often sniff the tea strainer multiple times before retreating from the site. This investigative behaviour was counted as vigilance and so contributed to the measure "duration of vigilance". There may be several benefits to approaching a predator scent including informing conspecifics of the potential threat (Parsons *et al.,* 2017). Animals may interact directly with the scent and release volatile compounds that assist with identification and assessment by licking or breathing onto the odour cue (Parsons *et al.,* 2017). This was seen in most of the species (brushtail possums, red necked wallabies, swamp wallabies and eastern grey kangaroos) where some would lick or attempt to eat the tea strainer. Therefore, it is important to understand that if a prey animal continues to approach and investigate odours, the deterrent may not necessarily have failed.

5.7 Limitations

5.7.1 Experimental design

My study was conducted in two experiments due to time delays with receiving some odours. An eastern quoll reintroduction also caused delays in fieldwork. This was a staggered translocation and I decided to wait until all quolls have been reintroduced to commence the second half of the study. This was to avoid biasing my results with more eastern quoll camera trappings collected towards the end. The need to have two separate experiments was a limitation. There could possibly have been some temporal and weather effects as the experiments were run with a gap of a couple of weeks between. Ideally, all odours with a rotating control would be put out in the same period to reduce the number of variables that may affect comparisons of behaviours between odours.

5.7.2 Camera issues

I had several technical issues with the cameras I was using. Although I changed the settings of each, removing delays between videos, some of the cameras settings defaulted where there were inconsistent delays. Several videos only captured an animal leaving a site, and in some cases, they were on the screen at the start of the video. This means there is uncertainty regarding true behaviour, because camera faults have led to poorer data quality. I believe the camera faults are caused by the age of the cameras and exposure to the elements out in MFWS for at least 18 months. Often cameras were bumped by animals and so the odour station would not be centered in the video. This highlights a need to better secure cameras, because animals often came to sniff them, they would get bumped by kangaroos feeding or by possums running down the tree they were attached to. Despite having camera issues I do not think this had a significant effect on the data because it was only a small number of cameras.

5.7.3 Novelty of field sites to animals

The cameras had been out in the landscape for approximately 18 months and the odour lure stakes were placed out into the field approximately 5 weeks prior to commencing the study. Whilst this may remove some effect of novel objects in the environment there is the possibility this led to curiosity and investigation by some animals. Attraction to novel structures in the landscape during the temporal control in Experiment 1 may have led to false positives where the visit may not have been due to odour.

5.7.4 Tampering by sanctuary visitors

On three occasions, there was evidence of tampering of field equipment by sanctuary visitors at different sites which may have altered results. During Experiment 2, one incident involved someone removing one of my cameras and changing the settings so that it stopped taking videos. This was in a site where I have previously captured eastern quolls on film, so this may have contributed to a small quoll dataset. Part of my experimental design involved using cameras that were not close to main tracks or common walkways, but being an open nature reserve, I did expect there may be some investigation of field sites. I decided not to place signage around the sites advising there was an experiment taking place because I thought that would probably draw more attention to a site.

5.8 Implications

This research has helped evaluate how the innate behaviour of resident and reintroduced prey species within a predator-free environment facilitated the detection and avoidance of introduced (foxes and cats), native (dingo) and extinct (thylacine) predators based on their odour cues. The position in the landscape was shown to affect how each marsupial in MFWS responded to odours, giving an indication of the vulnerability of each species to predation. This research therefore has conservation implications for considerations of reintroducing the eastern bettong or eastern quoll outside fenced areas.

Eastern bettongs, brushtail possums and eastern grey kangaroos all showed at least some level of naïveté. This was probably due to being isolated and having no experience of the novel threats, and being separated from historical predators for a period, resulting in a loss of any innate response. It would probably take deaths of conspecifics or a close call with a predator for an individual to be able to perceive predation risk. While attraction or lack of deterrence to the site with a predator odour attached would be highly dangerous in the wild, there was no threat attached to predator odours within MFWS. This research has demonstrated that isolated marsupials within the Sanctuary responded to different mammalian predators of which they have had no experience with in their life time.

It is critical to understand the level of predation risk in an area prior to a species reintroduction. Studies have shown that predator efficiency for a diverse range of predators is generally low, between 8-26%. At least 80% of the time prey escape (Laundré *et al.*, 2010). Rapid adaptations can occur in a short period where prey populations will shift their behaviour and learn to respond to predators accordingly. West *et al.* (2017) found this to be the case with burrowing bettongs. Another example is with the Lower Cotter Catchment eastern bettongs which have managed to survive, co-existing with low numbers of novel predators for approximately a year (Will Batson, pers. comm). A near death experience is an effective lesson for prey, particularly if habitat affects how narrow their escapes are. Landscape heterogeneity should therefore be considered when planning reintroductions of a species into an area that may have introduced predators present. The combination of naïveté and complex habitats could reduce the chances of success in the presence predators.

5.9 Further research

The complications I had with my experimental design and the results that emerged from my study lead to two main recommendations for further research. The first would be to replicate this study inside and outside the reserve (for example, within the Lower Cotter Catchment) at the same time for a comparison of responses of native fauna from those that have been isolated to those that have been exposed to mammalian predators. Whether repeated exposure to predator scents leads to habituation by animals could depend on whether there are predators associated with the odour cues (Parsons and Blumstein, 2010a). I would expect those outside of the reserve to display different responses compared to those inside the reserve. This would demonstrate that in these species it takes a short time for them to recover anti-predator responses.

Whilst there were low numbers of eastern quoll videos, there was some evidence of investigation to predator odours and so further research may give a clearer indication on eastern quoll behaviour. One visit by a quoll shows clear investigation of dingo odour; it leans against the odour pole and sniffs towards the tea strainer (Figure 4.23). Another video showed a quoll slowly approaching an odour station which held fox odour. It then stood on two legs leaning on the odour station pole sniffing the odour, climbed the odour station pole to get closer to the odour, sniffed the tea strainer, jumped down, then sniffed the ground around the odour pole and quickly retreated. Whilst fox is a novel odour to eastern quolls it may be recognised as another carnivorous competitor. Without knowing the threat or size of the fox, the quoll may have gone to investigate. This behaviour is known to occur in different competitive predators (Glen and Dickman, 2005).

While it seemed that quolls may be interested in the odour of foxes, further research is required to confirm this as the data were too low for statistical analysis. The sample size for quoll (n=4 in Experiment 1, n=8 in Experiment 2) was much smaller than expected, although the numbers of quolls present in the reserve during Experiment 1 were estimated to be ~15 and by the time Experiment 2 commenced, after the 2017 release, numbers were expected to be ~28 (Adrian Manning, pers comm). Replicating this study inside MFWS would ensure a larger dataset on quoll visits and behaviour, making it suitable to test results with statistical analysis. As this study was undertaken around the time that quolls started carrying pouch young, a study after the breeding period, once young disperse may lead to a different result. An important finding would be if, as carnivorous predators, quolls seek out novel fox and cat odour. If quolls were interested in fox odour, as foxes have been seen to seek out quolls (Andrewatha, 2017), it could affect translocation efforts. This attraction could increase their risk of predation if they are drawn to their predator. Results could inform decisions on translocating eastern quolls to areas with low numbers of predators outside of MFWS, such as the Lower Cotter Catchment.

My next recommendation would be to include a recent coevolved predator, such as the Tasmanian devil, for the reintroduced species to have more of an intermediate predator odour present. This could fill knowledge gaps of when innate responses disappear in the eastern quoll and eastern bettong. The experiment, if time permitted, should have all odours within the one experiment as well as a rotated control to prevent any chance of response differences due to temporal factors. Research to look at volatile chemicals within predator body odour may help explain responses to introduced predators. For example, the ‘common constituents hypothesis’ (Nolte *et al.*, 1994) suggests that prey may recognise even unfamiliar predators because odours of carnivores share common compounds (Tortosa *et al.*, 2015).

Figure 5.1: Eastern quoll leaning against odour station holding dingo odour in a high vegetation site. When a predator odour was not fully recognisable this behaviour is called predator investigation (Image: Author’s own)

Chapter 6: Conclusion

Fenced reserves keep vulnerable prey separated from novel predators that may otherwise have devastating effects on their numbers. With this isolation comes the risk of becoming naïve to predators that are coevolved. The implications occur at the time of reintroduction outside a predator free reserve, resulting in the inability to respond accordingly to any predators. This could lead to the rapid termination and subsequent failure of the reintroduction.

I set out to test how resident marsupials and reintroduced marsupials in a reserve free of mammalian predators responded to a range of predator odour cues. I also tested whether odour on its own or an interaction with vegetation cover influenced prey animals' behaviour.

My findings showed that a short period of isolation can remove innate anti-predator behaviour from prey species to their historical predators (e.g. brushtail possums to dingo odour). I also discovered that prey will often investigate unrecognisable odours, which may be detrimental. Vigilance tended to be more common in high vegetation sites, particularly for cat odour suggesting there was some level of recognition of risk. For fox odour, eastern bettongs and brushtail possums (two CWR species) spent more time at the sites. My results have shown that quantifying the landscape of fear can be useful in the management and conservation of wildlife populations because odour on its own often had no effect on the responses of prey animal to predator odour cues. Therefore, the landscape of fear model should be a valued management and conservation tool for understanding predator-prey interactions. Studying the effects of odour on their own may return incorrect results which can be problematic when considering conservation management strategies and particularly reintroduction programs for threatened species.

Inconsistences from past studies and the large amount of variation with my results demonstrate the need to study prey species responses to predator cues on a species by species basis. My results suggest that isolated marsupials can, to an extent, recognise predator odours, shown by reduced activity in areas compared to the controls, increased vigilance and differences in visit duration between low and high vegetation. The findings of this research have provided support for future research into comparison odour recognition studies, inside and outside a fenced reserve. My research has contributed to the understanding of predator-prey interactions between native marsupials and their potential predators, and has demonstrated all the species studied show at least some level of naïveté which could be detrimental to them outside MFWS. However, further research using an experimental reintroduction to a site with low numbers of predators may allow prey to gain exposure and quickly adapt to the environment.

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Appendix 1: List of the 30 Australian mammal species extinct since 1788

Common name	**Scientific name**
Western long-beaked echidna	*Zaglossus bruijnii*
Thylacine	*Thylacinus cynocephalus*
Pig-footed bandicoot	*Chaeropus ecaudatus*
Desert bandicoot	*Perameles eremiana*
Yallara (lesser bilby)	*Macrotis leucura*
Desert bettong	*Bettongia anhydra*
Nullabor dwarf bettong	*Bettongia pusilla*
Desert rat-kangaroo	*Caloprymnus campestris*
Broad-faced potoroo	*Potorous platyops*
Kuluwarri (central hare-wallaby)	*Lagorchestes asomatus*
Eastern hare-wallaby	*Lagorchestes leorides*
Toolache wallaby	*Macropus greyi*
Crescent nailtail wallaby	*Onychogalea lunata*
Dusky flying-fox	*Pteropus brunneus*
Lorde Howe long-eared bat	*Nyctophilus howensis*
Christmas Island pipistrelle	*Pipistrellus murrayi*
White-footed rabbit-rat	*Conilurus albipes*
Capricorn rabbit-rat	*Conilurus capricornensis*
Lesser stick-nest rat	*Leporillus apicalis*
Short-tailed hopping-mouse	*Notomys amplus*
Long-tailed hopping-mouse	*Notomys longicaudatus*
Large-eared hopping-mouse	*Notomys macrotis*
Darling Downs hopping-mouse	*Notomys mordax*
Broad-cheeked hopping-mouse	*Notomys robustus*
Long-eared mouse	*Pseudomys auritus*
Blue-gray mouse	*Pseudomys glaucus*
Gould’s mouse	*Pseudomys gouldii*
Bramble Clay melomys	*Melomys rubicola*
Maclear’s rat	*Rattus macleari*
Bulldog rat	*Rattus nativitatis*

All species were endemic to Australia except the western long-beaked echidna (Woinarski *et al.*, 2015).

Appendix 2: Rotation patterns of odour treatments every 4 days, spread over 30 cameras (Experiment 1)

Camera	Vegetation	Control	Odour 1	Odour 2	Odour 3
1	High	Control	Cat	Dingo	Rabbit
2	Low	Control	Dingo	Rabbit	Cat
3	Low	Control	Rabbit	Cat	Dingo
4	Low	Control	Cat	Dingo	Rabbit
5	Low	Control	Dingo	Rabbit	Cat
6	Low	Control	Rabbit	Cat	Dingo
7	High	Control	Dingo	Rabbit	Cat
8	Low	Control	Rabbit	Cat	Dingo
9	Low	Control	Cat	Dingo	Rabbit
10	High	Control	Rabbit	Cat	Dingo
11	Low	Control	Dingo	Rabbit	Cat
12	High	Control	Cat	Dingo	Rabbit
13	High	Control	Rabbit	Cat	Dingo
14	Low	Control	Dingo	Rabbit	Cat
15	High	Control	Rabbit	Cat	Dingo
16	High	Control	Cat	Dingo	Rabbit
17	Low	Control	Cat	Dingo	Rabbit
18	High	Control	Dingo	Rabbit	Cat
19	Low	Control	Cat	Dingo	Rabbit
20	Low	Control	Rabbit	Cat	Dingo
21	High	Control	Dingo	Rabbit	Cat
22	High	Control	Rabbit	Cat	Dingo
23	High	Control	Dingo	Rabbit	Cat
24	High	Control	Cat	Dingo	Rabbit
25	High	Control	Rabbit	Cat	Dingo
26	Low	Control	Cat	Dingo	Rabbit
27	High	Control	Dingo	Rabbit	Cat
28	Low	Control	Dingo	Rabbit	Cat
29	High	Control	Cat	Dingo	Rabbit
30	Low	Control	Rabbit	Cat	Dingo

Appendix 3: Rotation patterns of odour treatments every 4 days, spread over 30 cameras (Experiment 2)

Camera	Vegetation	Odour 1	Odour 2	Odour 3
1	High	Fox	Control	Thylacine
2	Low	Control	Thylacine	Fox
3	Low	Thylacine	Fox	Control
4	Low	Fox	Control	Thylacine
5	Low	Control	Thylacine	Fox
6	Low	Thylacine	Fox	Control
7	High	Control	Thylacine	Fox
8	Low	Thylacine	Fox	Control
9	Low	Fox	Control	Thylacine
10	High	Thylacine	Fox	Control
11	Low	Control	Thylacine	Fox
12	High	Fox	Control	Thylacine
13	High	Thylacine	Fox	Control
14	Low	Control	Thylacine	Fox
15	High	Thylacine	Fox	Control
16	High	Fox	Control	Thylacine
17	Low	Fox	Control	Thylacine
18	High	Control	Thylacine	Fox
19	Low	Fox	Control	Thylacine
20	Low	Thylacine	Fox	Control
21	High	Control	Thylacine	Fox
22	High	Thylacine	Fox	Control
23	High	Control	Thylacine	Fox
24	High	Fox	Control	Thylacine
25	High	Thylacine	Fox	Control
26	Low	Fox	Control	Thylacine
27	High	Control	Thylacine	Fox
28	Low	Control	Thylacine	Fox
29	High	Fox	Control	Thylacine
30	Low	Thylacine	Fox	Control

Appendix 4: Distribution of animals over sites in Experiment 1

Camera	Vegetation	Eastern Bettong	Eastern Quoll	Eastern Grey Kangaroo	Brushtail possum	Swamp Wallaby	Red-necked Wallaby	Total
1	High	12	0	2	9	0	2	25
2	Low	25	0	2	10	1	2	40
3	Low	1	0	0	4	0	2	7
4	Low	22	0	7	1	0	0	30
5	Low	31	0	1	3	0	0	35
6	Low	6	0	2	5	5	2	20
7	High	29	0	3	3	3	0	38
8	Low	2	0	4	2	6	3	17
9	Low	3	0	3	10	6	0	22
10	High	3	1	0	0	2	3	9
11	Low	20	0	1	3	7	5	36
12	High	43	0	15	3	4	3	68
13	High	2	0	4	4	3	0	13
14	Low	5	0	26	8	5	5	49
15	High	4	0	11	3	0	3	21
16	High	22	0	1	5	6	0	34
17	Low	1	2	2	7	0	0	12
18	High	3	1	2	2	0	1	8
19	Low	20	0	7	10	5	1	43
20	Low	18	0	4	3	1	0	25
21	High	4	0	2	4	4	0	14
22	High	6	0	1	0	0	1	8
23	High	12	0	6	6	1	2	27
24	High	1	0	19	6	5	2	33
25	High	21	0	6	23	0	0	50
26	Low	26	0	12	25	2	2	67
27	High	10	0	2	1	2	0	15
28	Low	7	0	4	1	0	0	12
29	High	2	0	0	0	0	0	2
30	Low	6	0	0	4	0	1	11

	Total	367	4	166	165	68	40	810
	Low	193	2	75	96	38	23	427
	High	174	2	91	69	30	17	383

Appendix 5: Distribution of animals over sites in Experiment 2

Camera	Vegetation	Eastern Bettong	Eastern Quoll	Eastern Grey Kangaroo	Brushtail possum	Swamp Wallaby	Red-necked Wallaby	Total
1	High	7	1	6	4	0	2	20
2	Low	22	0	1	3	0	0	25
3	Low	2	0	0	0	0	3	5
4	Low	4	0	3	0	0	0	7
5	Low	12	0	2	0	0	5	19
6	Low	4	0	2	2	1	3	12
7	High	18	0	0	4	0	0	22
8	Low	3	0	5	1	0	2	11
9	Low	0	0	6	4	1	0	11
10	High	20	0	19	0	6	2	47
11	Low	5	1	1	0	4	1	12
12	High	41	0	1	10	1	0	53
13	High	0	0	2	1	1	0	4
14	Low	4	0	20	2	3	2	31
15	High	0	0	6	0	0	0	6
16	High	13	2	4	0	9	0	28
17	Low	6	0	1	3	4	5	19
18	High	3	0	1	0	0	0	4
19	Low	7	1	11	0	0	0	19
20	Low	2	0	2	4	1	0	9
21	High	2	0	1	0	0	0	3
22	High	0	0	1	0	0	0	1
23	High	13	1	13	1	0	2	30
24	High	1	1	10	0	2	1	13
25	High	25	1	2	7	2	0	37
26	Low	7	0	2	11	0	3	13
27	High	1	0	3	0	0	1	5
28	Low	4	0	2	0	0	0	6
29	High	3	0	0	0	0	0	3
30	Low	1	0	0	0	0	0	1

	Total	230	8	125	57	39	32	491
	Low	83	2	58	30	18	24	215
	High	147	6	67	27	21	8	276