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Interspecific competition and olfactory communication between New Zealand's invasive predators

Unravelling and exploiting stoat behaviour for conservation

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A thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy in Biology Sciences (Animal behaviour and conservation), The University of Auckland, 2016.



This little animal has more spirit than body, and its courage supplying the deficiency of its strength, with a great heart actuating a slender frame, it is vindictive and relentless in its wrath - Giraldus Cambrensis during his visits to Ireland in the 12th century.

Abstract

Stoats (*Mustela erminea*), feral cats (*Felis catus*) and ferrets (*M. furo*) were introduced to New Zealand as agents of biological control and have subsequently decimated populations of many native species. Although the detrimental impacts of these predators are unequivocal, the potential limiting factor of competition among these invasive species is less well understood. Predator demographics can be influenced by several factors such as resource-consumer interaction, facilitation and mutualism, as well as the mechanisms that are the focus of this thesis - competition and predation. I investigated the consequences of interference competition and olfactory communication on the distribution and behaviour of the focal species (stoat), in a series of macrocosm and field experiments. Following a general introduction, Chapter 2 describes pen trials that examine changes in stoat foraging behaviour based on the perceived risk posed by larger predators (cats and ferrets). Olfaction, the dominant sense of many mammals, may mediate trophic interactions by allowing subordinate species to assess the risk of encounter. Chapter 3 therefore examines the importance of interspecific olfactory communication and quantifies behavioural changes of foraging stoats when they encountered the odour of apex predators. Chapter 4 tests whether behavioural responses of wild-caught stoats' are consistent with observations made in the macrocosm, and evaluates the importance of results for conservation. Finally, Chapter 5 investigates whether niche partitioning facilitates invasive predator coexistence and a removal experiment tests the responses of stoats to changes in the densities of larger predators. The thesis concludes with a general discussion and suggestions for future research. Although New Zealand is the main focus, my results may have worldwide conservation applications. Understanding interactions among invasive carnivores, and the communication mechanisms that maintain predator assemblages, is critical for native species protection in invaded ecosystems.

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CHAPTER 1 Introduction

1.1 Competitive interactions among carnivores

Competition is a powerful force in nature and scientists have theorised about its importance in shaping communities since the early 20th century (Gause, 1934; Lotka, 1932; Volterra, 1928). Competition occurs where the presence of one species alters the way in which a second species uses available resources, thus reducing their survivorship or fecundity (Birch, 1957; MacNally, 1983). These effects are often asymmetrical, based on the comparative size and/or age, with the weaker competitor typically being the smaller of the two interacting species (Connell, 1983; Schoener, 1974). Competition may occur between species (interspecific), or within species (intraspecific), but, only the former will be examined in this thesis.

Predators rarely exist in isolation, but instead are sympatric with species that have similar ecological requirements, with which they compete for finite resources (Gause 1934). Interspecific competition is a widespread interaction among mammalian carnivores and has been shown to influence community structure (Keddy & Shipley, 1989; Schoener, 1982). Predator interactions have always interested researchers, given their ecological consequences, as well as the conservation and management implications (Lourenço et al., 2014; Schmitz et al., 2000; Sergio et al., 2008). The idea that carnivores may drive ecosystems dates back more than a hundred years, but its pervasive nature has only recently been appreciated (Terborgh, 2015). Energy flow through an ecosystem is thought to be determined by bottom-up forces, while top-down forces determine the distribution of the energy among trophic levels (Estes et al., 2011). Traditionally, competition has been broadly described through two mechanisms: exploitation or interference competition (Schoener, 1983). It is argued that interference

competition is the more widespread form encountered in nature (Case & Gilpin, 1974) and this form is the focus of my research. Box 1 defines terms that are used throughout this thesis.

Box 1 Definitions

Apex predator: a predator occupying the highest trophic level in an ecosystem and these predators are primarily known for their role as inhibitors of population eruptions of prey and small mammals (Wallach et al., 2015a). This definition depends on the species' trophic position within the predator community. For example, feral cats (*Felis catus*) function as apex predators on many island ecosystems, but more frequently occur as mesopredators on continents where they coexist with larger predators (Crooks & Soulé, 1999; Rayner et al., 2007).

Apparent competition: the presence of one species limits population density of another species via an indirect interaction involving a third species. This may occur when two species share a predator, or are linked through the food web by some other causal chain (Connell, 1990; Holt, 1977).

Exploitative competition: occurs where an organism's use of a limiting resource deprives competing individuals of those resources (Pianka, 1974). Common resources that may be exploited include prey, den sites, habitat, light, soil nutrients, and mates (Levine, 1976).

Guild: a group of species that exploit the same class of environmental resources in a similar way (Root, 1967; Simberloff & Dayan, 1991)

Interference competition: where one individual excludes a competitor from a contested resource, for example, chemical interference, kleptoparasitism or direct aggression (Donadio & Buskirk, 2006; Lourenço et al., 2014; Schoener, 1974).

Interspecific competitive killing: an extreme form of interference competition in which an animal kills a competitor without consuming it (Lourenço et al., 2014).

Intraguild predation: a combination of competition and predation, where a species kills and eats a competing species (Polis & Holt, 1992). Intraguild predation is a common form of interaction among predators where the predator receives the dual gain of removing a competitor plus a nutritional benefit (Polis et al., 1989).

Kleptoparasitism: a form of interference competition where food is stolen from a sympatric species. Losing food to a competitor has associated fitness consequences as hunting is dangerous and energetically costly (Creel, 2001).

Mesopredator release: the expansion in density or distribution, or the change in behaviour of subordinate predators, as a result of declines in the density or distribution of an apex predator (Prugh et al., 2009; Soulé et al., 1988).

Mesopredator: any mid-ranking predator within a food web (Prugh et al., 2009). This definition is also context specific as a mesopredator in one system may be an apex predator elsewhere (Roemer et al., 2009).

Trophic cascades: interactions that extend through more than one link in a food web (Paine, 1980; Polis et al., 2000)

An encounter with an apex predator can have lethal or non-lethal consequences for a mesopredator. Lethal interactions (i.e. interspecific competitive killing, intraguild predation) frequently occur, as carnivores possess the physical and behavioural adaptations to kill other species efficiently (Creel & Creel, 1996; Palomares & Caro, 1999). These interactions can potentially affect the abundance and distribution of a mesopredator, which can, in turn, have cascading effects on lower trophic levels (Holt & Polis, 1997; Polis et al., 1989). A classic example that demonstrates how ecosystems can be structured through lethal interactions was observed following the reintroduction of grey wolves (*Canis lupus lupus*) to Yellowstone National Park (Laundré et al., 2001). Yellowstone's coyote (*C. latrans*) populations were reduced by 50% within three years, due primarily to interspecific competitive killing (Smith et al., 2003). This reduction in coyote abundance allowed small prey to flourish and species such as the beaver (*Castor canadensis*) recolonised the park, in turn creating new habitats that benefited other species (Laundré et al., 2001).

Encounters with an apex predator are not always fatal and a non-lethal interaction will instill fear in a mesopredator, leading to modifications of behaviours that have associated fitness costs (Brown et al., 1999; Hunter & Caro, 2008; Salo et al., 2008). Fear provokes spatial and/or temporal avoidance of the dominant predators, behaviours that have associated costs for the mesopredator, as they are forced to diverge from a foraging strategy that would optimise their fitness (Krebs, 1995; Sergio & Hiraldo, 2008). Spatial avoidance can affect range limits, increasing travel costs and reducing hunting opportunities for subordinate species (Creel, 2001; Lima & Dill, 1990). Shifts in temporal activity patterns are associated with predation risk (Rasmussen & Macdonald, 2012) or competition (Kronfeld-Schor & Dayan, 2003) and also lead to reduced foraging opportunities (Dickman, 1991; Rasmussen & Macdonald, 2012). Spatiotemporal avoidance is most apparent in guilds of large carnivores; cheetahs (*Acinonyx jubatus*) use spatial segregation and adjust activity patterns to minimise

interaction with dominant predators, such as lions (*Panthera leo*) and hyenas (*Hyaena* spp.) (Durant, 1998; Hayward & Slotow, 2009).

1.1.1 *Strength of interspecific competition*

The frequency and severity of interference competition depends on system productivity (Elmhagen & Rushton, 2007; Greenville et al., 2014). In periods of prey scarcity, intraguild predation by the apex predator can increase, with the mesopredator being an alternative prey resource (Amarasekare, 2008; Greenville et al., 2014). Reduced food availability also forces apex predators to forage across greater distances, increasing the likelihood of an encounter with a mesopredator (Prugh et al., 2009). However, interference competition may also become more prevalent where there are abundant resources, as greater prey availability supports more dominant predators, which results in the exclusion of the subordinate competitor (Polis et al., 1989). In Australia, dingoes (*C. dingo*) suppressed introduced foxes (*Vulpes vulpes*) most severely where productivity was greatest (Ritchie et al., 2012). Food stress can also change the behaviour of subordinate species, forcing them to take greater risks while foraging (Cozzi et al., 2012). In Africa, cheetahs and African wild dogs (*Lycaon pictus*) increase hunting activity on moonlit nights, even though the risk of an encounter with a dominant predator is exacerbated during hours of darkness (Cozzi et al., 2012).

Complex habitats can provide refuges for mesopredators, weakening the intensity of interspecific interaction (Finke & Denno, 2002). Species' coexistence may be facilitated when a refuge is provided for the subordinate predator and access to additional food resources increases a mesopredator's dietary breadth. For example, the spotted-tailed quoll (*Dasyurus maculatus*) favours arboreal prey, a class of food which is largely unavailable to canid competitors, and this vertical dietary partitioning facilitates coexistence (Glen &

Dickman, 2008). Structurally simple landscapes, such as those denuded for agriculture, may therefore increase the potential for interference competition (Finke & Denno, 2002).

1.2 Coexistence via niche partitioning

Over ecological timescales, competition may cause species to exploit separate niches, ameliorating interspecific competition (Tilman, 1982). A niche was defined by Hutchinson (1978) as an “n-dimensional hyper-volume”, where dimensions represent a resource or condition of importance for the species. However, a species’ niche also includes its relationship to food and enemies (Pulliam, 2000). Ecological theory has long held that niche differentiation in heterogeneous environments is a primary mechanism facilitating coexistence among competitors (e.g. MacArthur & Levins, 1964; MacArthur, 1958). In the absence of behavioural concessions, the competitive exclusion principle holds that two species with identical ecological demands cannot coexist without some degree of resource separation (Gause, 1934; Hardin, 1960; Schoener, 1982). Niche partitioning is effective in minimising the risk of being killed or injured, but defensive behaviours also incur fitness constraints, although these costs are evolutionarily preferable to extirpation for the subordinate species (Brown et al., 1999; Lima & Dill, 1990).

Partitioning can be achieved through differentiating the three main niche components: habitat use, temporal activity, and diet (Hurlbert, 1978). Niche theory holds that high resource overlap along one dimension requires resource divergence in another dimension for species to coexist (Fuentes & Jakšić, 1979; Hutchinson, 1978; Molsher, 1999). Habitat shift, by confining activity to different habitats or habitat strata, constrains the available niche and imposes demographic contractions ranging from local to continental scales (Durant, 2000; Newsome et al., 2015). Fine scale niche divergence was observed by MacArthur (1958); up to five species of warbler foraged on the same conifer trees by utilising different heights and

positions within the branches. Temporal partitioning facilitates coexistence in two ways: avoidance of direct encounters (interference competition) and/or reduction in resource-use overlap (exploitation competition) (Kronfeld-Schor & Dayan, 2003). Coexistence can also be facilitated by differentiating hunting strategies and by reproductive adaptations (Bonesi et al., 2004; King & Moors, 1979). For example, ecologically similar weasels (*M. nivalis*) and stoats can coexist, as the smaller weasels can reproduce faster in response to increases in prey availability and are capable of entering vole (*Microtus agrestis*) tunnels, including some that are inaccessible to larger stoats (King & Moors, 1979). Such coexistence supports the hypothesis that dominant and subordinate species can only be sympatric, when the subordinate species in interspecific interactions is the superior resource competitor in some instances (Holt & Polis, 1997; King & Moors, 1979; Revilla, 2002).

The theory of foraging behaviour is based on the principle that animals behave to maximise their energetic gain to increase lifetime fitness (Charnov, 1976; Stephens & Krebs, 1986). Foraging areas themselves may also vary in risk depending on the presence of refugia, which also influence behavioural responses (Creel & Christianson, 2008). Mesopredators balance the conflicting demands of finding resources while avoiding apex predators by allocating time among safe and risky habitats, or by increasing vigilance while active within a habitat (Ferrari & Chivers, 2009; Lima & Dill, 1990; Sih, 1980). These decisions affect the types and abundance of resources encountered so it is important that a mesopredator displays an appropriate level of vigilance and avoidance, corresponding to the true proximity of an apex predator (Brown et al., 1999). Fear can be measured by recording changes in vigilance or by measuring the food remaining in a depleted resource patch, to reveal the foraging cost of predation (Hunter & Skinner, 1998; Kotler et al., 2010).

1.3 Odour-mediated foraging

Uncertainty poses significant problems in life as it reduces an animal's ability to accurately estimate risk in a dangerous world (Dall et al., 2005). Olfaction, the primary sense of many mammals, can be used to gather information about the environment to reduce this uncertainty (Dall et al., 2005; Dusenbery, 1992). Every organism has metabolic processes creating waste products that are expelled into the environment, and odour cues are also deliberately deposited to communicate with conspecifics (Atema, 1995; Thom & Hurst, 2004). These cues are available for exploitation by 'eavesdropping' mesopredators that can detect and interpret the odorants (Hughes et al., 2010). Strong natural selection processes will shape the recognition of predator odour, as it provides a basis for risk assessment by reliably relaying an apex predator's previous location (Apfelbach et al., 2005; Dall et al., 2005; Kats & Dill, 1998; Schmidt et al., 2010). Species survival favours predator detection that leads to escape and, where selection pressures are strong, naive species may rapidly evolve anti-predator behaviours to reduce predation risk (Anson & Dickman, 2013; Kats & Dill, 1998).

1.4 Invasive species

Colonisation of new ecosystems by plants and animals is a natural process, but in recent millennia human activity has greatly accelerated the rate of introduction (Pimm, 1987; Pyšek et al., 2004). Dramatic increases in biological invasions have tracked the development of human transportation networks, with few habitats on earth now free from invasive alien species (Di Castri, 1989; Hulme, 2009). Invasive predators are associated with global declines in biodiversity, the disruption of ecological processes and the triggering of trophic cascades (Mooney & Cleland, 2001; Sax et al., 2007; Simberloff et al., 2013; Vitousek et al., 1997), as they impose intense suppression and maintain prey at lower densities than native predators (Clout & Veitch, 2002; Salo et al., 2007).

Impacts of invasive species are more severe on islands than continents. In the last 500 years, over 60% of vertebrate extinctions have occurred on islands and invasive species have been implicated in over half of these events (Tershy et al., 2015; Towns et al., 2006). Species are genetically adapted and/or behaviourally adjusted to the predators with which they evolved and high levels of endemism increase the vulnerability of native species in isolated systems (Blackburn et al., 2004; Pyšek & Richardson, 2010; Terborgh et al., 2001). Negative impacts on native animals can also be magnified via hyperpredation when invasive predators exploit introduced prey (Courchamp et al., 1999). In New Zealand, periodic mass-seedfall events cause irruptions in rodent numbers, which support high densities of stoats. Prey switching during subsequent periods of rodent decline leads to increased predation on native species (King, 1983). Complex native predator communities can buffer ecosystems against invasive species and, conversely, ecosystems with low predator diversity are particularly sensitive to disruption (Ritchie et al., 2012).

1.5 New Zealand invasion ecology

New Zealand is an isolated landmass that separated from the supercontinent Gondwana about 82 million years ago and now lies 2000 km east of Australia (McCulloch et al., 2010). New Zealand's terrestrial fauna is dominated by birds and insects and lacks the terrestrial mammals that are found in continental biomes, with the exception of three bat species (Worthy & Holdaway, 2002). New Zealand was the last major landmass to enter the Anthropocene, when Polynesians arrived circa 1280 AD, and the appearance of humans signalled a change in fortunes for native wildlife (Wilmshurst et al., 2008). Almost a third (at least 76 of 245) of bird species in pre-human times have become locally or globally extinct, and introduced mammals are the primary factor responsible for these declines (Innes et al., 2010). The kiore (*Rattus exulans*) arrived with Polynesian settlers and European ships

transported three additional rodent species: ship rats (*R. rattus*), brown rats (*R. norvegicus*) and the house mice (*Mus musculus*), which quickly spread throughout the country (Gibbs, 2009). European settlers also introduced two species of lagomorphs as food resources, the European hare (*Lepus europaeus*) and the rabbit (*Oryctolagus cuniculus*) (Thomson, 2011). Invasive mammals arrived to find vacant niches and this lack of competitors reduced the ecosystems' biological resistance (Shea & Chesson, 2002). The invaders prospered, free from the constraints of disease, parasites and native predators, and soon reached plague proportions (Mooney & Cleland, 2001). With livestock farmers demanding intervention to control invasive herbivores, the way was paved for an early attempt at biological control, and the arrival of mustelids signaled a further change in fortunes of native species (King, 1984).

1.6 New Zealand's terrestrial carnivores

Four terrestrial carnivores were introduced to New Zealand and established feral populations: three mustelids (ferret, stoat, weasel) and cats (Dowding & Murphy, 2001; King & Powell, 2007). Dogs were also introduced and while initially they may have been feral populations these no longer exist (Parkes & Murphy, 2003). The smallest of the introduced mustelids, the weasel, remain scarce in New Zealand despite being introduced in large numbers, as they encountered marginal habitat that lacked suitable small prey (e.g. voles) (King & Powell, 2007). This section will therefore focus on the biology of the three largest predators that established feral populations, after an initial introduction to the mustelid family.

1.6.1 *Mustelidae*

The family Mustelidae is the largest in the order Carnivora, and members are found on all continents with the exception of Australia and Antarctica (Powell & Zielinski, 1983). Mustelids are usually solitary foragers by nature, they range in size from the world's smallest carnivore, the weasel, to the wolverine (*Gulo gulo*), a tenacious apex predator capable of

stealing the kill of wolves (King & Powell, 2007; Prugh et al., 2009). Interspecific competition is common between mustelids, but coexistence is facilitated by partitioning the available habitat, as species can be primarily aquatic, arboreal, fossorial or terrestrial (Hunter & Caro, 2008; Powell & Zielinski, 1983). Olfaction is the main form of communication and some species are known to be capable of identifying conspecifics and responding to odours of sympatric mustelids (Clapperton, 1989; Erlinge & Sandell, 1988; Macdonald, 1985). Many mustelids are in decline within their natural range, for example 99.9% range contraction in the case of the black footed ferret (*M. nigripes*), and there are more threatened mustelids (25%) than any other mammalian family (IUCN, 2012; Jachowski & Lockhart, 2009). Mustelids are also destructive invasive species, demonstrated to have negative impacts on native fauna when they naturalise outside their natural ranges (Clapperton & Byrom, 2005; Macdonald & Harrington, 2003).

1.6.2 *Stoat*

The stoat is a mustelid native to Europe, North America and Asia (King & Powell, 2007). It is morphologically adapted for hunting prey in confined spaces, having a slender body, flexible skeleton, short legs and a long neck to facilitate prey transportation (King & Powell, 2007). In New Zealand, stoats are found in a range of habitats including forests, braided rivers, alpine tussock, grasslands, and coastal areas (Alterio et al., 1998; King et al., 1996; Moller & Tilley, 1986; Ratz, 2000; Smith et al., 2007).

Stoats are extremely powerful for their slender physique, capable of subduing prey much larger than themselves. Their ancestors evolved to prey on lemmings and voles, prey that display population fluctuations of large amplitude, which may have forced them to become generalist predators (King, 1983; Korpimäki et al., 1991). Stoats' diet varies with prey availability, but lagomorphs, rodents and birds are typically the main food resource, while

insects, lizards, amphibians and fish are also consumed (King & Murphy, 2005; Murphy et al., 2015). Solitary hunters, stoats are versatile predators pursuing a variety of prey in different habitat strata – rodents and rabbits are hunted underground (Jędrzejewski et al., 1993), lagomorphs are exhausted in long-distance pursuits (Hewson, 1990), birds are ambushed in tree cavities (King & Powell, 2007), and fish are hunted in rivers (Dowding & Elliott, 2003). Stoats hunt incessantly when active, exhibiting a zigzag search pattern and exploring every cavity when searching for prey in forested habitats (King & Powell, 2007). They avoid open areas that lack cover, using breaks in the landscape such as streams, walls, and hedges, to reduce the risk of encountering a larger predator (Murphy & Dowding, 1994). Apart from their hunting prowess stoats are renowned for their tenacity, intelligence and curiosity, possessing large brains relative to their body size (Healy et al., 2005; King & Powell, 2007; Radinsky, 1981).

Stoat abundance is driven primarily by bottom-up processes, with large population changes following pulses in prey resources (King, 1983; Korpimäki et al., 1991). Females reach sexual maturity when only a few weeks old, and most females within a population are mated during each breeding season (King & Powell, 2007). Food availability influences birth rates, and typically 6-13 offspring are born, but few of these will survive their first year, as natural mortality rates can be extremely high for juveniles (King, 1981; King, 1989). Stoats can be active at any time of the day, exhibiting primarily nocturnal (e.g. Debrot et al., 1985; Sidorovich et al., 2008), or diurnal activity patterns (e.g. Alterio & Moller, 1997a; Hellstedt et al., 2006). Seasonal variability may also influence temporal activity patterns (King & Powell, 2007).

Stoats are sexually dimorphic, with males considerably larger than females (King & Powell, 2007). The evolution of dimorphism is hypothesised to have been driven by reproduction

(Erlinge, 1979; King & Powell, 2007), or alternatively as a mechanism to reduce dietary overlap (Dayan & Simberloff, 1994), and dimorphism enables males to exploit more lagomorph prey and females to access more rodents. Stoats are territorial, although home ranges may shift depending on prey availability (King & Murphy, 2005).

1.6.3 *Stoat introduction to New Zealand*

Stoats were introduced to New Zealand in the early 1880s and are the most widespread and abundant of the three introduced mustelid species (King & Murphy, 2005; Wodzicki, 1950). Stoats are a considerable challenge to wildlife managers, due to their impacts as predators, cryptic nature, low population densities, and the virtual certainty that any female stoat will be pregnant, which facilitates recolonization (Choquenot et al., 2001; King et al., 2009). The impacts of stoats have been recognised by the IUCN (International Union for Conservation of Nature) as they are listed as one of the world's worst invasive species (Lowe et al., 2000).

Their arrival was not greeted universally with approval (Martin, 1885). Records from the period reveal an appreciation for the potential impacts of these generalist predators, “*stoats have no marked preference for any one species...and will certainly lead to the extermination of many species of birds*” and even an awareness of interference competition among predators, “*having no natural enemies here, there would be no natural check upon them, as in northern regions they are preyed on by larger beasts of prey*”(Martin, 1885). Unfortunately, discerning voices were ignored and in an outcome familiar to conservationists, the concerns for wildlife were trumped by the wishes of powerful lobby groups. However, twenty years after their introduction, stoats lost their privileged status and have since continued along the path of ‘political perdition’ and are now regarded as an unwanted organism under The Biosecurity Act (Wells, 2009).

1.6.4 *Ferret*

Ferrets, the domesticated form of the European polecat (*M. putorius*), were introduced from Britain in the 1880s to control rabbits (Clapperton, 2001). They are the largest mustelid in New Zealand and, in common with other mustelids, exhibit sexual dimorphism with males considerably larger than females. Ferrets achieve their highest densities in tussock grassland and improved pasture, but are also found along braided rivers, coastal areas, forest ecotones, and at low densities in forests (Gillies & Pierce, 1999; King et al., 1996; Ragg, 1998b). Rabbits (and/or hares) are their main prey, with ferret densities strongly correlated with those of lagomorphs, but they also hunt rodents, birds, insects, lizards, eels, frogs, hedgehogs and carrion, depending on food availability (Clapperton, 2001; Fitzgerald, 1964; Norbury et al., 1998b; Ragg, 1998a). Both fossorial and terrestrial prey are hunted, but poor climbing skills make arboreal prey inaccessible (Clapperton & Byrom, 2005). Activity is primarily nocturnal and intrasexual territories are maintained (Pierce, 1987; Tempero et al., 2007). Scent marking is the primary mode of social communication and they are capable of discriminating between familiar and unfamiliar conspecifics (Clapperton, 1989).

1.6.5 *Feral cat*

Cats have travelled widely as human commensals, establishing feral populations and becoming the most widespread carnivore on the planet (Todd, 1977). They accompanied European settlers to New Zealand in the latter part of the 18th century, having secured passage due to their ability to control rodents aboard ships. They are the largest invasive predator in New Zealand, found across a range of habitat types including forests, tussock grasslands, pastoral farmlands, and coastal areas (Daniel, 1972; Langham, 1990; Norbury et al., 1998c) Feral cats are opportunistic predators and constitute a major threat to biodiversity, having been directly implicated in the extinction of several animal taxa (Nogales et al. 2013).

In New Zealand, they are regarded as a pest both for their deleterious effect on native wildlife and as a carrier of disease such as bovine tuberculosis (Tb) and toxoplasmosis (Fitzgerald & Karl, 1979; Ragg et al., 2000). Cats evolved to be solitary hunters, ambushing or stalking prey, with vertebrates (rodents, lagomorphs, birds) the main components of their generalist diet, which is primarily determined by the relative abundance of prey species (Dickman, 1996; Fitzgerald, 1990). Moderate diurnal activity is sometimes recorded, but cats are typically crepuscular or nocturnal in New Zealand (Alterio & Moller, 1997a). In New Zealand, females give birth to two to four kittens in September/October, although a second litter may be born later in the year (Moors & Lavers, 1981). Prolific breeding and their hunting ability make cats a destructive invasive predator. For example, five cats were released on a South African island in 1949 and less than thirty years later an estimated 2139 cats were killing 450,000 burrowing petrels (*Procellariidae*) annually (van Aarde 1979, 1984).

1.7 Naturalisation of invasive predators

The fate of new arrivals into an ecosystem is uncertain, as only a fraction of introduced species survive the hazards of a novel environment to become naturalised (Mack et al., 2000). For the focal species in this study, there were a number of factors that contributed to their successful establishment in New Zealand. Stoats, ferrets and cats possess biological attributes that they share with other successful invaders: generalist diet, high reproduction, high mobility, and flexible habitat requirements (Pyšek & Richardson, 2010). Propagule pressure and the genetic diversity of the founder population also contribute to the successful establishment of an invader (Wilson et al., 2009). Humans released large numbers of these predators at sites throughout New Zealand and sourced founder individuals from across Britain, encompassing high genetic variability. New Zealand stoats, for example, are more

genetically diverse than their British counterparts, which went through a bottleneck after the introduction of *Myxoma* virus to Britain as a control measure for rabbits (Veale et al., 2015).

1.8 Competition and coexistence among introduced carnivores

Trophic interactions may alleviate or exacerbate the impacts of invasive species and are an important consideration when assessing stoat behaviour in New Zealand. Resource competition is apparent among the invasive predators, as studies show high dietary overlap (e.g. Alterio & Moller, 1997b) and similar denning requirements (Dowding & Elliott, 2003). Hunting strategies also overlap; stoats, in common with ferrets, are fossorial hunters, and stoats may also stalk terrestrial prey, similar to a foraging cat. Niche differentiation may be achieved in complex habitats as stoats can access arboreal prey, such as cavity nesting birds, and vertical niche partitioning can facilitate coexistence of species (Glen & Dickman, 2005). There is no evidence of spatial partitioning at a landscape scale with distributions of these predators frequently overlapping (Alterio et al., 1998; Murphy & Dowding, 1995; Norbury et al., 1998a; Ragg, 1998b). Localised spatial partitioning may occur as there is evidence of reciprocal distributions (Alterio et al., 1998; Ratz, 2000), although these alternative patterns are not consistently documented (Keedwell & Brown, 2001). Studying the drivers of predator community structure is important as the assemblage of predators determines the susceptibility of prey as well as their behavioural traits (Parlato et al., 2015).

As one of the smallest members of the order Carnivora, stoats suffer high mortality and intense persecution from larger predators, particularly canids, felids, and raptors (Jedrzejewska & Jedrzejewski, 1998; King & Powell, 2007). New Zealand's two largest predators are from taxonomic families that frequently engage in intraguild predation (Palomares & Caro, 1999). Cats rely on stealth and agility to capture prey, making them efficient hunters of small animals, and there are frequent reports of cats killing stoats (e.g.

Fitzgerald & Karl, 1979; Gillies & Clout, 2003; Sleeman, 1987; Wodzicki, 1950; Woods et al., 2003). Reports of ferrets killing stoats are infrequent, but have been documented (Wodzicki, 1950). Dietary studies support the existence of intraguild predation, as stoat remains were discovered in the scat of cats and polecats, although scavenging offers an alternative plausible explanation (Erlinge, 1983). However, despite their diminutive size, stoats are tenacious animals and capable of defending themselves against larger predators. They possess a strong bite and can expel a pungent odour as a defensive weapon, so if predators can be identified prior to an interaction a stoat's chances of survival increase (King & Powell, 2007).

Although not the focus of this study, reports of interspecific interactions between ferrets and cats illustrate the nature of the relationships between New Zealand's predators. Both species are frequently sympatric in ecosystems with high rabbit abundance (Alterio et al., 1998; Norbury et al., 1998c). Coexistence may be facilitated by ferrets and cats using different habitat strata and contrasting hunting strategies; ferrets are almost exclusively fossorial hunters, while cats stalk or ambush terrestrial prey. In New Zealand, interspecific competition has been recorded between the species; attempted kleptoparasitism was observed where a large cat tried to steal prey from a ferret, but the prey was eventually retained by the ferret without harm to either predator (Peach, 2005). A study by Ragg (2000) recorded interactions of adult cats and ferrets attracted to carrion and in 7 out of 8 instances, when both species appeared simultaneously at a carcass, ferrets maintained possession or displaced cats. In another incident, a ferret and a kitten were captured together in the same live trap, but both appeared unharmed (Ragg, 1998a).

1.9 Invasive species management

Invasive species are notoriously difficult to control and often impossible to completely eliminate, so long-term management is frequently required (Hulme, 2006; Norton, 2009; Pyšek & Richardson, 2010; Towns & Broome, 2003). Control or monitoring of invasive mammals is currently undertaken across almost 45% of New Zealand and continued management intervention is required to prevent further extinctions of native species (Russell et al., 2015). Eradicating New Zealand's invasive predators is currently not feasible, given the available technologies and resources, although the aspirational goal of creating a 'predator-free' country is gaining momentum (Russell et al., 2015). The conservation objectives of effective long-term management or eradication of predators could be greatly assisted by research on invasive predator dynamics and the development of new control tools.

Relatively little is known about the consequences of removing a single species in ecosystems comprised of multiple invasive predators as complex linkages make it difficult to predict the outcome of control (Glen & Dickman, 2005; Ruscoe et al., 2011). However, experimental removal of top predators has demonstrated the ecological release of mesopredators in forest (Ruscoe et al., 2001) and dryland (Norbury et al., 2013) ecosystems, with potentially detrimental consequences for particular native species (e.g. Rayner et al., 2007). Control of New Zealand's predators can lead to trophic cascades within invaded communities, so a greater understanding of interspecific interactions is essential to ensure that control programmes do not have unforeseen negative consequences for native fauna.

Invasive species management is limited by current resources, relying on technologies and techniques developed decades ago, and new measures are required to help reverse species loss (Campbell et al., 2015). Recently, a conceptual framework has been developed to link behavioural and sensory ecology, including studies of foraging behaviour and predator-prey

interactions, to conservation biology (Berger-Tal et al., 2011). The application of behavioural ecology in conservation requires both an understanding of biological phenomena and the conservation management issues (Blumstein & Berger-Tal, 2015). Species' responses to odour have been exploited for diverse management objectives, from reducing human-animal conflicts by deterring African elephants from crop raids (Rasmussen & Riddle, 2004), to attracting bears for genetic sampling in Canada (Woods et al., 1999). Exploiting the behavioural responses associated with olfactory communication in predators is an avenue of research that has not been extensively explored (Banks et al., 2014; Blumstein & Berger-Tal, 2015; Price & Banks, 2012). Stoats possess keen olfactory senses, complemented by well-developed cognitive capacities, suggesting that they may respond strongly to sympatric predator odour.

1.10 Research Aims and Overview

Studies on invasive species that interact on the same trophic level are rare and competition between New Zealand's largest invasive predators has not been studied extensively. For this thesis I investigated interspecific competition, olfactory communication, niche partitioning, and the mesopredator release hypothesis (*sensu* Soulé et al. 1988). The thesis is presented as papers or manuscripts at various stages of publication (published, in press or manuscript form). The aims were:

- To expand our understanding of invasive carnivore behaviours in New Zealand,
- To identify the mechanisms of coexistence among invasive predators, and
- To investigate the role of interspecific scent communication and its potential applications for the management of invasive species.

A series of experiments were used to test hypotheses about interactions between predators and investigate the underlying mechanisms that could lead to their observed distribution. The

initial research phase, undertaken at Landcare Research's Animal Facility, investigated the behaviour of captured stoats using experimental manipulation in a controlled environment. Pen trials informed the design of field experiments to measure intraguild interactions, niche partitioning and the effects of olfactory communication within the guild consisting of mustelids and feral cats. Observing species interactions can be challenging, but interpreting these observations can also be problematic, so alternative interpretations of the results are discussed wherever possible.

Chapter 2 provides an insight into wild-captured stoats' fear of larger predators by documenting their foraging behaviour in a controlled environment. The perceived risk of predation was manipulated so that food remaining at a location near a dominant predator could be used as a measure of foraging cost. The stoat was allowed unrestricted movement within the enclosure but animals were segregated from each other to avoid injury. In addition to depleted food, vigilance and time allocation patterns were recorded to assess stoats' fear in the presence of a guild member. Given the risk of intraguild predation by apex predators, it was predicted that mesopredators would forage in a pattern similar to that of other potential prey species and avoid the larger predator.

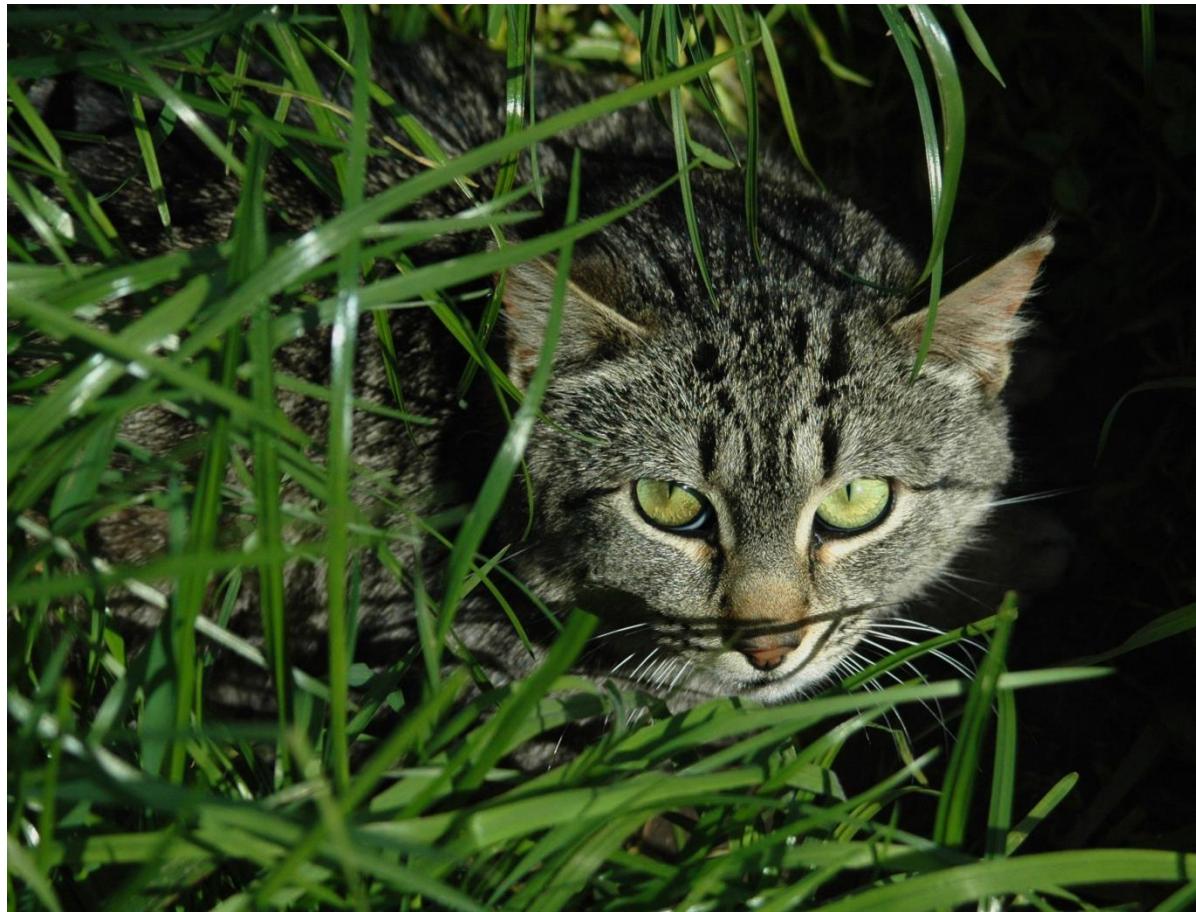
Mammalian carnivores' highly developed olfactory senses are used to locate prey and, potentially, avoid agonistic encounters with sympatric guild members. Chapter 3 investigates whether or not wild-captured stoats recognise the scent of a dominant predator and consequently adjust their feeding behaviour, based on whether they perceive the scent to signal an imminent threat. Stoats were exposed to the odour of cats, ferrets and a novel apex predator (African wild dog) and reactions were quantified by recording behavioural responses while foraging. It was anticipated that stoats would avoid dominant predator odour due to the associated risk of agonistic encounters.

Chapter 4 investigates the responses of wild mesopredators to dominant predator odour. Odour deposited by an apex predator can supply information about shared resources or reveal the location where a predator has recently foraged. A field experiment was devised to test whether ferret odour would alter the behaviour of three of New Zealand's common invasive mesopredators: stoats, hedgehogs (*Erinaceus europaeus*), and ship rats. Active response to the scent of a competitor has repercussions for predator assemblages and consequently for native species survival. I anticipated that stoats, and other mesopredators, would display responses consistent with those displayed by stoats in the macrocosm and the implications of findings for conservation are discussed.

Chapter 5 investigates coexistence of stoats and larger predators in two pastoral farmlands in New Zealand. Theory predicts that stoats could only coexist with dominant ferrets and cats through niche partitioning. Spatiotemporal partitioning reduces the risk of aggressive interactions, and studying predator distribution and activity patterns provides evidence of interspecific interactions. A large scale camera trapping study enabled us to document temporal activity patterns and spatial distribution using occupancy modelling. Habitat complexity and ecosystem productivity are important considerations when assessing trophic interactions and measures relating to habitat (habitat quality) and productivity (prey) were included in the analysis. The prediction was that larger predators would dominate the most productive resources and stoats would show preferences for heterogeneous habitats likely to provide refuge from predation. Removal experiments are required to provide unequivocal evidence of interference competition. The effects of selectively removing cats and ferrets from one site were measured by recording whether changes occurred in the abundance and/or activity of stoats. In accordance with the mesopredator release hypothesis, the prediction was that observations of stoats would increase in the removal area and/or changes would be observed to their spatiotemporal extent, relative to an untreated area.

Theoretical questions can be explored using invasive species, where similar research with native species would be difficult due to their scarcity or untenable due to ethical or funding reasons. The small guild of mammalian predators in New Zealand provides an excellent opportunity to conduct research on species interactions. Stoats are also an ideal focal species, as they exhibit the behavioural repertoire and cognitive abilities to adjust to the presence of dominant predators. The overarching aim of this thesis is to provide knowledge that can inform management decisions and to discover new tools to help solve conservation problems.

CHAPTER 2 Foraging Ermine Avoid Risk: behavioural responses of a mesopredator to its interspecific competitors in a mammalian guild



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2.1 Abstract

Interference competition between predators strongly influences the structure and composition of ecological communities. These interactions are usually asymmetrical as larger predators dominate in aggressive encounters. Smaller predators are forced to balance the conflicting demands of obtaining food while reducing the risk of a confrontation. We tested the behavioural responses of 16 wild captured stoats (*Mustela erminea*) to the presence of a feral cat (*Felis catus*) and a ferret (*M. furo*), which we refer to as “larger predators” due to their superior body size. Stoats were released individually into an outdoor arena and nocturnal activities were recorded on infra-red video cameras. On treatment nights, one of the larger predators was placed inside a segregated holding cage on one side of the arena, while an empty cage was placed on the opposite side as a control. A stoat’s daily food allocation was divided into two equal portions, one placed in front of each holding cage to form a food “patch”. Stoats’ perception of risk was assessed by comparing behaviour in the risky patch (close to the caged predator) versus the safe patch (close to the empty cage). Stoats harvested less food at the risky patch. They avoided the area containing the larger predator, both spatially and temporally, and increased vigilance at the risky patch. The results show that stoats alter their foraging behaviour due to perceived interference competition when they encounter larger predators. Understanding trophic interactions between invasive species will help to inform conservation decisions and maximise the effectiveness of management intervention.

2.2 Introduction

Interference competition is a widespread interaction among mammalian carnivores, altering the shape of ecological communities and food webs (Caro & Stoner, 2003; Donadio & Buskirk, 2006; Palomares & Caro, 1999). These interactions are typically asymmetrical, with larger predators dominating smaller species in confrontations. There are a number of mechanisms by which interference competition may occur, including: (1) lethal interactions (Donadio & Buskirk, 2006; Palomares & Caro, 1999; Polis et al., 1989) (2) harassment (Creel & Creel, 1996), and (3) kleptoparasitism (Kruuk, 1972). These mechanisms are particularly important among carnivores as natural selection has equipped them with the behavioural and physical adaptations necessary for killing their prey (Creel, 2001). Lethal interactions may take two distinct forms: intraguild predation, where the victim is killed and eaten; and interspecific killing where the dominant species kills a competitor, but does not consume the victim (Lourenço et al., 2014; Polis et al., 1989). Both mechanisms lead to the same outcome for the victim, but the intraguild predator obtains the additional benefit of an energetic gain. Lethal interactions are widespread among mammalian carnivores, but are especially common among felids, canids and mustelids (Palomares & Caro, 1999). The likelihood of this interaction increases with the degree of dietary overlap and taxonomic relatedness, as niche similarities justify expending energy in order to remove a competitor (Donadio and Buskirk 2006). Lethal interactions also increase where the body size of the aggressor is 2 to 5.4 times that of the smaller species (Donadio and Buskirk 2006). In this range the predator with the body size advantage has a reduced risk of injury during an attack (Mukherjee and Heithaus 2013).

Subordinate species reduce the risk of an agonistic encounter by engaging in spatial and temporal avoidance (Durant, 1998; Fuller & Keith, 1981). Mesopredators seek refuge from

dominant competitors by occurring in different areas, habitats or habitat strata or by temporally partitioning their activity to avoid the dominant predator (Hunter & Caro, 2008; Palomares & Caro, 1999). The constraints imposed by apex predator avoidance reduce feeding opportunities, habitat availability and ultimately the fitness of the submissive species (Durant, 1998; Lima & Dill, 1990). The potential for an encounter also induces fear in the smaller predator, and this non-lethal effect may have stronger impacts on mesopredator abundance than direct predation (Preisser et al., 2005). Harassment and kleptoparasitism by apex predators increase the costs of foraging, thereby forcing mesopredators to avoid the most productive areas (Creel & Creel, 1996). For example, cheetahs (*Acinonyx jubatus*) avoid areas with high densities of their preferred prey, as these habitats also correspond to locations where their dominant competitors, lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*), are most common (Durant, 1998). In Finland, the American mink (*Neovison vison*), an invasive mustelid, significantly reduced its swimming activity between islands in response to an increased risk of sea eagle (*Haliaeetus albicilla*) predation (Salo et al., 2008).

Modification of an optimal survival strategy carries physiological, foraging and fitness costs for the subordinate species (McArthur et al., 2012). A mesopredators' perception of this risk can be measured both qualitatively and quantitatively, as they adjust their foraging behaviour in response to the landscape of fear (Laundré et al., 2001; Mukherjee et al., 2009). To gain an insight into this perception of danger, we can study changes in vigilance and foraging activities and use these observations as a surrogate measure of fear. As animals search for food they might be forced to move outside areas of safety, and vigilance is therefore the most important anti-predator behaviour in this context (Allen & Bekoff, 1999). Besides its primary role in detecting predators, vigilance is also important for observing conspecifics, acquiring food, and to prevent kleptoparasitism (Quenette, 1990). Increased vigilance improves the probability of detecting and avoiding an attack, but may reduce the time available for feeding.

(Frid, 1997; Lima & Dill, 1990). A forager needs to balance risk with its requirements for energy and therefore it should capitalise on safe feeding opportunities (Lima & Bednekoff, 1999; Sih, 1980).

This study examines the interactions among three invasive species, which are actively managed in New Zealand. Cats (*Felis catus*) were brought to New Zealand by European settlers from the late 18th century onwards, while mustelids were introduced from Britain in the 1870s (King & Powell, 2007). Feral cats, ferrets (*Mustela furo*) and stoats (*M. erminea*) are the largest wild terrestrial carnivores in New Zealand, and are responsible for the decline, in some cases to extinction, of many native species (Parkes & Murphy, 2003). Intensive control is undertaken to protect a range of vulnerable species (Parkes & Murphy, 2003) and an understanding of the consequences of pest control may help mitigate the possible negative impact of trophic cascades in an invaded ecosystem. We predict that a hierarchy exists within the assemblage of mammalian predators in New Zealand, and is enforced by agonistic encounters and/or predator recognition and avoidance. Our hypothesis that interference competition exists between the two mustelid species is based on the following factors: a difference in body weights (ferret = 3.8 x stoat), taxonomic and morphological relatedness (Clapperton & Byrom, 2005; Donadio & Buskirk, 2006; King & Murphy, 2005), propensity for interspecific killing in mustelids (Palomares & Caro, 1999) and high dietary overlap where the species coexist (Alterio & Moller, 1997b; Murphy et al., 2004). Interference competition is anticipated to occur between cats and stoats as both species belong to families frequently involved in interspecific killing (Palomares & Caro, 1999) and occupy similar niches (Alterio & Moller, 1997b; Murphy et al., 2004). The average weight of a feral cat is 14.3 times heavier than that of a stoat (Gillies & Fitzgerald, 2005; King & Murphy, 2005). This would imply a low benefit to a cat in killing the smaller competitor due to an expected low niche overlap (Donadio & Buskirk, 2006). However, unlike most solitary

hunters, stoats regularly kill prey animals much heavier than themselves, potentially putting them in direct competition with cats for resources.

Our objective is to quantify stoats' vigilance, foraging and avoidance behaviour in a risky area close to an apex predator in comparison to a safe area without a predator. We predict that: stoats will harvest less food in the risky area; stoats will harvest food in the safe area first; and, in order to avoid an apex predator, stoats will reduce the number of visits and spend less time in the risky area. Additionally we anticipate that stoats will increase vigilance in close proximity to the predator, which will correspond to a slower feeding rate in the risky area. Stoats will behave submissively towards the larger predators and a stoat's behaviour will be independent of its sex or age. This final prediction is based on the assumption that fear of the larger predator will be an intrinsic behavioural response of all stoats.

2.3 Materials and methods

Animals used in this trial were captured by professional trappers on the South Island of New Zealand. Trappers have an obligation to abide by the Animal Welfare Act 1999 section 36. The cat and ferret were trapped locally (within 70 km from the Landcare Research Animal Facility, Lincoln) while the 16 stoats (8 males/ 8 females) were captured at two locations on the South Island. All three species are known to be sympatric at the sites where stoats were captured. The cat and ferret were housed in large cages $5.5 \times 6.5 \times 3$ m (D \times W \times H) constructed from wire with a timber frame, and each animal had its own nest box, which was placed within a galvanised shelter measuring $1 \times 2.5 \times 1.5$ m. Stoats were housed for at least 6 months prior to the start of the experiment in individual cages ($0.6 \times 1.5 \times 0.9$ m) under an outside shelter at the animal facility. Each stoat was supplied with a nest box ($0.4 \times 0.33 \times 0.15$ m) containing shredded paper as nesting material.

All animals were sexed, weighed and physically inspected upon arrival at the animal facility. The average body weight of stoats was 0.326 kg for males (range: 0.297 kg - 0.374 kg) and 0.206 kg for females (0.130 kg - 0.260 kg). Weights were recorded monthly thereafter, which enabled us to classify stoats into adult and sub-adult groups, using previously described methods (King & Powell, 2007). Sympatric guild species were represented by a wild-captured female ferret (0.962 kg) and a wild-captured male cat (3.5 kg).

Study species were fed on an alternating daily diet of either dead day-old chickens or chicken mince and domestic cat biscuits. Animals remained healthy and their weights did not fluctuate over the course of the trial. All animals were weighed within their nest box, which was subsequently weighed separately after an animal had been returned to its pen. It was not necessary to handle any of the animals as they were moved within their nest box and a sliding door prevented an animal from escaping while it was being transported between the experimental arena and the housing cage. After the trial was completed the ferret and cat were humanely euthanised by intracardiac injection of pentobarbital following anaesthesia with isofluorane. This procedure was carried out by experienced technicians in accordance with Landcare Research standard operating procedures, based on the Animal Welfare Act. Stoats remained in captivity at the facility as they were healthy and were required for further experimental work not connected with this study.

2.3.1 *Experimental arena*

The experiment was conducted at Landcare Research from August to October 2012. The arena consisted of three adjoining outdoor pens ($9 \times 7.5 \times 2$ m) (Figure 2.1). Open doors (2×1 m) allowed a stoat's unobstructed movement between the three pens. Two holding cages ($0.6 \times 1.5 \times 0.9$ m) were added to the arena, one placed in each of the end pens. These holding cages segregated the ferret or cat from the stoat and prevented injury during

interactions. Both the cat and the ferret were assigned to a specific holding cage for the entirety of the experiment, which ensured there was no cross contamination with predator odours. During the trial the cat or ferret was placed in a holding cage for a maximum of 14 hours at a time. Markers were placed in the ground at a distance of 1.5 m and 0.5 m, to allow us to assess the proximity of a stoat to the holding cage. The height of grass in the pens was maintained at 5 cm to ensure animals were clearly visible to the observer, and to each other.

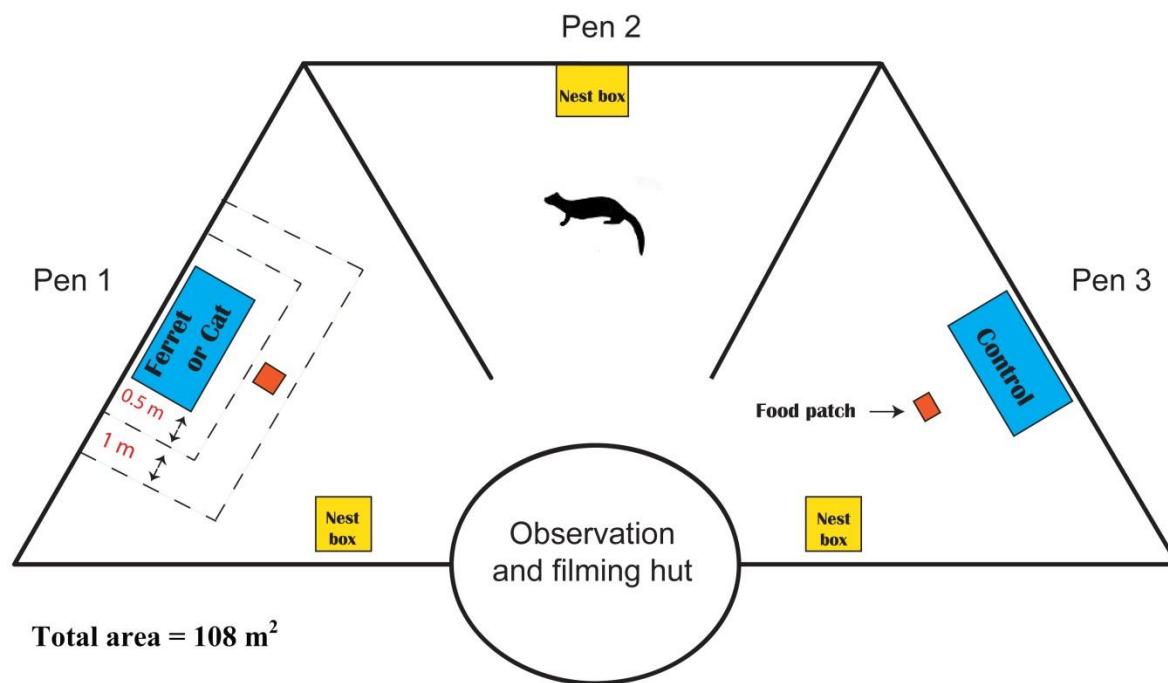


Figure 2.1 Experimental arena (not to scale) used for interaction experiments between three invasive predators (stoat/ ferret/ cat) in New Zealand. During a trial a stoat released into Pen 2 can choose to feed at either end of the experimental arena, but there is a cat or ferret in the holding cage in Pen 1, while an empty holding cage in Pen 3 serves as a control.

2.3.2 Trial design

Each stoat was released individually into the arena and remained there for three consecutive nights. The first night of the trial allowed the stoat to acclimate, and also provided an opportunity to test if stoats displayed a pen preference. On the second night either a ferret or cat was placed within its assigned holding cage, at a randomly selected end of the arena. A

second holding cage was placed in the other peripheral pen and used as an experimental control. Sacks were placed on the floor of the holding cage to prevent the pen from being contaminated with scent. On the final trial night whichever of the two larger predators was not used on the second night was introduced as the last treatment. All animals were moved within their familiar nest box to avoid the need for sedation and had 24-hour access to drinking water.

Nocturnal activities were recorded on Bosch Dinion day/ night video cameras (Bosch Security Systems, Sydney, Australia) from an observation hut adjoining the arena, which was dimly lit by an infrared spotlight. Three cameras used wide angle lenses to record the entire arena, while two additional lenses focused on the area of the holding cages, to give clear recordings of any interactions. All cameras ran continuously for 15 h from 5pm to 8am the following morning. Video footage was stored and viewed using a GeoVision 1248 digital video-recording system (GeoVision Inc, Neihu Rd., Neihu District, Taipei 114, Taiwan).

2.3.3 *Food*

Every day, just before sunset, we placed an artificial food patch in each of the peripheral pens. The daily food requirement of stoats in captivity has been calculated at 19 to 37% of an individual's mass and stoats in this experiment were given mince at a standard rate of 25% of their bodyweight per day (Müller, 1970). Allocations were split into two equal portions, placed 1 m from each of the holding cages, creating two energetically equal food patches. Standardised amounts of food were provided so that we could isolate stoats' behavioural responses to predation risk, without variations in feeding opportunities influencing these behaviours. The food allocated was a conservative measure based on a stoat's daily energetic requirement. Animals were provided with food in proportion to body weight so that each

animal had an equivalent incentive to approach the food patches. Food was presented on a 0.2 m² plate of Perspex so that it remained clearly visible to the infra-red cameras.

Chicken-neck mince was used because it could be divided easily and because it was part of a stoat's regular diet at the facility. Also mince could be spread thinly across the Perspex plate to prevent the stoat from removing large pieces to consume elsewhere. As a control, an identical portion of mince was left outside the arena under the same environmental conditions, to account for the changes in weight over the course of the trial night, due to evaporation or absorption of moisture. Latex gloves were worn at all times when handling food and moving cages. Both the ferret and the cat were supplied with food as per their normal daily allocation of 0.1 kg and 0.15 kg respectively.

Each morning food eaten in the pens, as well as the control sample, was collected and weighed. Intake was calculated by subtracting the mass remaining at each of the food patches from the mass of the control sample. Nocturnal foraging and predator interactions were assessed by reviewing video on GeoVision software and analysed using the software package JwatcherTM (v. 1.0, Animal Behaviour Laboratory, Macquarie University, Sydney, Australia).

2.3.4 *Data recording and analysis*

Data were analysed for differences in stoat behaviour when in close proximity to the 'risky' (close to predator) and 'safe' (empty holding cage) food patches on each of the two treatment nights (ferret or cat present). The acclimation night was used to assess if stoats displayed a pen preference, which was tested with the response variable proportion of 'food eaten'. A total of 12 stoats were used for all three-night trials, with 4 additional animals tested on the acclimation and cat treatment nights. The following variables were recorded: (1) food eaten, (2) time until first feeding, (3) total visits to food patch, (4) total time feeding at patch, (5)

time at patch per visit, (6) feeding rate ((intake g)/(total time feeding)), (7) vigilance while feeding (body angle of a stoat at the food patch relative to the holding cage), (8) total visits to 0.5 or 1.5 m marked areas within the first two hours of activity. All variables were recorded over the entire 15 h trial period with the exception of this final variable.

Vigilant behaviour (variable 7) was assessed by observing a stoats' orientation in relation to the holding cage on each separate occasion that a stoat fed. Consecutive feeding incidences were a minimum of 15 min apart during which time the stoat vacated the marked area. The marked areas (variable 8) were used to compare close visits to the risky versus safe patch during a trial night. Each food patch was contained within the marked boundary of 1.5 m, so that a stoat crossed this boundary to feed. An approach within 0.5 m of a treatment cage was only undertaken if a stoat investigated the larger predators. Visits to the marked areas were recorded after 'first active' to ensure that all animals were mobile during the recording period and data collection was limited to 2 h. A pilot study revealed that incursions into the marked areas peaked during the initial investigation phase, when a stoat appeared to quantify the threat presented by the larger predators. Avoidance of marked areas near the risky patch increased over the course of a trial night and recording visitations for the entire 15 h would not have provided additional insights. We also recorded the orientation of a visible larger predator in relation to the stoat on each occasion that the food was harvested at the risky patch, and noted any behavioural changes in response to the stoat's presence. Larger predators were not visible on the infra-red camera, or to a stoat, if they remained in their nest box or climbed into the hessian sack.

Pairwise correlations between the dependant variables were determined using Pearson's correlation coefficient. This allowed us to exclude response terms that are correlates of one another. We tested for the effect of the larger predators on a subset of uncorrelated variables

from each of the categories of feeding, vigilance and avoidance (closeness of approach). Where inspection of mixed models residuals revealed deviations from homoscedasticity or normality, transformations were used to normalize their distribution before analyses. All statistical analysis and plots were created in the R environment (version 2.14.1, R Development Core Team, 2015).

We analysed the data on the proportion of ‘food eaten’ using linear mixed-effects models (the ‘lme’ function from the nlme package), which enabled us to assess the influence of fixed and random effects. Food eaten was analysed as a proportion of total food given so that the greater food allocations to males, based on sexual dimorphism, did not influence the results. We included ‘patch’ (risky or safe), ‘treatment’ (ferret or cat), and ‘sex’ (male or female), as fixed effects in our model, as well as the interactions between these terms. Stoat age (juvenile or adult) was originally included in our models but, as all stoats could not be aged, this was subsequently removed. ‘Stoat ID’ was entered into the model as the random effect, to account for the non-independence of errors associated with repeated measures recorded on the same individuals. Data on vigilance (‘vigilance while feeding’) and avoidance (‘total visits < 0.5 m’) were analysed using generalized linear mixed models (GLMM) with a quasi-Poisson error distribution (Venables & Ripley, 2002), as there was overdispersion in the data. The same fixed and random effects were included in the models with the exception of the model for ‘vigilance while feeding’, which did not include sex as a fixed factor, as there was insufficient power to assess the influence of this variable. Models were simplified by removing non-significance ($p > 0.05$) terms in a reverse-stepwise manner, and significant levels are reported based on the entire and minimal adequate models. Maximum-likelihood (ML) estimates were used to allow us to compare models. After the best model was selected it was fitted by restricted maximum likelihood (REML), to provide unbiased estimates (Zuur

et al., 2009). This allowed us to separate the influence of fixed and random effects, and maximum likelihood estimates enabled us to compare between models.

2.4 Results

Pearson's correlation revealed that 8 of the 21 pairwise comparisons were strongly correlated (Table 2.1). The uncorrelated predictor variables chosen for further analysis were: 'food eaten', 'total visits < 0.5 m' and 'vigilance while feeding'. These predictors allow us to quantify feeding, avoidance and vigilant behaviours, which can be used to assess whether interference competition is likely to occur.

Table 2.1 Testing for correlations where values indicate Pearson's correlation coefficient (r) for each dependant variable measured during experimental treatments. Derived variables ('time at patch per visit'; 'feeding rate') are not included. Asterisks (*) denotes significant correlation at $p < 0.01$.

Response variables	Food eaten	Time to first feeding	Total visits	Total time feeding	Vigilance	Total visits to 1.5m
Time until first feeding	-0.79*	-	-	-	-	-
Total visits to food patch	-0.72*	-0.76*	-	-	-	-
Total time feeding at patch	-0.75*	-0.79*	0.81*	-	-	-
Vigilance	0.29	-0.76*	-0.18	-0.25	-	-
Total visits to 1.5m	-0.19	-0.3	0.37	0.11	-0.32	-
Total visits to 0.5m	-0.24	-0.38	0.34	0.16	-0.25	0.83*

2.4.1 Feeding

Stoats did not display a pen preference while foraging as assessed by comparing proportion of 'food eaten' at each of the food patches on the acclimation night ($t_{15} = 1.22$, $P = 0.28$). Stoats significantly reduced their consumption of food at the risky patch in comparison to the safe patch (Table 2.2, Figure 2.2) on trial nights. At the end of the 15 hour trial night over half of all stoats tested had not consumed the food at the ferret (7 of 12) or cat patch (9 of 16),

while the food at the safe patch was eaten on almost every occasion (27 of 28). Of the 11 stoats that did not eat at the risky patch 8 were female and 3 male, although the sex of the stoat did not significantly influence food harvesting. One quarter of all stoats did not eat at the risky patch across both treatment nights. In situations where food was consumed, ‘time until first feeding’ was on average 7 times earlier at the safe patch compared to the ferret patch and 3 times more rapidly in comparison to the cat patch (Figure 2.3). On every occasion across both treatment nights food was never eaten at a risky patch until all food was finished at the safe patch.

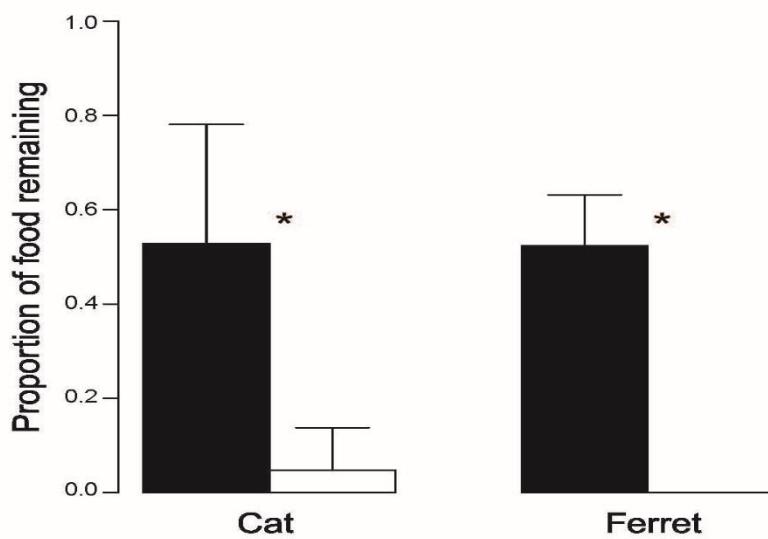


Figure 2.2 Proportion of food that was not consumed by stoats (mean \pm standard error) at the risky treatment patch (black bar) and safe control patch (white bar), when either a cat or a ferret used as the treatment. An asterisk (*) denotes a significant difference between patches at $p < 0.05$.

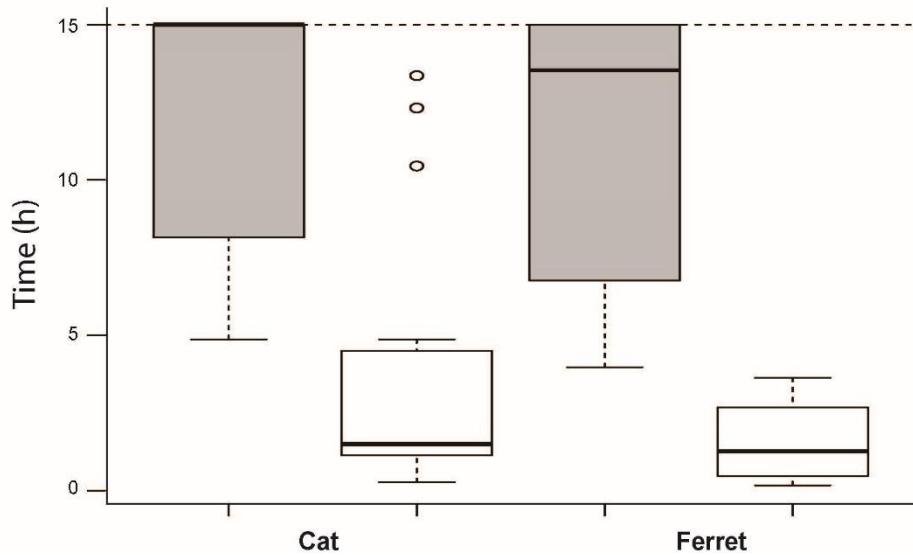


Figure 2.3 Time until first feeding by a stoat at the food patch near the cat (treatment vs. control) and ferret patch (treatment vs. control), for the predator treatment nights. Maximum of 15 h is equal to the duration of one trial night. Boxplot whiskers represent the limit of the nominal range of the data inferred from the upper and lower quartiles, with points outside this displayed as outliers.

Stoat feeding rates (intake g/total time feeding) did not differ between treatments (lme: $t_{19} = -0.03$, $P = 0.98$) or patch type (lme: $t_{19} = -0.30$, $P = 0.77$). As feeding rates did not differ between patch types, “total visits to food patch” mirrors the results for “total time feeding at patch” (Figure 2.4).

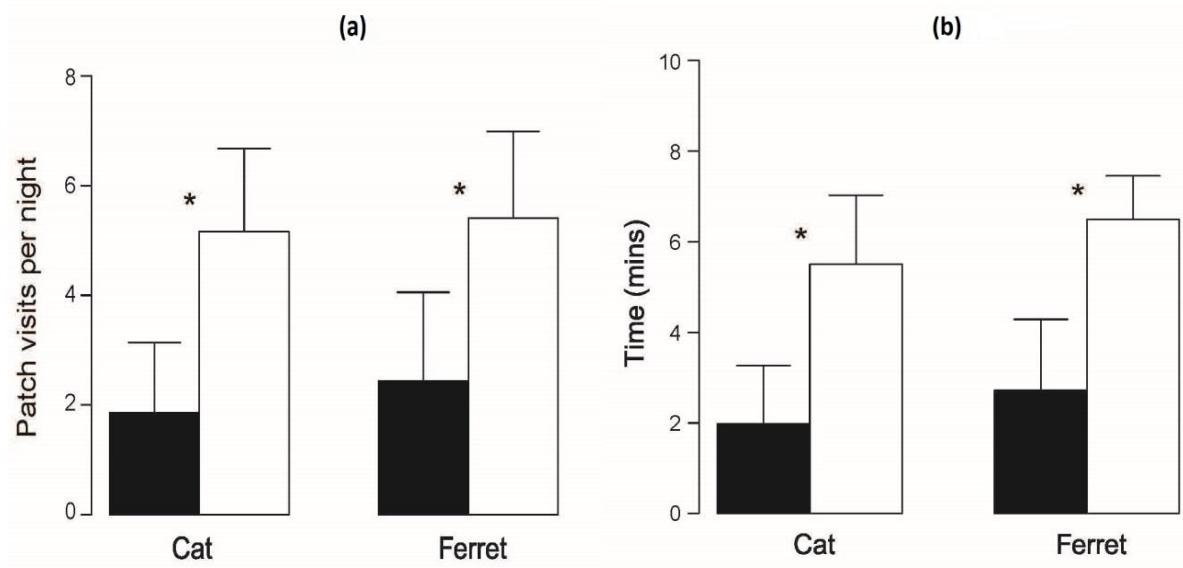


Figure 2.4 Total visits (a) and total time feeding (b) by a stoat, at the treatment (black bar) and control (white bar) food patches, per treatment night with either a cat or a ferret. Columns show mean \pm SE. An asterisk (*) denotes a significant difference between patches at $p < 0.05$.

2.4.2 Avoidance

Stoats significantly avoided the 0.5 m area, close to both larger predators, in comparison to the equivalent 0.5 m at the safe patch (Table 2.2, Figure 2.5). The results were similar at the greater distance of 1.5 m. Stoats distinguished between the treatments as they selected for the safe area significantly more often when the ferret was the larger predator in comparison to the cat (Table 2.2). Additionally, stoats made fewer visits to within 0.5 or 1.5 m of the marked area when the larger predator was the ferret.

Table 2.2 LME and GLMM results for measures of stoat behaviour: feeding at risky or safe patches, avoidance of the larger predator and vigilance while feeding. Statistical significance for differences between treatments is indicated for $p < 0.01$ (*), $p < 0.001$ (**), and $p < 0.0001$ (***)�.

Source of variation	Value	SE	df	t value	p value
Feeding (model: LME)					
<i>Dependent variable: Proportion of food eaten (arcsin transformed)</i>					
Patch (Safe or Risky)	34.73	13.34	34	2.6	0.01*
Treatment (Ferret or Cat)	15.62	13.88	34	1.13	0.27
Sex (Male or Female)	-7.55	14.74	15	0.51	0.62
Patch × Treatment	-6.94	19.53	34	0.36	0.72
Patch × Sex	15.14	18.87	34	0.8	0.43
Treatment × Sex	-34.23	20.79	34	1.65	0.11
Patch × Treatment × Sex	23.94	29.05	34	0.82	0.42
<i>Reduced model: Proportion of food eaten</i>					
Patch (Safe or Risky)	43.05	7.47	38	5.77	<0.0001***
Avoidance (model: GLMM)					
<i>Dependent variable: Number of visits < 0.5 m (quasi-Poisson)</i>					
Patch (Safe or Risky)	2.15	0.92	27	2.33	0.0274*
Treatment (Ferret or Cat)	0.03	1.28	27	0.02	0.98
Sex (Male or Female)	0.71	1.13	13	0.63	0.54
Patch × Treatment	0.7	1.33	27	0.52	0.61
Patch × Sex	-2.31	1.34	27	-1.72	0.1
Treatment × Sex	-0.1	1.63	27	-0.06	0.95
Patch × Treatment × Sex	1.79	1.83	27	0.98	0.34
<i>Reduced model: Number of visits < 0.5 m</i>					
Patch (Safe or Risky)	2.06	0.5	31	4.15	0.0002**
Treatment (Ferret or Cat)	1.06	0.35	31	3	0.0053*
Vigilance (model: GLMM)					
<i>Dependent variable: Vigilance while feeding (quasi-Poisson)</i>					
Patch (Safe or Risky)	-1.52	0.4	10	-3.81	0.0034*
Treatment (Ferret or Cat)	-0.05	0.2	10	0.23	0.82
Sex (Male or Female)	-0.01	0.24	10	-0.06	0.95
<i>Reduced model: Vigilance while feeding</i>					
Patch (Safe or Risky)	-1.15	0.19	15	-5.97	<0.0001***

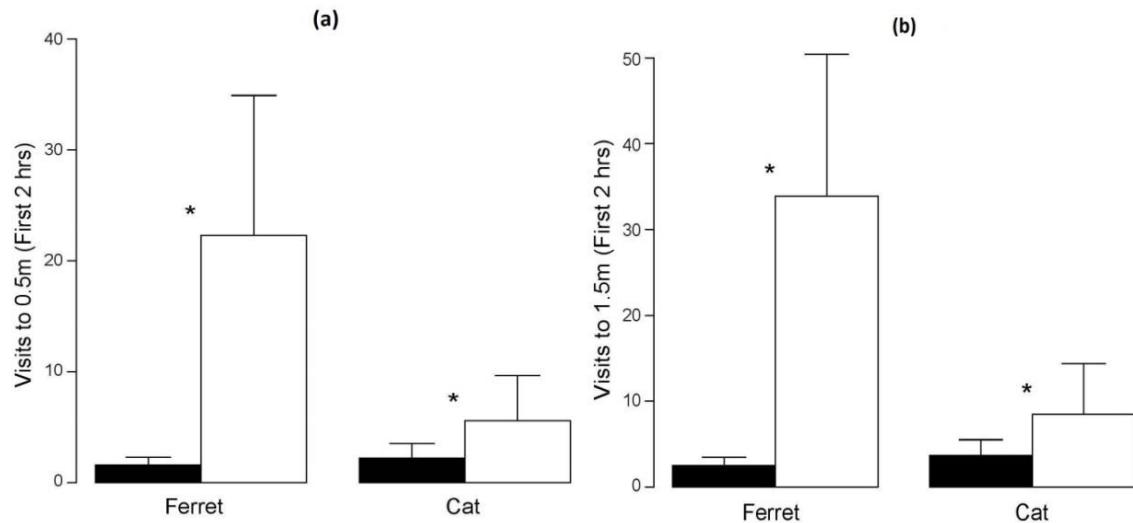


Figure 2.5 Mean number of stoat visits to within 0.5 m (a) or 1.5 m (b) of the holding cage containing a ferret or a cat (black bars for both) compared to an empty holding cage (white bar). Asterisks (*) denotes significant correlation at $p < 0.01$.

2.4.3 Vigilance

Stoats displayed vigilant behaviour by orientating themselves toward the holding cage while feeding. Forward facing eyes enable a stoat to observe the larger predator in this position. There was a highly significant difference in vigilance at the safe and risky patches (Table 2.2). Stoats regarded both larger predators as a threat and the sex of the stoat did not significantly influence the degree of vigilance displayed. Stoats faced directly towards the holding cage 89% of the time when it contained the ferret ($n = 18$) and 93% of the time ($n = 27$) when it contained the cat, as displayed in video recording (Appendix I: S1).

2.4.4 Response of large predators to stoats

The behaviours of both larger predators were recorded on every occasion that a stoat harvested at the risky patch. The ferret was only visible 20% of the time when the stoat harvested food ($n=20$) and oriented itself towards the smaller mustelid just 10% of the time it was visible. The ferret displayed no obvious signs of aggression but occasionally exhibited

piloerection of the tail, which is an indication of excitement (Vinke & Schoemaker, 2012). In contrast, the cat was visible 90% of the time when a stoat harvested food ($n=29$) and on the other three occasions it emerged from its nest box and stalked, with a slow purposeful approach, to the centre of the cage. Cats oriented themselves towards the stoat the entire time it was feeding. The cat attempted to pounce on a female stoat (0.216 kg) that approached the edge of the holding cage (Appendix I: S2) and also attempted to catch a full sized male stoat (0.392 kg) that climbed onto the holding cage (Appendix I: S3).

2.5 Discussion

Behavioural patterns exhibited by predators in this experiment are consistent with the mechanisms that underlie interference competition. Foraging Ermine Avoid Risk (FEAR), and this was evident in stoats' behaviour, as they adjusted their foraging activity to the presence of both larger predators. In line with our predictions, there was significantly less food harvested at both of the risky patches, and food was consumed in its entirety at the safe patch before any food was eaten in close proximity to either predator. Stoats displayed the anticipated avoidance behaviour to the presence of a cat or a ferret as measured by: time until first feeding, number of visits to the patch, total time spent at the risky patch per night, and visits to the two marked areas (0.5 m and 1.5 m) around the predator's cage. Although stoats avoided both predators, there were subtle differences in their behavioural responses. Stoats had greater visitation rates to the control cage, and fewer approaches to the treatment cage, when a ferret was present in comparison to the cat (Figure 2.5). The control cage was the furthest point in the arena from the large predator and increased stoat activity at the control cage may have been influenced by efforts to maximise distance from a perceived threat. Consistent with our predictions, stoats displayed subordinate behaviours (concealment/ avoidance/ freezing/ fleeing) but no overtly aggressive behaviours in the presence of both

large predators. Stoat sex did not have an influence on behavioural responses as both sexes significantly avoided the larger predators. Pairwise correlations revealed that the three measures we used for feeding behaviour were highly correlated: ‘time until first feeding’ is therefore an easily measured variable that conveys a stoat’s perception of the threat that the larger predator represents. Our results show that food was consumed in its entirety at the safe patch before any food was ingested at the risky patch; this is consistent with optimal foraging theory, which predicts that an animal will maximize its energy intake while minimising its exposure to risk (Kotler, 1984; Nonacs & Dill, 1990; Sih, 1980).

As expected, stoats increased the level of vigilance at the risky patch, but in contrast to our prediction this did not correspond to slower feeding and hence an increased feeding duration at a patch per visit. It was long held that feeding and vigilance were mutually exclusive, but this view was subsequently challenged (Lima & Bednekoff, 1999) and it is now recognised that foragers can synchronise these activities. Stoats adjusted their orientation while feeding, which enabled them to maintain their feeding rates while still remaining vigilant.

The results of our study are similar to observations of behavioural interactions between members of the family Canidae (Scheinin et al., 2006; Vanak et al., 2009) and this research suggests that interference competition is likely to occur where stoats, ferrets and cats are sympatric. Although it has been suggested that stoats avoid areas frequented by cats and/or ferrets (Keedwell & Brown, 2001; Moller & Alterio, 1999), avoidance has been inferred only indirectly due to the difficulties in observing interference competition in the wild. The importance of interference competition is also difficult to quantify compared to other processes such as resource competition. We controlled for resource availability in our experiment by providing equal amounts of food at both patches. The spatial avoidance of an

apex predator, as displayed by stoats in this experiment, would reduce the risk of an aggressive interaction, but ultimately could correspond to a reduction in resource availability.

Observations made during this experiment suggest a high likelihood of interspecific killing, as the cat clearly attempted to catch two stoats that ventured close to the holding cage (Appendix I: S2 & S3). Asymmetrical killing has been documented previously between these species (Flux, 2007; Gillies & Clout, 2003), while larger mustelids occasionally have been known to kill smaller ones (Polderboer et al., 1941). Donadio and Buskirk (2006) found that the frequency of lethal interactions tended to be highest at intermediate body size differences between members of the same family. Body size difference is calculated as $(Mb_l - Mb_s)/Mb_l$, where Mb_l is the mass of the larger species and Mb_s is the mass of the smaller one. Relative to stoats, ferrets fall into the intermediate class, with a body size difference of 72%, where the probability of interspecific killing between family members is at its maximum. Although cats are proportionally much heavier than stoats, the body weight difference (93%) again puts them into a category with a high expectancy of interspecific killing, when the predators are from different families (Donadio & Buskirk, 2006). The combined competitive force of these two predators, that vary both in preferential hunting terrain (surface vs. subterranean) and strategies (ambush vs. cursorial predators), may preclude stoats from certain habitats with both larger predators. Nevertheless, these three species do co-exist in New Zealand (Keedwell & Brown, 2001; Reardon et al., 2012). Mesopredators may adjust their behaviour, using spatial or temporal avoidance, to reduce the risk of an encounter (Ritchie & Johnson, 2009). Stoats are common in forested areas, where there are abundant refuges from larger predators, while in open habitats stoats may use fine scale avoidance (King & Powell, 2007; Moller & Alterio, 1999). Where arboreal refuges are scarce, such as in tussock grasslands or pastoral farmlands, stoats are predominantly diurnal, while ferrets and cats are primarily nocturnal (Alterio & Moller, 1997a). Although they may co-exist in close proximity, habitat

restriction imposed by apex predator avoidance may lead to dramatic effects on the population dynamics of the subordinate species (Sergio & Hiraldo, 2008).

There were discrete differences in the behavioural responses of stoats to both larger predators in this trial. Individual variations in how members of the same species respond when feeding under predation risk (Bell, 2005) or when inspecting a predator (Dugatkin, 1992) have been attributed to the shy–bold continuum where boldness is measured by the inclination to take risks in challenging or novel situations (Sloan Wilson et al., 1994). One quarter of the 16 stoats tested consumed the food at the risky patch on both treatment nights, but conversely one third did not consume any food at the risky patch. Anti-predator behaviour is known to vary between individuals that are part of the same population (López et al., 2005), and bold individuals are hypothesised to have a higher risk of mortality where interspecific killing is common (Scheinin et al., 2006). Therefore, based on our evidence of substantial variation in stoats' boldness, we predict there should be a lower proportion of bold stoats in areas with abundant cats or ferrets compared to areas without these larger predators. Unfortunately the densities of ferrets and cats at the sites where the stoats were captured are unknown and our sample sizes at each site were insufficient to test this prediction.

The experimental design proved to be effective at eliciting behavioural responses of stoats. Allocating food portions based on a conservative measure of a stoat's daily energy requirements encouraged interactions between the predators. Non-predatory animal species were not used as a control in place of a cat or ferret, and thus an assumption is that stoats were fearful because they recognised both predators as threats, as opposed to being fearful due to the novelty of a caged animal. A study with segregated mustelids showed that stoats were not intimidated by the presence of a smaller predator, the weasel (*M. nivalis*), and demonstrated clear dominance in encounter tests (Erlinge & Sandell, 1988). Stoats in New

Zealand prey upon species that are relatively greater in size, such as lagomorphs (Murphy et al., 2004), and there is also anecdotal evidence of stoats attacking brushtail possums (*Trichosurus vulpecula*) (Veale, 2013), a large (~5kg) aggressive omnivore. Therefore, in this trial, the greater size of the larger predators was unlikely to be the attribute that provoked the significant avoidance behaviour observed for stoats. Furthermore, previous research on interactions between two canid species assessed interference competition based on interactions observed in pen trials (Rudzinski et al., 1982). Their conclusions have proven robust because subsequent research has confirmed that the red fox (*Vulpes vulpes*) dominates the smaller artic fox (*Vulpes lagopus*) in competitive interactions. Thus, we believe it is unlikely that stoats would have reacted similarly to the presence of a caged animal that was not a potential predator. A useful extension to this study would be to test whether stoats use visual, olfactory or auditory cues, or a combination of these, to assess the threat. A number of studies have found that these senses are important for predator recognition in both terrestrial and aquatic systems (Ferrari et al., 2005; Miller & Surlykke, 2001; Mukherjee et al., 2009).

2.5.1 *Management applications*

Mustelidae species are of special interest to conservation, as they have members on both the IUCN red list of threatened species and the list of the world's worst invasive species (IUCN, 2012; Lowe et al., 2000). Understanding competitive interactions between mustelids and apex predators can help with conservation strategies relating to both of these issues. A high proportion of the Mustelidae are considered to be threatened or already extinct (IUCN, 2012). The two terrestrial species at greatest risk are the endangered black-footed ferret and the critically endangered European mink (*M. lutreola*). Both these species are being managed with re-introduction programs in areas where they have been extirpated. In a recent re-introduction attempt 80% of known mortalities of black-footed ferrets and their ecological surrogate, Siberian polecats (*M. eversmanii*), were caused by interspecific killing (Biggins et

al., 2011). Repatriation of the European mink has encountered similar high mortality rates with 75% of all recorded deaths attributed to apex predators (Maran et al., 2009). Understanding and managing interference competition is critical for re-establishment of both these species. Individual variability in the fear response to a larger predator was displayed by stoats in this study. Understanding the proliferation of individual traits, or selectively breeding animals with desirable characteristics, could improve survival rates during re-introduction programs for species threatened by predation. Additionally this experimental design might have potential as a tool for training endangered animals to avoid dominant predators, and hence improve post release success. This sort of behavioural conditioning has been used for reintroductions of naïve animals with no prior exposure to predators (Kleiman, 1989; Moseby et al., 2012; Smith & Blumstein, 2012).

In New Zealand interference competition between invasive cats, ferrets and stoats is an important consideration when making conservation decisions. In the absence of large carnivores, ferrets and particularly cats have assumed the role of apex predators. The low diversity of native mammalian and terrestrial bird fauna leads to a high likelihood of dietary overlap, which is one of the main drivers of interference competition (Donadio & Buskirk, 2006). In these circumstances, management of an invasive predator species in isolation can have unwanted consequences due to mesopredator release (Ritchie & Johnson, 2009; Soulé et al., 1988). Even when managing a suite of predators simultaneously, differences in trappability, succession and re-colonisation rates imply that interference competition warrants consideration. Increased stoat abundance can have detrimental consequences for native species in certain habitats, as stoats are the primary predators of many birds that nest on the ground or in tree cavities (Clout et al., 1995; McLennan et al., 1996; Wilson et al., 1998). It is therefore important that management programs take into consideration the consequences of control operations that target ferrets and/or cats, especially during the breeding season of

native birds, as nests located in burrows, tree hollows and tree canopies, may be at greatest risk from stoat predation.

2.6 Acknowledgements

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2.6.1 Ethical standards

This research was approved by the Landcare Research Animal Ethics Committee (AEC approval number 12/06/01). Approved applications comply with the Animal Welfare Laws 1999, Animal Code of Welfare 2012 and all additional New Zealand legislation.

CHAPTER 3 Dominant predator odour triggers caution and eavesdropping behaviour in a mammalian mesopredator



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3.1 Abstract

Mesopredators need to satisfy their energetic requirements while avoiding potentially lethal encounters with apex predators. Predators release odours into the environment through natural processes and many antipredator adaptations are induced by the detection of these scents. We tested whether a mesopredator adjusted its behaviour when it encountered dominant predator odour in an outdoor arena. Eighteen wild-captured stoats (*Mustela erminea*) were exposed to the body odour of three predators: two previously encountered sympatric apex predators (cat *Felis catus* and ferret *M. furo*), and a novel apex predator (African wild dog *Lycaon pictus*). Foraging areas were created that varied in perceived risk, based on the presence or absence of predator odour. Detection of kairomones (chemical cues from predators) triggered cautious inspection and altered the mesopredator's foraging activity. However, in contrast to our predictions, dominant predator odour was an attractant rather than a deterrent; food was consumed earlier in foraging areas with apex predator odour than in unscented controls. Sympatric predator odour elicited the most pronounced behavioural changes, with stoats cautiously approaching, but readily investigating, the odour source. Ferret odour stimulated the most marked changes. Mesopredators may benefit from exploitative eavesdropping as detection of predator odour primes antipredator behaviours, avoids the energetic cost of unnecessary flight and may also help a mesopredator to locate resources. This experiment highlights the role of odour in the assessment of risk, and its capacity to alter foraging behaviour by a subordinate member of a predator guild.

3.2 Introduction

Mesopredators (which are both predators and prey) must balance the conflicting demands of meeting their energetic requirements while remaining safe (Kats & Dill, 1998; Sih, 1980). Interference competition is a widespread interaction among mammalian carnivores, with larger predators dominating smaller species in confrontations (Palomares & Caro, 1999). Survival within a predator guild therefore requires keen senses, as an agonistic encounter may lead to injury or death. Olfaction, the dominant sense of many mammals, may mediate these interactions by providing reliable information on an apex predator's proximity (Apfelbach et al., 2005; Parsons & Blumstein, 2010). Selection pressure may therefore benefit individuals that recognise and respond to odours (Apfelbach et al., 2005).

Predator odours are deposited either deliberately or as a by-product of metabolic processes (Wyatt, 2010). These odours are a class of chemical cues known as kairomones, which moderate interspecific competition to the benefit of the detecting species (Ferrero et al., 2011). Sources of kairomones include urine, faeces, exfoliated skin cells and glandular secretions (Gorman & Trowbridge, 1989). Studies on rodents have found that predator cues derived from skin and fur elicit stronger endocrine and behavioural responses than odours derived from excreta (Apfelbach et al., 2005; Masini et al., 2005; Takahashi et al., 2005). Odours from skin and fur may indicate a higher likelihood that the depositing animal is nearby compared to odour from faeces or urine (Blanchard et al., 2003a).

A species may display a range of responses when predator odour is encountered including freezing, vigilance, escape, avoidance and the use of refuges (Lima & Dill, 1990). These behaviours are not specific to any animal group and have been documented in primates, rodents, lagomorphs and artiodactyla (Apfelbach et al., 2005). Avoidance strategies are costly, as they may reduce the time available for foraging, so individuals need to make an

accurate assessment of the true risk (Preisser et al., 2005). Unlike visual or auditory stimuli, kairomones indicate that a given area was risky at some point in time, but not necessarily at present (Kats & Dill, 1998). Odour attenuates as volatile components disperse, so variation in odour strength can give an indication of its age (Bytheway et al., 2013). Many mammals can distinguish between the odour deposits of different predator species (Apfelbach et al., 2005; Lledo et al., 2005). Odour recognition may be learnt through past experience or be innate due to recognition of components of a carnivorous diet (Blumstein et al., 2002; Ferrari et al., 2005). Once a predator has been identified, the detecting species can respond to the threat with an appropriate defence, based on the hunting strategy or lethality of the identified species (Schoeppner & Relyea, 2009)

Mustelidae have highly developed olfactory senses, as chemical communication is of particular importance to solitary carnivores (Gorman & Trowbridge, 1989). Species-specific chemical composition of secretions makes exchange of information possible between coexisting mustelid species (Brinck et al., 1983). American mink (*Neovison vison*) are attracted to the scent of polecats (*Mustela putorius*) and have a similar level of response to polecat odour as to that of a conspecific (Harrington et al., 2009). Stoats (*M. erminea*) and weasels (*M. nivalis*) are sometimes sympatric, with stoats having an advantage in interspecific competition by virtue of their larger size (King & Powell, 2007). In behavioural studies, weasels distinguished between their own scent and that of a stoat, and they responded by avoiding the scent of the dominant predator (Erlinge & Sandell, 1988).

As one of the smallest members of the Carnivora, stoats are vulnerable to interference competition from larger predators. They co-exist with cats (*Felis catus*) and ferrets (*M. furo*) in many parts of the world including Europe, North America and New Zealand. Feral cats typically function as mesopredators in continental ecosystems (Crooks & Soulé, 1999), but

are apex predators on many islands, including New Zealand (Bergstrom et al., 2009). Ferrets and cats dominate stoats in aggressive encounters. Stoats avoided the larger predators when they were detected visually and displayed behaviours consistent with fear for the duration of encounters in pen experiments (Chapter 2). Odours from both larger predators have been used as stimuli in laboratory experiments and elicited pronounced behavioural responses in *Rattus* species (Staples, 2010). A comprehensive series of experiments show odour from ferret fur and skin induce acute physiological and behavioural reactions in rats (Masini et al., 2005). Similarly, cat body odour triggered defensive responses in rats (Dielenberg & McGregor, 2001).

The objective of this study was to investigate the behavioural responses of foraging stoats to the odour of a larger competitor. We exposed stoats to fresh odour cues from: sympatric predators (cat and ferret), a novel predator (African wild dog - *Lycaon pictus*), a pungency control (cinnamon), and a non-odour control (distilled water). Studies on Mustelidae and other mammals suggest that sympatric predator odour will provoke the strongest behavioural responses, with diminishing responses to novel predator odour and no discernible behavioural change when stoats encounter pungent or non-odour controls (Apfelbach et al., 2005; Harrington et al., 2009). We predicted that sympatric predator odour would result in: (1) avoidance, (2) prolonged survival time of artificial prey (i.e. food items close to predator odour), (3) brief encounter, (4) increased risk assessment, and (5) fear behaviour (Table 3.1). Based on results of a previous trial (Chapter 2), we anticipated that (6) responses of male and female stoats would be similar across all measures. It is possible that initial detection of dominant predator odour may spur further investigation of the source rather than rapid departure. Therefore, an alternative to prediction (1) is that detection of kairomones will lead to odour inspection (7), as a stoat attempts to gain further information about the donor (Hurst et al., 1997).

3.3 Methods

3.3.1 Study animals

Eighteen wild stoats (9 males and 9 females) were captured by professional trappers at various locations across the South Island of New Zealand. All trappers have an obligation to abide by the Animal Welfare Act 1999 section 36. Stoats were trapped in areas where they were highly likely to have encountered sympatric ferrets and cats or traces of their odour, prior to capture. In addition, during a pen trial completed three months before this study began, all test stoats were in close proximity to cats and ferrets while foraging (Chapter 2). This removed lack of previous experience with both sympatric predators as a potential source of variability amongst study animals. The study was conducted between mid-November and January, a period immediately after the breeding season of stoats in New Zealand. Animals arrived at the facility in December 2011, with the exception of two stoats that were supplied in April and September of that year. The trial took place from August-September 2012, so sixteen animals were housed for seven months and the maximum duration that a stoat remained in captivity was sixteen months. Stoats were housed in individual cages ($0.6 \times 1.5 \times 1.9$ m) under an outside shelter at the Landcare Research Animal Facility, Lincoln, New Zealand. Stoats were held in a semi-natural environment, albeit in pens, and with an absolute minimum of human contact. All animals were sexed, weighed and physically inspected upon arrival at the animal facility. The average body weight of stoats was 0.329 kg for males (range: 0.310 kg – 0.431 kg) and 0.198 kg for females (0.140 kg – 0.273 kg). All animals were fed an alternating daily diet of dead day-old chickens or chicken mince and domestic cat biscuits.

3.3.2 Trial design

Pen trials were undertaken at Landcare Research, Lincoln, New Zealand. The experiment was conducted in an arena of three adjoining outdoor pens (Figure 3.1), with each pen covering an area of $9 \times 7.5 \times 2 \text{ m}$. Open doors ($2 \text{ m} \times 1 \text{ m}$) allowed a stoat's unobstructed movement between the three pens. The height of grass in the pens was maintained at about 5 cm to ensure a stoat was clearly visible to the observer.

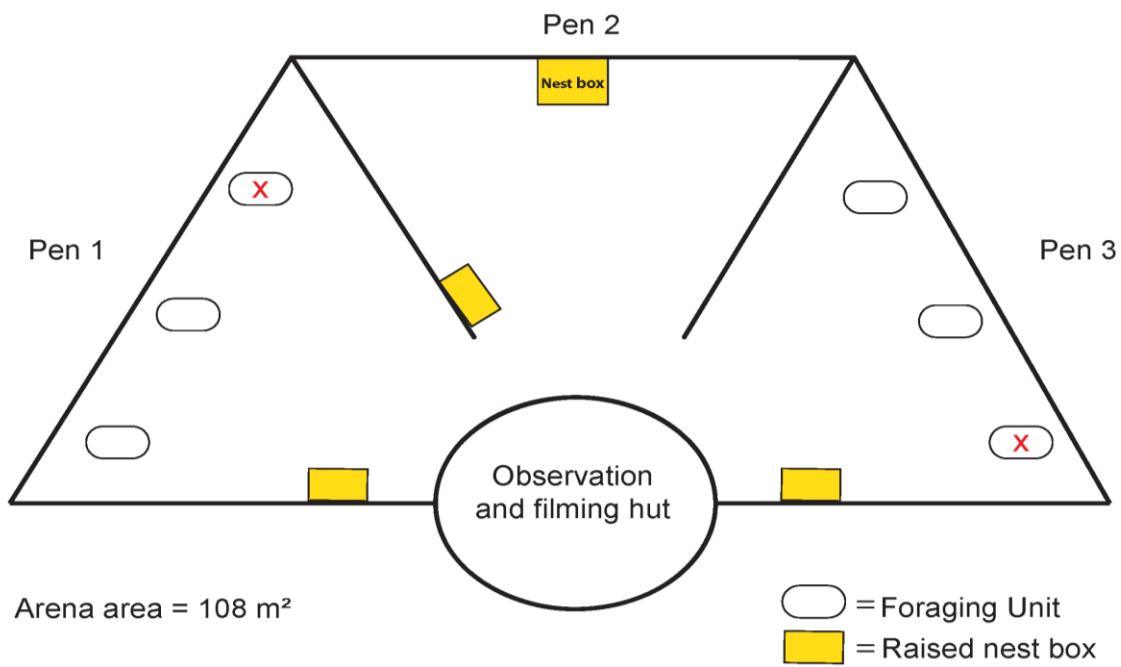


Figure 3.1 Experimental set-up on a treatment night. The 'X' represents the random location of one of the four odour treatments (ferret/ cat/ wild dog/ pungent control). The other four foraging units each contained a cloth with non-odour control (distilled water). All foraging units contained a dead baby rat as a food resource.

Each stoat was released individually into the experimental arena for three consecutive nights. All animals were moved into the arena within their familiar nest box to avoid the need for sedation and had 24-hr access to drinking water. A stoat's familiar box remained in the arena for the duration of the trial and each animal had access to three additional nest boxes that

were fixed to wire mesh at 1.5 m above the ground (Figure 3.1). When not being used in the trial, stoats were housed elsewhere in pens adjacent to other stoats, so it was anticipated that any residual scent left in the arena would not influence foraging activity. This assumption was tested subsequently to ensure residual scent did not influence the results. Stoats were placed in the arena for an average of 5.37 hours (range 4.82 - 5.96 h) before the start of the experiment. Three ‘foraging units’ were subsequently placed in each of the two peripheral pens (Figure 3.1). These units (described in detail below) were designed to provide a structurally complex environment where a stoat could search for food. Thus, the experimental arena, consisting of pens and foraging units, was a microcosm where stoats could forage and, during this process, encounter the odour of a large predator. We expected that more natural behaviours and a greater range of behavioural responses would be exhibited when encountering predator odours in this trial design than those elicited from forced alternative choices imposed in a Y or plus maze (Blanchard et al., 2003a). The first night of the trial provided a baseline measure of undisturbed activity and foraging behaviour. On the second and third nights, one foraging unit in each peripheral pen was selected randomly to include one of the four odour treatments (ferret/ cat/ wild dog/ pungent control), while the other two foraging units received towelling material sprayed with distilled water as a non-odour control (Figure 3.1).

Individual stoats received different sequences of treatments in a randomised order to minimise carryover effects and to facilitate comparisons between pairs of treatments. This enabled us to test whether the sequence of treatments unduly influenced the stoats’ behaviour. Treatments were set out each evening at least an hour before dusk and collected the following morning. Nocturnal activities were recorded on day and night video cameras (‘Bosch Dinion’, Bosch Security Systems, Sydney) from an observation hut adjoining the arena, which was dimly lit by an infrared spotlight. Three cameras had wide angle lenses (2.8 – 11

mm) to record the entire arena, while two additional lenses were focused on the area containing the treatment odour. All cameras ran continuously for 15 hours from 5pm to 8am the following morning. This recording period included an average of 69 minutes (range 40-99) of light after dawn and 66 minutes (range 48-85) before dusk. Video footage was stored and viewed using a Geovision-1248 digital video-recording system (Geovision Inc., Taipei). To minimize observer bias, blinded methods were used when all behavioural data were analysed. Nocturnal foraging behaviours were assessed by reviewing video on GeoVision software and analysed using the software package JWatcher (v. 1.0, Animal Behaviour Laboratory, Macquarie University, Sydney, Australia).

3.3.3 *Olfactory stimuli*

Body odour was collected from three mammalian predators by placing towels in direct contact with the donor animals. Hand towels (30 cm × 61 cm) were first washed in warm water to ensure they were free from any pre-existing scent. Ferret odour was collected over 12 days from four wild-caught ferrets (2 male and 2 female) by placing a clean towel in each animal's nest box for three days. Towels were positioned so that they were exposed directly to the fur on the body and neck of the donor animal. Odour was collected from four feral cats (2 male and 2 female) using the same method. Body odour was collected from six African wild dogs kept as part of a breeding program at Orana Wildlife Park, Christchurch, New Zealand. Towels were placed in communal denning beds of wild dogs for two weeks to ensure the material was impregnated with sufficient odour. All towels were inspected to check that there were no obvious excreta present.

Towels were cut into segments immediately after collection and each segment was wrapped in a plastic oven bag (Glad brand, Clorox New Zealand Ltd., Auckland). Large 15 cm x 12 cm segments were used because previous research concluded that the amount of odour affects

the extent of fear-related behaviour displayed by a mesopredator (Takahashi et al., 2005). Each segment was subsequently rolled in a polyethylene based wrapping material to prevent loss of volatile compounds, and placed in an airtight plastic box. Containers were stored in a –80 °C freezer until needed. Fresh plastic gloves were worn at all times during odour collection. For the pungency control, cinnamon oil was added to a clean segment of towel prior to usage. The non-odour control was a clean segment of towel treated with distilled water.

3.3.4 *Foraging unit*

Three tunnels were placed in parallel to form a ‘foraging unit’ (Figure 3.1). Each tunnel consisted of an 800-mm length of non-perforated agricultural drainage tubing, 65 mm in diameter and sealed at one end using a 65-mm end cap. The lack of perforations ensured that odour only escaped from the tunnel entrance, and also prevented light entering into the sealed end. Odour-impregnated material was at the sealed end of the foraging tunnel, so that there was no possibility of cross contamination with the second treatment that was located a minimum of 15 m away. The length of a foraging tunnel ensured that a stoat would have to enter in its entirety before it could retrieve a prey item (average head-body length of a male stoat was 285 mm). Separate foraging units were used for each odour treatment to ensure there was no cross-contamination of scents. A marker was placed in the ground 0.5 m from the entrance to a foraging unit to assist in estimating approach distances. To apply a treatment to a foraging unit, a segment of towel, impregnated with one of the four odours, was passed through a tunnel three times before being placed inside at the capped end. All three tunnels within a foraging unit received the same treatment. It was anticipated that this lack of visibility and the body odour emanating from the entrance of a tunnel would indicate to a stoat that there was (or had been) a predator. Tunnels were stored separately and washed thoroughly after each stoat had completed its three consecutive nights.

Latex gloves were worn at all times when handling food and foraging tunnels. Frozen baby rats were used as prey items, with a mean weight of 15.1 g (range 5.25 g – 25.4 g). Although rats were a novel food item for stoats at the animal facility, rodents are commonly eaten in the wild. The daily food requirement of a stoat in captivity is 19-37% of an individual's mass (King & Powell, 2007). Six baby rats were chosen so that collectively they weighed 25-30% of the stoat's body weight. One tunnel within a foraging unit was randomly selected and a rat was placed inside at the capped end. Stoats received the same food portion on all three trial nights. A fishing swivel was tied to one end of 300 mm of fishing line and used to secure the prey item. The fishing line passed through a small hole, and a 30-mm square metal tag was secured to the other end, outside the tunnel. This prevented the prey from being cached and also served as a marker as movement of the metal tag gave a clear visual indicator of the moment when the prey item was seized (Appendix II: S1). In each tunnel entered by a stoat, the rat was eaten on a single visit.

3.3.5 *Behaviour and food harvesting measures*

The behaviour of 18 stoats was recorded individually for three consecutive nights. We related all response variables to specific predictions (Table 3.1), which were developed based on observations from the pen trial (Chapter 2) and a comparable study (Blanchard et al., 1991). Odour inspection was measured by the two continuous variables: *time until first approach*, which was defined as the time elapsed in minutes from a stoat's first activity until it approached to within 0.5 m of a foraging unit and *time spent at foraging unit*, which was defined as the total time in seconds that a stoat spent, on its initial visit, within 0.5 m of a foraging unit. We defined *time when food eaten* as a continuous variable measured as the interval in units of hours between the time of first activity and when the visual indicator was triggered at a foraging unit. *Prey remaining at end of night* was a categorical variable as the prey was either entirely consumed or remained untouched. *Foraging tunnels entered* was a

discrete variable measured as the number of times a stoat entered a foraging unit within the first two hours of activity. Several behavioural responses to predator odour were tallied as discreet variables at the end of each trial night. Cautious approach was characterised by slow forward movements towards the stimuli with the body pressed low to the ground and we recorded any instance that occurred within 0.5 m of a foraging unit. Similarly, scanning was defined as an interruption in odour investigation when a stoat raised its head and looked around repeatedly, within 0.5 m of a foraging unit. Any instance where a stoat suddenly became motionless anywhere in the pen, while oriented towards the odour source, was defined as *freezing*. This was the only measure to be recorded outside of the marked 0.5 m area, as we anticipated that detection of predator odour from a distance may result in freezing. However, this behaviour was not recorded during the trial. The behaviour *hiding* was defined as a visit by a stoat to within 0.5 m of a foraging unit and then an immediate retreat to one of the four nest boxes in the arena. Continuous variables were measured from first activity, which we defined as the time that a stoat appeared on any camera after a trial night started at 5 pm. When we observed changes in behaviour due to the initial detection of odour volatiles, we used the 0.5 m marker to provide an estimate of this detection distance. Behaviours were recorded until the food was eaten in each of the foraging units. Additional behaviours that were not anticipated, but occurred in response to the treatments, were also recorded. Scent marking was recorded on five occasions, involving two males and one female stoat. Marking occurred only when stoats encountered sympatric predator scent: four times with ferret odour and once with cat odour.

Table 3.1 Prediction and associated response variables used to measure each prediction.

Prediction	Response variables
(1) Avoidance ¹	(i) Time until first approach (ii) Time spent at foraging unit ²
(2) Prey survival ³	(ii) Time when food eaten, (iii) Prey remaining at the end of the night
(3) Encounter	(v) Foraging tunnels entered, (vi) Time spent at foraging unit
(4) Risk assessment	(vii) Cautious approach ⁴ , (viii) Scanning ⁵
(5) Fear behaviour	(ix) Freezing ⁶ , (x) Hiding ⁷
(6) Gender response	(xi) Male or female
(7) Odour inspection ⁸	(i) Time until first approach (ii) Time spent at foraging unit

1 Avoidance was measured as the interval between the time when a stoat first became active and the *time until first approach* to within 0.5m of a foraging unit.

2 *Time spent at foraging unit* was defined as total time in seconds, within 0.5 m of a foraging unit, on the first visit by a stoat.

3 Prey survival time was measured as the interval between the time of first activity and the *time when food eaten*.

4 *Cautious approach* was characterised by slow forward movements towards the stimuli with the body pressed low to the ground.

5 *Scanning* was defined as an interruption in odour investigation, within 0.5 m of a foraging unit, when a stoat raised its head and look around repeatedly.

6 *Freezing* was defined as any instance that a stoat became motionless, while orientated towards an odour source.

7 *Hiding* was defined as when a stoat visited within 0.5 m of a foraging unit and then immediately retreated to one of the four nest boxes in the arena.

8 Odour inspection was measured by the interval between the time when a stoat first became active and the *time until first approach* to within 0.5m of a foraging unit.

3.3.6 Data analysis

Data were analysed for differences in stoat behaviour in response to odour detection at a foraging unit. On a treatment night each of the variables associated with the four ‘control’ foraging units were averaged, as stoats had access to all units simultaneously. Generalized linear mixed models (GLMM) were used to compare stoats’ responses to the odour treatments, based on the response variables *time until first approach*, *time when food eaten* and *time spent at foraging unit*. Models were fitted by maximum likelihood (ML) to compare competing models. After the best model was selected it was fitted by restricted maximum likelihood (REML), to provide unbiased estimates (Zuur et al., 2009). This allowed us to separate the influence of fixed and random effects, and maximum likelihood estimates enabled us to compare between models. ‘Treatment’ (non-odour control, pungent control, cat,

ferret and wild dog) and sex (male or female) were used as fixed effects, as well as the interactions between these terms. The term night, which was a categorical variable with two levels (first/ second), was added to the GLMM as a way of testing if stoat behaviour changed over time due to a) greater requirement for food on the second night after forgoing prey on the first night or b) lack of a fear response on the second night after the predator was not physically encountered on the first trial night. Stoat ‘age’ (juvenile or adult) was originally included in our models, but as it was not possible to age all stoats, age was not included as a factor. ‘StoatID’ was entered into the model as the random effect, to account for the non-independence of errors associated with repeated measures of the same individuals. The acclimation night was used to test if stoats displayed a pen preference: this was tested with a GLMM and the response variable *time when food eaten*. The fixed effect ‘pen’ (pen 1 or 3) and the random effect StoatID were added to the model. A similar model with ‘trial’ (1st half/2nd half) added as the fixed effect tested whether stoat foraging activity varied across the experiment, which could indicate that residual odour was affecting behaviour. We tested random variables to ensure that the scent combinations or the order of scent presentation did not influence the results of the trial. These factors were found to be non-significant so subsequently only ‘StoatID’ was used as a categorical random factor in the analysis. Inspection of the residuals for the response variables *time when food eaten* and *time spent at foraging unit* revealed heteroscedasticity and we controlled for this with a varPower function of the form ‘fitted(.)’ (Zuur et al., 2009).

Pairwise correlations between the dependent variables were calculated using Pearson’s correlation coefficient to identify any response terms that were highly correlated and therefore non-independent. Statistical analysis was conducted on *prey remaining at the end of a night, cautious approach* and *scanning* by converting variables to a contingency table and analysing these response variables using Fisher’s exact test. All analyses were undertaken

with this test as the count in some cells in the table was less than 5, which precluded the use of Pearson's chi-square. This enabled us to test for differences in behaviour between the controls and treatments. In contrast to our prediction, *freezing* or *hiding* behaviours were not displayed and were removed from the analysis. All statistical analysis and plots were created in the R environment (version 2.14.1, R Development Core Team, 2015).

3.4 Results

Pearson's correlation revealed that 1 of the 15 pairwise comparisons of response had a high inter correlation (Appendix II: S2). The discrete variable *foraging tunnels entered* and the continuous variable *time spent at foraging unit* effectively measured the same aspect of stoat behaviour and this was confirmed with a positive correlation between these variables of 0.72. We therefore dropped *foraging tunnels entered* from the analysis.

There was no evidence that stoats displayed a pen preference, as assessed by comparing *time when food eaten* across foraging units during the acclimation night (GLMM: $P = 0.29$). The *time when food eaten* ranged from 2 to 810 minutes (mean = 264 minutes \pm SE 0.34) in pen 1 and 5 to 860 minutes (mean = 310 minutes \pm SE 0.37) in pen 3. There was also no evidence that stoats varied their foraging behaviour in the first half (mean = 273 minutes \pm SE 0.23) of the trial in comparison to the second half (mean = 304 minutes \pm SE 0.22), based on *time when food eaten* (GLMM: $P = 0.19$). The sex of the stoat did not significantly influence any of the results and stoat behaviour remained constant across treatment periods, as the term 'night' was non-significant (Table 3.2).

Table 3.2 Generalised linear mixed model (GLMM) of stoat behaviour using response variables *time until first approach* and *time when food eaten*. Statistical significance for differences between treatments is indicated for $p < 0.01$ (*), $p < 0.001$ (**), and $p < 0.0001$ (***)�.

Source of variation	Value	SE	df	t value	p value
<u>Time until first approach</u> (model: GLMM)					
<i>Treatment odours compared to control:</i>					
Pungent	-8.95	14.72	82	-0.61	0.55
Ferret	-33.74	10.09	82	-3.34	0.0013*
Cat	-15.42	13.08	82	-1.18	0.24
Wild Dog	-17.67	12.55	82	-1.41	0.16
Night	-2.65	3.24	82	-0.82	0.42
Sex (Male or Female)	-6.07	4.5	82	-1.35	0.18
<u>Time when food eaten</u> (model: GLMM)					
<i>Treatment odours compared to control:</i>					
Pungent	-0.42	0.85	72	-0.5	0.62
Ferret	-2.53	0.73	72	-3.49	0.0008**
Cat	-1.21	0.82	72	-1.49	0.14
Wild Dog	-0.7	0.84	72	-0.83	0.41
Night	-0.32	0.53	72	-0.59	0.56
Sex (Male or Female)	0.69	1	72	0.69	0.49
<u>Time spent at foraging unit</u> (model: GLMM)					
<i>Treatment odours compared to control:</i>					
Pungent	9.3	10.05	82	0.93	0.36
Ferret	104.92	9.68	82	10.84	<0.0001***
Cat	37.08	9.71	82	3.82	0.0003**
Wild Dog	14.64	9.68	82	1.51	0.134
Night	14.22	12.19	82	1.17	0.2465
Sex (Male or Female)	0.83	0.69	82	1.22	0.23

3.4.1 Initial detection

Stoats first became active 2 to 180 minutes (mean = 67.08 minutes \pm SE 10.07) after the trial began. Stoats moved freely throughout the arena: both pen 1 (mean = 12.65 minutes \pm SE 6.56) and 3 (mean = 15.21 minutes \pm SE 5.58) (Figure 3.1) were entered within the first hour by 16 of the 18 stoats and 90% of the foraging units were also visited within the first hour. *Time until first approach* was influenced by treatment as stoats approached and inspected foraging units containing predator odour more expediently than control units, with ferret odour provoking the most pronounced behavioural response (Table 3.2, Figure 3.2a).

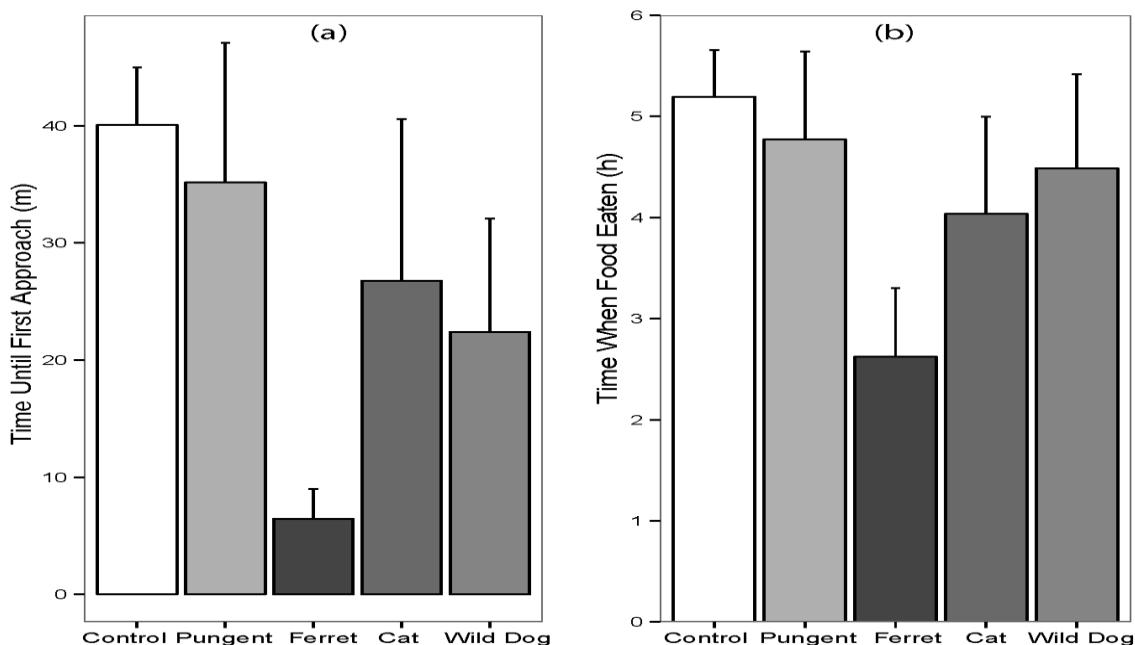


Figure 3.2 (a) *Time until first approach* is the time elapsed in minutes (mean \pm standard error) from a stoats' first activity until its initial approach to within 0.5 m of a foraging unit (control, pungent, ferret, cat and wild dog). (b) *Time when food eaten* is the time elapsed in hours (mean \pm standard error) from a stoats' first activity until the food item was eaten at each of the foraging units (control, pungent, ferret, cat and wild dog).

3.4.2 Prey survival

Stoats consumed 94% (203/216) of the food presented based on *prey remaining at the end of the night*. There was no significant relationship between treatment and food remaining (mean = 0.36 prey \pm SE 0.18) at the end of a trial night (Fisher's exact test, P = 0.89). *Time when food eaten* was significantly shorter at foraging units with ferret odour, while other treatments were similar to the controls (Table 3.2, Figure 3.2b).

3.4.3 Encounter

Stoats spent significantly more time at foraging units containing the scent of known sympatric predators (ferret or cat) than with odour of the novel predator (wild dog) or either of the controls (Table 3.2, Figure 3.3), which is consistent with inspection behaviour. Ferret odour incited the most prolonged initial investigation (mean = 141.44 seconds \pm SE 23.22) followed by cat odour (mean = 103.76 seconds \pm SE 20.72).

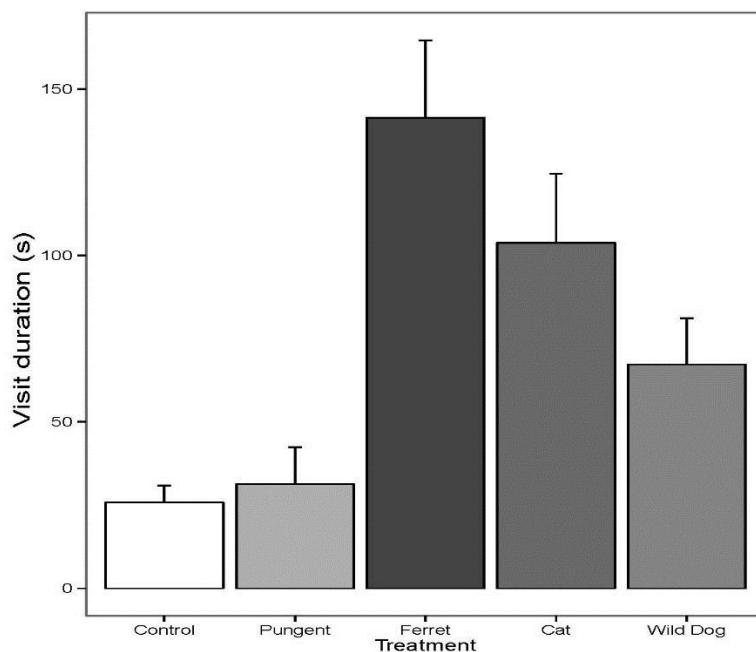


Figure 3.3 *Time spent at foraging unit* is the total time in seconds (mean \pm standard error) that a stoat spent, on its initial visit, within 0.5 m of a foraging unit (control, pungent, ferret, cat and wild dog).

3.4.4 Risk assessment

Risk assessment behaviours were only exhibited during the initial approach to the treatment. A *cautious approach*, characterised by slow careful movements or standing on hind legs, was most often observed with ferret odour (Appendix II: S3), less often with cat odour (Appendix II: S4), occasionally with wild dog odour, and never with non-odour or pungent controls (Figure 3.4a). The difference from the non-odour controls was significant for both cat (Fisher's exact test $P=0.031$) and ferret odour (Fisher's exact $p<0.0001$), but not for wild dog odour (Fisher's exact test $P=0.4706$). Ferret odour was detected by some stoats at a distance of >2 m, based on sudden changes in behaviour and the initiation of a *cautious approach*. Significant increases in *scanning* were observed when stoats investigated cat odour (Fisher's exact test $P=0.0072$), but not ferret (Fisher's exact test $P=0.10$), wild dog (Fisher's exact test $P=0.23$), or pungent (Fisher's exact test $P=1.00$) foraging units (Figure 3.4b).

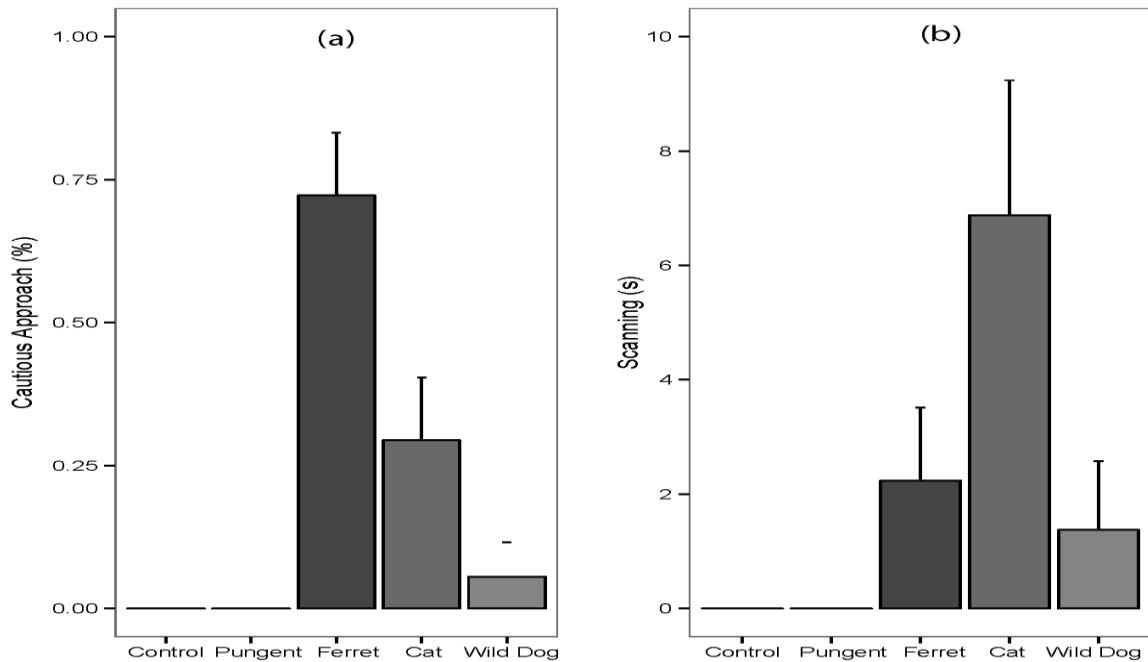


Figure 3.4 (a) *Cautious approach*: the percentage of stoats (mean \pm standard error) that displayed this behaviour when an odour was initially encountered. (b) *Scanning*: the number of seconds (mean \pm standard error) that a stoat engaged in scanning behaviour when a foraging unit was initially approached.

3.5 Discussion

Odour provoked clear behavioural responses in a subordinate carnivore, with sympatric dominant predator scent eliciting the greatest deviation from the baseline measure (non-odour control). Stoats did not avoid treated foraging areas (Prediction 1), but instead were attracted to the kairomones, carefully inspecting (Prediction 7) the odour source. Ferret odour provoked the most pronounced behavioural changes, with stoats approaching three times faster than to the second most alluring odour. This was reflected in shorter survival times of prey (Prediction 2), again in contrast to our prediction. The *time spent at foraging units* was positively correlated with the *cautious approach* response variable, and the results for this variable indicate that, contrary to Prediction 3, stoats spent more time in close proximity to

odour from sympatric predators than odour from a non-sympatric predator or the pungent odour or non-odour controls. Visits to foraging units were brief, rarely more than two minutes, which suggests time spent at one type of odour did not reduce a stoat's ability to investigate the alternative odour. In line with our prediction, risk assessment behaviour increased (Prediction 4) when stoats detected predator kairomones, with a *cautious approach* strongly associated with sympatric predators (Appendix II: S3 & S4). We expected that the stimuli of greatest risk would be avoided, but ferret odour, which was approached cautiously by 75% of stoats, was investigated for the longest duration. Stoats scanned more frequently when encountering cat odour than ferret odour (Appendix II: S4). Fear behaviours (Prediction 5) such as *freezing* or *hiding* were never observed during the trial. Reaction to predator odours may be affected by gender (Dickman & Doncaster, 1984), but there was no evidence that stoat sex (Prediction 6) influenced any behavioural responses.

The attraction displayed by stoats to the body odour of a dominant sympatric predator may at first appear counterintuitive. Stoats detected predator scent emanating from inside a foraging unit, but then undertook close inspection to verify that the depositing predator was absent. Mammals, particularly carnivores, are sometimes known to respond to odours with increased interest (Albone & Shirley, 1984), which is thought to relate to information acquisition (Hurst, 2005). Stoats are likely to have investigated the odour to evaluate the risk. Heightened vigilance presumably ensured a quick response should a threat have materialised. A 'full predator stimulus', where the dominant predator is encountered, may elicit a strong fear response whereas a 'partial stimulus' from odour may elicit uncertainty and a need to gather further information (Dielenberg & McGregor, 2001). Overestimation of the threat when dominant predator odour is encountered would have associated fitness costs. An animal behaving optimally should only respond to real threats rather than wasting energy and foraging opportunities in unnecessary flight (Kats & Dill, 1998). High metabolic rates force

stoats to forage frequently (King & Powell, 2007), and animals with high metabolism must constantly trade off the risks of starvation and predation (Higginson et al., 2012). Also, despite their diminutive size, stoats are capable of defending themselves against larger predators. If they can identify a dominant predator prior to an encounter their chances of survival increase dramatically (King & Powell, 2007).

Behavioural responses displayed in this trial are consistent with stoats using multi-modal signalling to process olfactory information and select an appropriate behavioural response. A stoat encounters a myriad of odours as it traverses the landscape, and decision making can be improved by augmenting the chemical information with evidence from additional sensory modalities (Ward & Mehner, 2010). Stoats use olfaction as their dominant sense when hunting, yet the persistence of chemical cues may lead to outdated or inaccurate information (King & Powell, 2007; Ward & Mehner, 2010). Detection of volatiles from sympatric predator odour prompted a cautious approach and prolonged investigation, but this failed to provide additional visual or auditory confirmation. With no further evidence of a threat, stoats ceased cautious behaviour, which was not subsequently displayed on any successive visits to the foraging unit.

Ferret odour provoked the most pronounced response across all variables measured, with the exception of scanning. Stoats reacted differently to cat and ferret odour, showing that they can distinguish between them and respond accordingly. Stoats may perceive cats as a greater threat above ground (so visual scanning is an appropriate response) whereas ferrets may be a greater threat below ground (where visual scanning may not be an appropriate response). This variation in response appears consistent with the threat-sensitive predator avoidance hypothesis (Helfman, 1989). Ferret odour provoked the greatest changes to baseline behaviours and yet cats, by virtue of their larger size and hunting strategies, could pose a

more serious threat to a foraging stoat. This variation in response may possibly be explained by the pungency of ferret odour, leading to more expeditious detection of the scent. Ferrets and stoats are both members of the genus *Mustela*, with comparable ecological niches. Chemicals in mustelid ventral glands may allow interspecific recognition. A study of seven mustelid species revealed that secretions of ferrets and stoats have the most complex range of chemical compounds (Brinck et al., 1983). This suggests that these species possess heightened olfactory acuity and stoats may be attracted to the complex (and possibly similar) odour emitted by a closely related species (Erlinge & Sandell, 1988). However, stoats' attraction to the odour of dominant ferrets conflicts with the avoidance displayed by weasels towards odour from dominant stoats (Erlinge & Sandell, 1988).

The attraction displayed may also relate to the source of the odour, as scent was collected from ferret body fur, a source where ventral glands are associated with scent marking in two distinct situations: after caching food and when a den site is occupied (Clapperton, 1989). Interceptive eavesdropping is known to occur between species that occupy the same trophic levels (Peake, 2005), and stoats may be attracted to the odours of a competing predator in order to locate shared resources. Scent marking was predominantly recorded in response to ferret odour and mammals may direct scent marks at both conspecifics and heterospecifics (Hughes et al., 2010). In our experiment stoats that investigated ferret odour encountered 'cached' food, which was consumed significantly faster at ferret foraging units than at other treatments. This could also explain the stronger response to ferret kairomones in comparison to those of cats. Further indirect evidence is provided by a study on wild mustelids, where nine dens were identified that were occupied sequentially by ferrets and stoats, sometimes within the same month (Dowding & Elliott, 2003). Stoats may therefore eavesdrop on ferret odour to help locate resources such as den sites, and the pronounced attraction exhibited may be a positive response towards chemical compounds of the scent, rather than any negative

connotations. Further research is required to disentangle the responses to ferret odour and to ascertain the motivation behind the apparent attraction.

In trials with tracking tunnels, track prevalence of stoats and ferrets had a significant inverse relationship (Ratz, 2000). Based on the results from our pen experiment it would appear that tunnels previously entered by a ferret were not avoided due to stoats recognising odour deposits. However, stoats avoided ferrets during visual encounters in a controlled environment (Chapter 2). This suggests that the inverse relationship between records of stoats and ferrets at tracking tunnels may be due to stoats avoiding areas where they had encountered ferrets (i.e. spatial avoidance) rather than temporal avoidance within a jointly used area (as they would be attracted to the ferret odour).

3.5.1 *Comparison with other studies*

Several previous studies report weak responses to the odour of a dangerous predator and a number of potential explanations have been proposed.

Prior experience may be necessary before anti-predator behaviours are exhibited in response to chemical cues (Griffin et al., 2001; Sih et al., 2010). Stoats used in this experiment would almost certainly have encountered both sympatric predators in the wild and had encountered both predators in an earlier foraging experiment (Chapter 2). Lack of avoidance could therefore not be ascribed to stoat naivety, as the same individuals that avoided a ferret or cat when physically present were attracted to the kairomones of these species.

Harrington et al. (2009) hypothesised that the lack of avoidance of polecat odour by mink may relate to the inability of mink to discriminate odours, although the authors concluded this scenario was unlikely. Stoats clearly discriminated between novel and sympatric predator

cues, based on their behavioural responses. Lack of avoidance was therefore not due to an inability to distinguish between familiar and unfamiliar predator odours.

The lack of avoidance by a mesopredator of dominant predator odour while foraging has been hypothesised to relate to the fitness costs of avoiding a potential food source (Ward et al., 1997). The cost of avoidance in our study was low, as foraging units were available with prey and without predator odour, but stoats preferentially consumed the food at foraging units scented with the coevolved predator odour. However, Ward et al.'s explanation could still apply if this is an evolved behaviour, as opposed to a calculated decision.

Apfelbach et al. (2005) suggested that the lack of avoidance observed in some trials may relate to the age or amount of odour utilized. Odour was collected in this trial from a number of individual donors, with cloth being in direct contact with the donor animal immediately prior to freezing. We also used a large segment of cloth to maximise the potential of the predator odour provoking a fear response (Takahashi et al., 2005). Thus, neither the age nor amount of odour probably affected behaviours exhibited by stoats in this experiment. These comparative studies all differed from the present one in that they used anal gland secretion or excreta as the predator odour source. Body odour may therefore elicit different responses.

3.5.2 *Practical applications*

Our results could have practical and commercial applications for wildlife management. Lures derived from mustelid odours have been used previously to capture pest animals. In the outer Hebrides, the scent gland of a conspecific improved capture rates of American mink (*Neovison vison*) by an order of magnitude compared to a fish-based lure (Schemnitz, 2005). In New Zealand, stoats are an invasive species and a major threat to the survival of many native animals (Clout et al., 1995; O'Donnell, 1996). Synthetic lures, derived from anal gland compounds that are common to both ferrets and stoats, have been deployed in trapping

operations and proved as effective at capturing ferrets as a food-based lure (Clapperton et al., 1994). A long-life scent lure would have a number of advantages over traps baited with food. First, stoats have colonised some areas that are difficult to access for pest control, and cost savings would accrue from the need for less frequent re-setting of traps. Cloths impregnated with ferret body odour continue to exude pungent volatiles detectable to a human for over six months (P. Garvey, personal observation), and hence might attract target animals substantially longer than fresh meat baits. Second, management of invasive mustelids often needs to deal with low predator densities resulting from *in situ* survivors of previous control operations or reinvasion of treated areas. Using a scent-based lure increases the likelihood that the few remaining animals will enter a trap. Third, mustelids become difficult to trap with meat or egg baits when alternative food is readily available. Under these conditions – such as in an invasion scenario on a mammal-free island – a scent-based lure that is not related to food may improve the effectiveness of a trapping programme.

3.6 Acknowledgements

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3.6.1 Ethical standards

Pen trials were carried out within all the necessary guidelines and were in accordance with the relevant animal welfare regulations. We received ethical clearance from the Landcare Research Animal Ethics Committee (AEC approval number 12/06/01). The authors declare that they have no conflict of interest.

CHAPTER 4 Exploiting interspecific olfactory communication to monitor predators



Publication status: Submitted

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4.1 Abstract

Mesopredators may exploit olfactory cues left by dominant predators to facilitate co-existence. These chemical cues can act as repellents or attractants and may therefore have applications for wildlife management. A field experiment was devised to investigate whether dominant predator (ferret *Mustela furo*) body odour would alter the behaviour of three common invasive mesopredators: stoats (*M. erminea*), hedgehogs (*Erinaceus europaeus*), and ship rats (*Rattus rattus*). We predicted that the addition of apex predator odour would lead to increased detections and results support the hypothesis that kairomones (chemical cues from a predator) would provoke ‘eavesdropping’ by mesopredators. Stoats exhibited the most pronounced responses, increasing engagement with monitoring devices, so that their occupancy estimates changed from rare to widespread. A long-life lure derived from apex predator pheromones could have practical value, especially when there are plentiful resources that reduce the efficiency of food-based lures for a subordinate predator. These results have application for pest management in New Zealand and conservation efforts in other parts of the world.

4.2 Introduction

Apex predators shape and drive community structure, either directly through agonistic encounters or indirectly as mesopredators alter their behaviour in response to predation risk (Ritchie & Johnson, 2009). Natural selection will encourage the development of mechanisms for subordinate species to recognise dominant predators and avoid confrontations (Kats & Dill, 1998; Monclús et al., 2005). Olfaction, the primary foraging sense of most mammals, may mediate trophic interactions by allowing subordinate species to assess the risk of encounter (Roberts & Gosling, 2001). Predators deposit odour into the environment, either deliberately for communication or unintentionally as by-products of metabolic processes (Ferrari & Chivers, 2009; Wyatt, 2010). These odours, termed ‘kairomones’, are primarily produced for intraspecific communication but are also available to “eavesdropping” sympatric species, increasing the receivers’ fitness relative to the depositing species (Ferrari & Chivers, 2009; Peake, 2005). For example, temporal variation in scent quality can indicate the time elapsed since an odour was deposited (Bytheway et al., 2013) or odour can facilitate predator identification, which may then be related to the risk of encountering this predator (Schoeppner & Relyea, 2009). Kairomones may additionally supply guild members with information about shared resources or reveal a location where a competitor has recently foraged (Hughes et al., 2010; van Dijk et al., 2008). Unlike visual or auditory cues, odour deposits indicate that a location was risky at some point in the past, but this may not relate to present risk (Kats & Dill, 1998). Therefore odours can be ambiguous and require careful inspection to elicit all the information contained in a scent (Hemmi & Pfeil, 2010).

Mammalian chemical communication has been exploited for a range of wildlife management applications: to reduce human-wildlife conflicts, improve population monitoring, influence habitat selection, reduce predation, increase the welfare of captive animals, encourage captive

breeding, and to improve the success of release programmes (Campbell-Palmer & Rosell, 2011). Olfactory attractants are primarily food based, but occasionally non-prey pheromone lures such as beaver (*Castor canadensis*) castoreum or muskrat (*Ondatra zibethicus*) scent glands are deployed to attract target species (Long et al., 2012). Intraspecific (pheromones) lures, that stimulate territorial or social responses in conspecifics, have been deployed for wildlife management; for example, lures derived from the scent gland of culled American mink (*Mustela vison*), an alien species in Europe, were used to attract mink to traps and proved as successful as a food based lure during control operations (Roy et al., 2006). Interactions between predator and prey have also been exploited to create deterrents, as predator odour may induce avoidance behaviours, reducing foraging damage by prey species (Apfelbach et al., 2005). Lures have yet to be developed that exploit interspecific communication between carnivores.

New Zealand has one of the highest proportions of threatened taxa in the world, a trend primarily driven by introduced invasive species (Clout, 2001; Towns et al., 2006). Island faunas are particularly vulnerable to extinction, as many evolved in the absence of mammals and therefore lack appropriate defensive mechanisms to avoid predation. New Zealand's mammalian carnivores were introduced in the hope that they would act as biological control agents for pests such as rabbits (*Oryctolagus cuniculus*) but, as generalist predators, they attack vulnerable native species as well as introduced mammals (King & Powell, 2007; Wallach et al., 2015b; Wodzicki, 1950). Trophic interactions also occur within this novel invasive predator guild, influencing behaviour through interference competition, which will in turn cascade to lower trophic levels (Chapter 2). Since sympatric predator odour is likely to provoke a response in these mesopredators there may be an opportunity to exploit olfactory communication to improve wildlife management outcomes.

Laboratory and field experiments on a range of different taxa have predominantly found that predator odour provokes anti-predator responses, often leading to avoidance by the subordinate species (Apfelbach et al., 2005; Monclús et al., 2005). However, in pen trials stoats were attracted to apex predator odours, with ferret body odour provoking the most marked response (Chapter 3). We devised a field experiment to test whether ferret (*M. furo*) odour would alter the behaviour and detection rates of three of New Zealand's most common invasive mesopredators: stoats (*M. erminea*), hedgehogs (*Erinaceus europaeus*), and ship rats (*Rattus rattus*). Hedgehogs and rats are important prey items for ferrets, while ferrets dominate stoats in interspecific encounters and are known to kill the smaller mustelid (Smith et al., 1995; Wodzicki, 1950). Common prey consumed by these four invasive species include: invertebrates, small mammals, reptiles, amphibians, and the eggs of ground nesting birds (Jones et al., 2005; Murphy & Dowding, 1994; Smith et al., 1995; Wodzicki, 1950). Additionally, stoats compete with ferrets for lagomorph, rodent and avian prey (King & Powell, 2007). Although these species form novel invasive guilds in New Zealand they are sympatric in parts of their native northern hemisphere range, which is important as evolutionary history is thought to influence the intensity of interactions (Connell, 1983).

We examined how ferret odour affected detectability and activity of the three mesopredator species. We predicted that ferret kairomones would provoke eavesdropping behaviour in mesopredators as measured by: (1) increased detections at monitoring sites (i.e. site occupancy), (2) increased total number of observations across all monitoring sites, and (3) increased activity (measured as time spent investigating a lure). We anticipated that mesopredators (4) would approach the ferret odour before approaching a food-based lure at a monitoring site, and that (5) ferret odour would remain attractive for longer than a food-based lure. In the field experiment, deer (*Cervus* spp.) served as a procedural “control”, as detections of this large herbivore should be unaffected by ferret odour. We predicted that deer

would (6) show no change in occupancy, number of observations or activity in response to ferret odour.

4.3 Methods

4.3.1 Study location

This study was conducted on Toronui station, a sheep and cattle farm in the Hawke's Bay region of the North Island, New Zealand ($39^{\circ} 10' S$, $176^{\circ} 46' E$). The landscape is dominated by pasture, with patches of forest consisting of mixed broadleaf angiosperm species at lower elevations and mānuka (*Leptospermum scoparium*) and kānuka (*Kunzea robusta*) at higher elevations. There was no recent history of predator control at this site.

The study ran for 64 days, from January to March 2014. Twenty camera monitoring sites were established within and adjacent to forest patches ≥ 50 ha. Average distance between sites was 2.44 km, with a minimum distance of 700 m, to maintain spatial independence and to ensure that olfactory responses at a monitoring site were unlikely to be biased by other sites. Fourteen sites were established at the forest/pasture margin and a further six sites were placed within a forest patch. Forest margins are known to be used extensively by cryptic predatory species (Morris & Davidson, 2000), so these areas were selected to maximise the likelihood of detection.

4.3.2 Study species

In New Zealand, ferrets are the second largest terrestrial predator after feral cats (*Felis catus*) and the largest of the three introduced mustelid species (Wodzicki, 1950). Ferrets predominantly use olfaction to communicate, depositing enduring odours that mediate social behaviour, proclaim territorial boundaries and signal reproductive receptiveness (Clapperton, 1989). Chemicals secreted from glands on the chin and neck are deliberately rubbed onto

surfaces, often when caching food or after a new den site has been established (Clapperton, 1989). Ventral glands are present in all mustelids (Macdonald, 1985) and odour volatiles designed to convey detailed information to conspecifics about the owner's social, reproductive, and health status that can be relayed to the receiver (Hughes et al., 2010).

Stoats are a highly successful invasive predator, designated as one of the world's 100 worst invasive species (Lowe et al., 2000). They occur predominantly in forests, but also in grassland, and are one of the primary agents of decline for over half of all forest birds currently threatened in New Zealand (Innes et al., 2010; King & Powell, 2007). Stoat populations can fluctuate due to resource pulses of prey, making them elusive when at low densities in certain environments, seasons or in particular years (King & Powell, 2007). They have keen olfactory senses that are employed to track prey, and for intraspecific communication (Erlinge & Sandell, 1988).

Hedgehogs were introduced primarily to help reduce garden pests, but have become major pests themselves, preying on native insects, reptiles and the eggs/fledglings of ground nesting birds (Jones et al., 2005). Introduced onto offshore islands in the UK, hedgehog predation resulted in dramatic declines in wading birds (Jackson & Green, 2000). Hedgehogs are found across a range of habitats and primarily employ olfaction while foraging for food (Wodzicki, 1950).

Ship rats arrived as stowaways on ships and have successfully invaded many islands worldwide, including those of New Zealand (Innes, 2005). They are generalist foragers and are associated with extinctions or declines of numerous indigenous species including reptiles, flightless invertebrates, burrowing seabirds and passerines (Towns et al., 2006).

Home range sizes (male-female) for pasture and native bush vary considerably among these three mesopredators in New Zealand: stoats, 145-75 ha; hedgehogs, 9.6-4.2 ha; and ship rats,

3.76-1.06 ha (Innes, 2005; Jones & Sanders, 2005; King & Murphy, 2005). The size of a species' home range is an important consideration when deciding on the spacing of monitoring sites (Rovero & Marshall, 2009). Smith et al. (2015) recommended a spacing of <700 m to ensure a control device is encountered by a female stoat. Because stoats have the largest home ranges of the 3 mesopredators, we set the spacing of monitoring sites at a minimum of 1 km to minimise multiple recordings of the same individuals, although two sites were just over 700 m apart due to logistical constraints.

4.3.3 *Ferret odour*

Body odour from captive ferrets was collected by placing a clean towel in their bedding area, where it would be in direct contact with the donor animal. Predator body odour has stronger endocrine and behavioural effects on prey than other odours such as urine or faeces, as it may indicate a high likelihood that the predator is nearby (Apfelbach et al., 2005). Male ferrets were selected as donor animals as male body odour is more pungent due to greater concentrations of an aromatic compound (indole), and males are a greater threat to mesopredators by virtue of their size (Clapperton et al., 1988). Towels were placed in the bedding area of individual ferrets for one month to ensure the material was thoroughly impregnated with odour. Towels were inspected to remove any excreta before being cut into 15-cm² segments and stored in a freezer (-80° C) until required, up to a maximum duration of 2 months.

Ferret odour was tested alongside rabbit meat, which is the standard lure used for carnivores in New Zealand (Pierce et al., 2007; Wodzicki, 1950), to assess whether it could improve the detection rate of mesopredators. A previous pen trial had tested stoats' response to three odour treatments: rabbit meat, ferret odour, and rabbit meat + ferret odour combined (Grant Morriss unpublished data). The rabbit meat + ferret odour combination provoked the greatest

attraction for stoats, so we compared this combination against rabbit meat in the field study. Comparing various bait types for stoats, Pierce et al. (2007) found that fresh rabbit meat was the most effective. Rabbit meat typically remains in traps for periods ranging from 1-3 weeks, but this can be extended for up to several months where site access is constrained (McMurtrie et al., 2011).

Perforated plastic vials were used to allow odour volatiles to disperse while preventing removal of the lure. Each vial (9 cm x 3 cm) was drilled with ~50 holes that were 5 mm in diameter. Two vials were used at each monitoring site, one placed at the base of a steel post, with the second placed 20 cm from the base, enabling us to distinguish between approaches to a specific container. Vials were secured to the ground using pegs to ensure that the camera remained trained on the container. The standard size of a vial was used as a reference to estimate the head–body–tail length of *Rattus* spp., which facilitates identification. We randomly deployed one of two possible treatments at each site. For the first treatment one vial received a portion of rabbit meat (3 g), while the second vial remained empty. For the second treatment, rabbit meat was again added to one vial, but the second vial contained 10 cm of towel that had been impregnated with ferret body odour. Each treatment was deployed at half the sites for the first 32 days, and rotated across sites for the second 32-day period, which ensured all sites received each treatment over the study.

4.3.4 Camera trapping

A total of 40 infrared cameras, triggered by heat and/or motion, were deployed for the study. Cameras were placed in pairs (matched by model type) at each monitoring site, one mounted horizontally and one vertically. Four types of cameras were used: Reconyx Hyperfire PC 900 (26) (Reconyx Inc, Holmen, Wisconsin), LTL Acorn Ltl 5210A (10) (Shenzen LTL Acorn Eletronics Co., Ltd), Moultrie M990i (2) (Moultrie, New Zealand) and Bushnell (2)

(Bushnell Outdoor products, Overland Park, KS). Detection efficiency may vary between models (Glen et al., 2013), but cameras were assigned to a monitoring site for the entire study, to ensure consistency across treatments.

The optimum orientation when photographing small mammals depends on the target species, although the most suitable orientation has even been shown to vary between studies on the same species (Smith & Coulson, 2012; Taylor et al., 2014). We therefore evaluated two orientations and decided *a posteriori* on the optimum configuration for our target mesopredators. Vertical cameras were mounted on a steel post, facing downwards from 1.5 m above the ground, with the vials placed in the centre of the field of view. Horizontal cameras were mounted on timber stakes 1.5 m away from the base of the steel post. These cameras were mounted 5 cm above ground level, which is approximately the shoulder height of the target mesopredators. All cameras had identical settings, or as close as possible where slight variations existed between models: high sensitivity, 3 photographs per trigger and no delay between triggers. Vegetation was removed to allow for an unobstructed field of view and to minimise false triggers. Camera batteries and memory cards were replaced after the first month. Meta data (date, time, location) were extracted from the images using R v. 2.14.1 (R Core Team, 2011); the function designed for this process, and associated information is provided in supporting material (Appendix III: S1).

4.3.5 *Data recording and analysis*

Cameras that were oriented horizontally documented the greatest number of species, both in terms of observations (independent record of an individual) and total number of photographs, while also having the fewest photographs with no animal in the field of view. We therefore preferentially chose this orientation at all sites, with the vertical orientation only selected when the horizontal camera was out of commission. If cameras mounted vertically had to be

used, this orientation was matched for both treatments at a monitoring site. We considered the selected camera at each monitoring site to be an independent sampling unit.

Data were analysed for differences in observations or behaviour of the target mesopredators, following the addition of ferret odour. To distinguish photographs of separate animals from repeated photographs of the same individual we plotted histograms of the time elapsed between consecutive photographs for each species (Brook et al., 2012). Most consecutive photographs of the same species occurred <5 minutes apart, suggesting that these were repeated detections of an individual during one visit to the monitoring site. We considered records of a species to be independent at a monitoring site if they were separated by more than 30 minutes, unless individuals could be distinguished. The following variables were calculated: (1) observation rate, (2) triggers per observation, (3) site occupancy and (4) observations per period. *Observation rate* was defined as the number of observations per 100 trap days (1 trap day = 1 camera trap set for 24 h) (Glen et al., 2014; Rovero & Marshall, 2009). Cameras were set to record in bursts of three photographs each time they detected motion; we refer to each burst with at least one image of an animal as a trigger. *Triggers per observation*, an index of a species activity within the camera's field of view, were calculated at each monitoring site: number of camera triggers divided by number of independent observations. *Site occupancy* is a binary response variable with 1 indicating a species was detected at the monitoring site at least once during the study, and 0 indicating non-detection. Occupancy models that explicitly account for imperfect detection provide an index of abundance for species without identifiable markings (Meek et al., 2014). *Site occupancy* was used as the binomial presence/absence measure where there were sufficient detections (MacKenzie, 2006). Monitoring periods were divided into intervals of 5 days and we ran a single species single season model framework to estimate occupancy in the software package PRESENCE 9.0 (Hines, 2006). We also divided the 32-day treatment period into four

intervals of eight days. An eight-day interval is comparable to the weekly re-baiting protocol used for most trapping operations (e.g. McMurtrie et al., 2011) and this enabled us to analyse change over an operational time scale. *Observations per period* are the independent observations in each period of eight days for each species, and cameras active for shorter durations were excluded from the analysis.

Behaviours recorded that may help to explain mesopredator responses to dominant predator odour include; cautious approach, scent marking, contact sniffing, self-anointing and biting of a lure vial. We were able to categorise these behaviours from images as they each had distinct, recognisable, body movements. Cautious approach was assessed by the mesopredator's body posture on its initial approach and also by the time taken for the individual to reach the vial after triggering the camera. Contact sniffing was defined as touching a vial with the nose or tongue. Self-anointing behaviour is defined as an animal spreading its odour through its pelage by licking, which may act as a deterrent to predators (Weldon, 2004).

We analysed the effect of the ferret odour using generalized linear mixed models (GLMM), from the MASS package in R (Venables & Ripley, 2002), which enabled us to assess the influence of fixed and random effects. The response variables for the analysis were *observation rate* and *triggers per observation*. A Poisson error distribution was selected as we had continuous count data (Venables & Ripley, 2002). The fixed effect included in the model was 'treatment' (rabbit only or rabbit + ferret) and 'site' was entered as a random effect, to account for the non-independence of errors associated with repeated measures on the same monitoring site. Models were assessed by plotting the residuals and testing for overdispersion and significance levels are reported at $p<0.05$. Where results of the GLMM revealed significant treatment effects we constructed additional species models for the four 8-

day time periods, with the response variables *observations per period* and *triggers per observation*, to assess each period's contribution to the significant result. Differences in mesopredator *site occupancy* and the additional behavioural measures (cautious approach, etc.) were assessed using Fisher's exact test. All statistical analyses were performed in the R environment (version 2.14.1, R Development Core Team, 2015).

4.4 Results

4.4.1 Camera trapping effort

Sampling effort totalled 1,834 trap days for the 20 paired cameras, when both orientations were included. Two monitoring sites were removed from the analysis, one due to cattle disturbance and a second due to flooding. With the horizontal camera preferentially selected, there were 1,090 trap-days for analysis.

4.4.2 Observation rate and observations per period

Collectively across all sites there were 465 independent observations of the three mesopredators: 288 with the ferret odour and 177 without, a 63% overall increase with the addition of the kairomone (Table 4.1). There was a corresponding increase in the overall *observation rate* for all three mesopredators. Also the number of mesopredator *observations per period* was greater with the addition of the ferret odour, and these differences were significant in periods 3 & 4 (Figure 4.1)

Table 4.1 Summary of sampling effort and camera trapping results for the response of mesopredators (stoat, hedgehog and ship rat) to the body odour of a dominant predator (ferret). The definitions of *trigger*, *observation* and *observation rate* are given in the text. Statistical significance for differences between treatments is indicated for $p < 0.01$ (*), $p < 0.001$ (**), and $p < 0.0001$ (***)�.

Species	Cameras set (functioning)	Camera days (mean)	Cameras with at least one detection	Total number of triggers	Total number of observations	Observation rate
<u>Treatment – Rabbit</u>						
Stoat	20 (19)	566 (29.78)	4	26	7	1.41
Hedgehog	20 (19)	566 (29.78)	17	318	95	16.78
Rat	20 (19)	566 (29.78)	13	258	74	13.07
Deer	20 (19)	566 (29.78)	6	86	26	4.59
<u>Treatment - Rabbit + Ferret</u>						
Stoat	20 (19)	524 (27.57)	11	155	28	5.34***
Hedgehog	20 (19)	524 (27.57)	16	856	162	30.92*
Rat	20 (19)	524 (27.57)	13	281	98	18.7
Deer	20 (19)	524 (27.57)	7	97	28	5.34

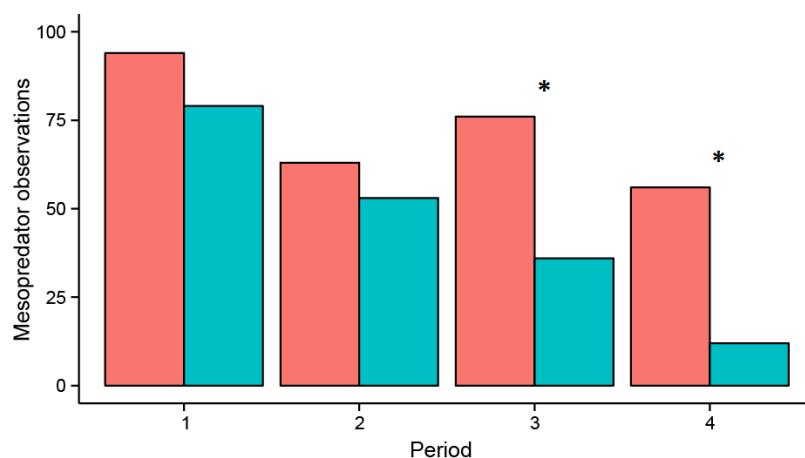


Figure 4.1 Mesopredator (cat/ stoat/ rat) observations per period for each of the four 8-day time periods. Treatments are represented by red bar (rabbit + ferret) and blue bar (rabbit). Asterisks denote a significant difference between treatments at ($p < 0.05$).

Most observations were of hedgehogs (55%), followed by rats (37%) and stoats (8%). There was a significant increase in stoat and hedgehog *observation rates* with the addition of ferret odour (Figure 4.2, Table 4.2). Stoats made up 10% of observations with rabbit + ferret odour and 5% with rabbit meat only. Treatment type did not significantly influence the number of observations or the *observation rates* for rats or deer (Figure 4.2, Table 4.1). Stoat *observations per period* were higher at sites with ferret odour than those without, and there was a particularly marked difference after the first period (Table 4.3). Significant increases were also recorded for the hedgehog *observation rate*, with the deviation most pronounced in the 3rd and 4th period (Table 4.3).

Table 4.2 GLMM results for responses by mesopredators to ferret odour based on: *observation rate* and *triggers per observation*. Statistical significance for differences between treatments is indicated for $p < 0.01$ (*), $p < 0.001$ (**), and $p < 0.0001$ (***)�.

Source of variation	Value	SE	df	t value	p value
Observation rate (model: GLMM – Poisson distribution)					
<u>Stoat</u>					
Treatment (Rabbit or Rabbit+Ferret)	1.46	0.27	18	5.34	<0.0001***
<u>Hedgehog</u>					
Treatment (Rabbit or Rabbit+Ferret)	0.57	0.21	18	2.7	0.0158
<u>Rat</u>					
Treatment (Rabbit or Rabbit+Ferret)	0.22	0.2	18	0.83	0.29
<u>Deer</u>					
Treatment (Rabbit or Rabbit+Ferret)	0.15	0.35	18	0.44	0.66
Triggers per observation (model: GLMM - Poisson distribution)					
<u>Stoat</u>					
Treatment (Rabbit or Rabbit+Ferret)	1.1	0.49	18	2.23	0.0397
<u>Hedgehog</u>					
Treatment (Rabbit or Rabbit+Ferret)	0.81	0.28	18	2.94	0.0091*
<u>Rat</u>					
Treatment (Rabbit or Rabbit+Ferret)	0.32	0.26	18	0.51	0.62
<u>Deer</u>					
Treatment (Rabbit or Rabbit+Ferret)	0.37	0.24	18	1.53	0.14

Table 4.3 GLMM results for total observations, *observations per period* and *triggers per observation* for stoats and hedgehogs in each period. These two species displayed significant treatment effects (Table 4.2). Statistical significance for differences between treatments is indicated for $p < 0.01$ (*), $p < 0.001$ (**), and $p < 0.0001$ (***)�.

Source of variation	Value	SE	df	t value	p value
<u>Total mesopredator observations (Poisson)</u>					
Period 1 (Rabbit vs Ferret + Rabbit)	0.17	0.2	17	0.85	0.41
Period 2 (Rabbit vs Ferret + Rabbit)	0.2	0.32	16	0.65	0.52
Period 3 (Rabbit vs Ferret + Rabbit)	0.82	0.23	15	3.61	0.0025*
Period 4 (Rabbit vs Ferret + Rabbit)	1.67	0.41	8	4.06	0.0036*
<u>Stoat observation per period (Poisson)</u>					
Period 1 (Rabbit vs Ferret + Rabbit)	0.61	0.49	17	2.05	0.06
Period 2 (Rabbit vs Ferret + Rabbit)	20.07	0.28	16	411.98	<0.0001***
Period 3 (Rabbit vs Ferret + Rabbit)	1.86	0.8	15	2.32	0.0348
Period 4 (Rabbit vs Ferret + Rabbit)	26.07	0.151	8	171.52	<0.0001***
<u>Hedgehog observation per period (Poisson)</u>					
Period 1 (Rabbit vs Ferret + Rabbit)	0.18	0.26	17	0.68	0.5
Period 2 (Rabbit vs Ferret + Rabbit)	0.33	0.28	16	1.17	0.26
Period 3 (Rabbit vs Ferret + Rabbit)	0.95	0.34	15	2.74	0.015
Period 4 (Rabbit vs Ferret + Rabbit)	1.1	0.048	8	2.22	0.056
<u>Stoat triggers per observation (Poisson)</u>					
Period 1 (Rabbit vs Ferret + Rabbit)	0.88	0.48	17	2.42	0.027
Period 2 (Rabbit vs Ferret + Rabbit)	21.24	0.37	16	450.38	0
Period 3 (Rabbit vs Ferret + Rabbit)	2.19	0.41	15	2.48	0.026
Period 4 (Rabbit vs Ferret + Rabbit)	27.49	0.98	8	3475	0
<u>Hedgehog triggers per observation (Poisson)</u>					
Period 1 (Rabbit vs Ferret + Rabbit)	0.94	0.34	17	2.74	0.015
Period 2 (Rabbit vs Ferret + Rabbit)	2	0.43	16	4.66	0.0003**
Period 3 (Rabbit vs Ferret + Rabbit)	0.47	0.34	15	1.38	0.18
Period 4 (Rabbit vs Ferret + Rabbit)	0.43	0.43	8	1	0.34

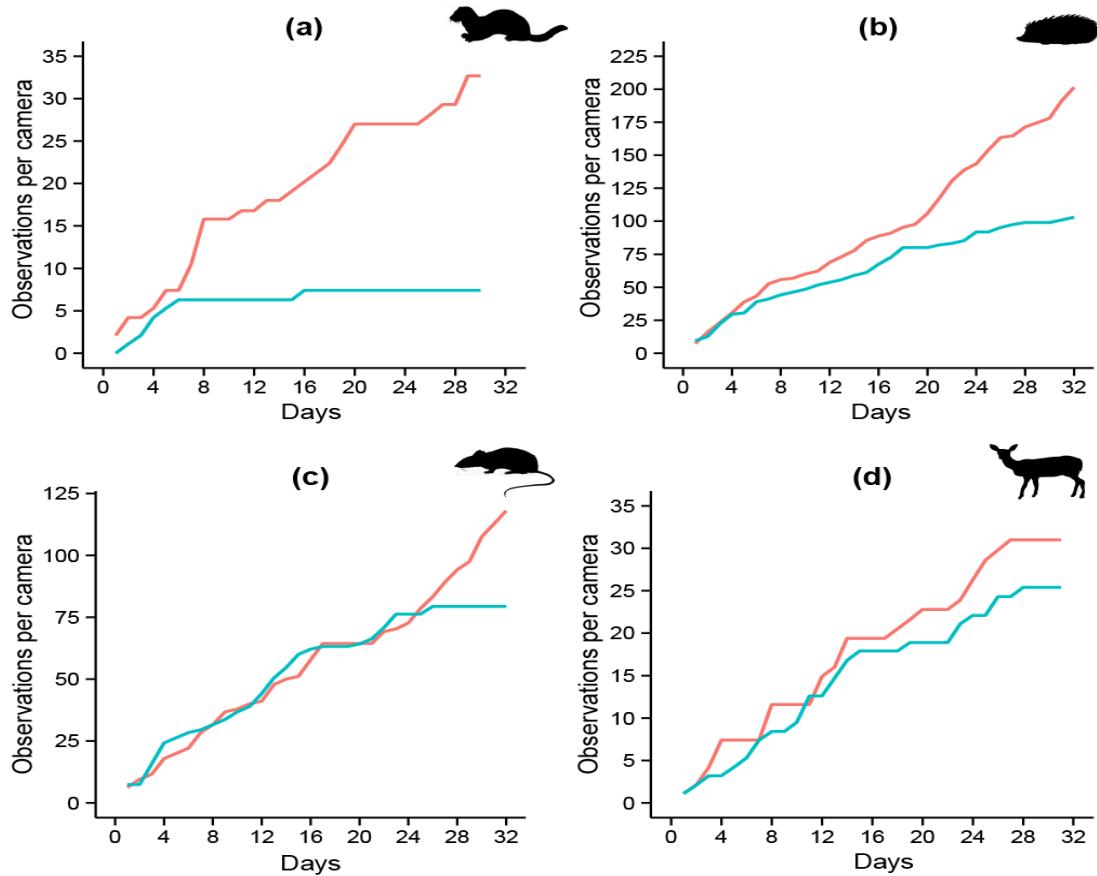


Figure 4.2 Cumulative observations per active camera, recorded over the 32-day treatment period for (a) stoat, (b) hedgehog, (c) rat, and (d) deer. Treatments are represented by red line (rabbit + ferret) and blue line (rabbit).

4.4.3 Triggers per observation

There were 6,861 photographs taken of the target mesopredators, 4,744 with the ferret and rabbit combination and 2,117 with rabbit only, an overall increase of 124% with the addition of the ferret odour. The most photographed mesopredators were hedgehogs (71%), followed by rats (22%) and then stoats (7%). For both stoats and hedgehogs, *triggers per observation* were significantly higher with the addition of the ferret odour: for stoats this occurred in all four monitoring periods, and for hedgehogs in the 1st and 2nd period (Table 4.3, Figure 4.3). Rats had fewer *triggers per observation* with the lure in period 1, but there were no differences in subsequent periods (Figure 4.3).

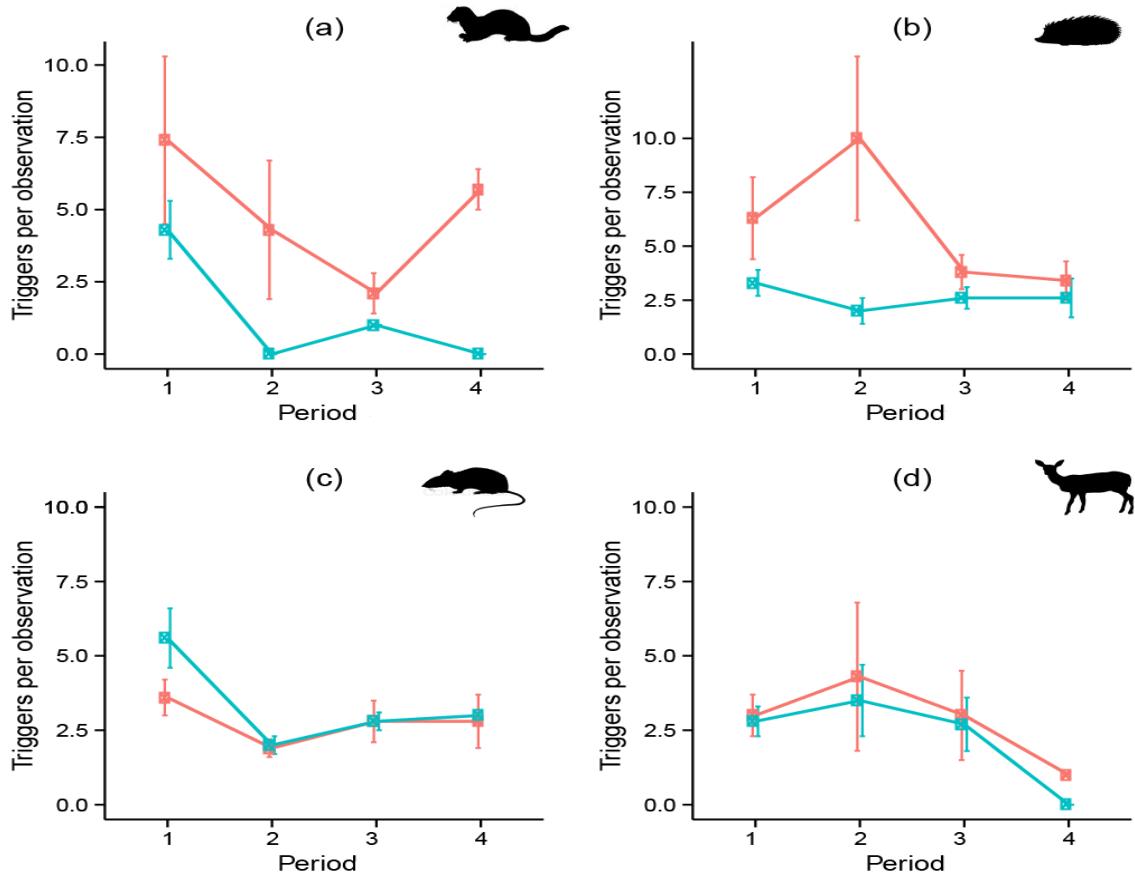


Figure 4.3 Mean \pm SE (error bars) *triggers per observation* for the four time periods for (a) stoat, (b) hedgehog, (c) rat, and (d) deer. Treatments are represented by red line (rabbit + ferret) and blue line (rabbit).

4.4.4 Site occupancy

Fisher's exact test showed a significant increase ($P = 0.04$) in the number of sites where stoats were detected using rabbit + ferret odour, as compared to rabbit only. There was no difference in the number of sites with detections of hedgehogs ($P = 0.65$), rats ($P = 0.95$) or deer ($P = 0.93$). Stoats were detected at 11 of 19 sites with the ferret odour, yielding a naïve site occupancy estimate of 58% (Figure 4.4). Using rabbit meat only, stoats were detected at 4 of 19 sites (21%) (Appendix III: S2).

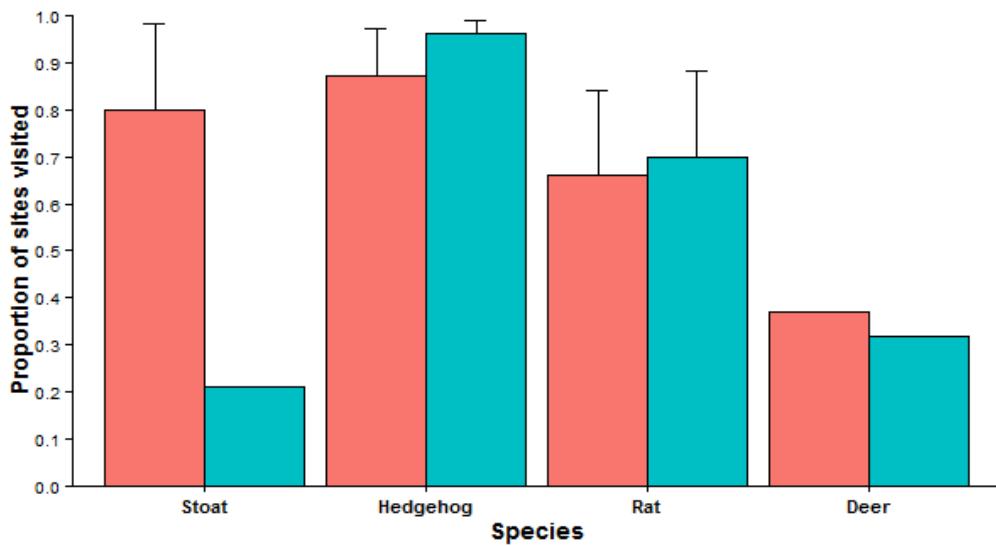


Figure 4.4 Occupancy estimates ($\pm 95\%$ CI) and naïve occupancy rates (no error bars) for the three target mesopredators and the procedural control (deer). Treatments are represented by red bar (rabbit + ferret) and blue bar (rabbit).

4.4.5 Mesopredator behaviour

In instances where the treatment employed was lure and rabbit, we recorded 20 occasions where a stoat made contact with a lure vial on its first approach. The vial containing ferret odour was contacted on 15 of these occasions, whereas the rabbit meat lure was contacted on 5 occasions. There were 5 instances where stoats cautiously approached the ferret odour vial, yet similar slow deliberate movements were never recorded when rabbit meat was the sole lure. Scent marking, when the treatment was lure and rabbit, was observed on 6 occasions, once by body rubbing with the head/neck and otherwise by anal drag (Appendix III: S3). Scent marking was not observed when rabbit meat was the only lure.

Hedgehogs engaged with the ferret lure for greater durations than any other mesopredator, repeatedly circling the vial. Self-anointing was recorded on 33 occasions at monitoring sites

with ferret odour, but never with the rabbit meat treatment. This behaviour appears not to be age-specific as it was recorded for hedgehogs of all sizes (Appendix III: S4).

Rats attempted to bite into the vial containing ferret lure on nine occasions; this behaviour was only recorded for vials with ferret odour (Appendix III: S5).

4.5 Discussion

Our results support the prediction that kairomones from an apex predator should provoke eavesdropping by mesopredators, increasing detections for all species (although the increase was not significant for rats). Ferret pheromones remained attractive for the duration of the experiment whereas rabbit lure appeared to lose attraction for stoats after 1 week. Apex predator kairomone was engaged by hedgehogs for shorter durations as its freshness diminished, while stoats continued to maintain their interest in the latter stages of the trial. Inspection of aged predator cues is a relatively low-cost activity, but the quality of information available in a scent recedes as the freshness declines (Bytheway et al., 2013). The most marked responses to ferret odour were discerned for stoats. Stoat observations increased six-fold, their estimated *site occupancy* changed from rare to widespread, and stoats engaged with the ferret odour lure for substantially longer than a rabbit meat lure. Hedgehogs also approached lures containing ferret odour more frequently and for longer periods than lures with rabbit, while rats displayed slight aversion to the fresh kairomone, with observations increasing only in the final period. These results concur with other field trials where predator odour failed to elicit a strong response in rats (e.g. Banks, 1998).

Chemical cues make an uncertain world more predictable and olfaction is particularly important for species that are solitary, inhabit complex habitats or are nocturnal (Kats & Dill, 1998). When prey encounter predator scent, avoidance may be the optimum defence, and this behaviour is frequently reported (e.g. Dickman & Doncaster, 1984; Jędrzejewski et al., 1993).

However, mesopredators, particularly highly mobile species, encounter a myriad of chemical cues that potentially provide a rich source of information (Bytheway et al., 2013). Careful evaluation of a kairomone is needed to determine the direction in which a predator travelled, which can be assessed by variation in odour intensity along a scent trail. Informed prey are more difficult to capture and as stoats and hedgehogs are predominantly solitary foragers, these species should gain greater benefit from eavesdropping than gregarious species that can be warned by conspecifics (Ridley et al., 2014). However, inspection behaviour is not without risk as the predator may remain in the vicinity. The persistence of this behaviour suggests it provides fitness benefits for the eavesdropping species.

Close approach to the predator odour may be necessary to activate the appropriate olfactory receptors. The vomeronasal organ, which is a chemoreceptor, detects non-volatile compounds and requires direct physical contact with the source (Papes et al., 2010). Mesopredators may approach the predator scent to assess non-volatile compounds encoded in the chemosignal. This need for direct contact suggests that predator odour could be an effective lure, as it increases the likelihood of a target species interacting with a camera trap or control device.

4.5.1 Can mechanisms apart from mitigating predation risk explain observed behaviours?

Animals co-exist in assemblages of closely-related species that often use similar communication systems (Hughes et al., 2010), facilitating the possibility of bidirectional olfactory communication. Stoats and polecats (*M. putorius*), species that are naturally sympatric in Europe, display commonalities in gland secretions and may have evolved communication networks that allow for information exchange (Brinck et al., 1983; Erlinge & Sandell, 1988; King & Powell, 2007). Counter-marking by stoats was observed on several occasions in close proximity to the pheromone vial and this behaviour is difficult to explain if the subordinate species wished to remain inconspicuous. Encounters between members of the

same guild are dangerous as potential gains are unknown and the risks of a confrontation are great (Hutchings & White, 2000). Interspecific olfactory communication may diminish these risks by providing knowledge of a competitor without requiring a direct interaction.

Mesopredators may be attracted to dominant predator odour to locate prey, carrion or den sites, as eavesdropping for resources occurs between species that occupy the same trophic levels (Peake, 2005; van Dijk et al., 2008). Stoats do not make their own dens, but use those of other animals (King & Murphy, 2005) and may eavesdrop on ferret scent to help locate appropriate sites. In support of the resource acquisition hypothesis, one study that radio-tracked mustelids recorded nine occasions where dens were shared sequentially by both ferrets and stoats (Dowding & Elliott, 2003). Scavenging for food may also potentially explain attraction to kairomones, as stoats, hedgehogs and rats may associate aging ferret odour with the possibility of locating the partial remains of prey.

Our study fell within the breeding season of hedgehogs in New Zealand (Jones & Sanders, 2005) and the attraction displayed by hedgehogs, i.e. repeatedly circling the pheromone vial, is a behaviour that appears very similar to the ‘cartwheeling’ performed by males during courtship (Jones & Sanders, 2005). Hedgehogs were also photographed self-anointing on more than 30 occasions: they are known to self-anoint with a range of novel, strong smelling or toxic substances. The basis of this behaviour is unknown; it may act as a deterrent to predators or alternatively self-anointing may play a role in mating behaviour (Jones & Sanders, 2005; Weldon, 2004).

4.5.2 *Management applications*

Responses to a dominant predator odour, such as increased attraction and engagement, can be exploited to improve conservation outcomes and the reliability of monitoring information. A major challenge for controlling invasive species is monitoring populations at low densities.

Exotic species that decline after intervention, or invade new ecosystems, are acutely aware of established competitors and conspecifics (Pyšek & Richardson, 2010). New Zealand's pest-free islands are important refuges for native animals and a kairomone lure could be deployed for long term monitoring and interception. For example, a stoat that invaded Kapiti Island, 5km off the coast of New Zealand, proved extremely difficult to locate and expensive to remove (Prada et al., 2014). Eventually, after an extensive operation, the stoat and its offspring were captured, with the sole male offspring entering a trap that was treated with the pheromones of a female stoat. Reduction in intra- and interspecific competition in managed ecosystems leads to greater resource availability and a non-food based attractant would be advantageous in these situations (Glen et al., 2013). Stoats are extremely difficult to detect at low densities (Choquenot et al., 2001) and monitoring in this study using only a rabbit lure would have substantially underestimated their prevalence. When eradicating an invasive population, it is essential to put all animals at risk and variability between members of a population leads to inconsistent responses to chemical signals (Réale et al., 2007). Costs of eliminating the last few survivors may be disproportionately high (Nugent et al., 2007) so increasing the range of lures may improve capture rates, thereby ameliorating the costs of mop-up operations. In addition to the management of invasive species, animals are also live-trapped for translocation, to collect biological samples, and to fit monitoring devices. The scent of a dominant competitor may always be worth investigating, so a kairomone lure could function effectively in these situations.

Camera traps are being used increasingly in wildlife monitoring, and can operate for extensive periods (Meek et al., 2014); however, most scent lures do not remain attractive for such long periods. This incongruence between camera capabilities and lure viability may lead to inefficient monitoring devices or require labour-intensive refreshing of lures. Ferret pheromones have evolved to endure in the environment to maximise the probability of

interception (Clapperton, 1989), making pheromones an ideal natural long-life lure. Camera traps can also help assess wildlife populations by identifying naturally marked animals, a powerful nonintrusive technique requiring clear images to distinguish among individuals (Trolle & Kéry, 2003). Increasing an animal's engagement at a monitoring site would help to reduce the number of unidentified individuals. Similarly, hair collected for DNA analysis requires the target species to interact with sampling devices. The significant increase in engagement observed by two mesopredators in our study suggests that dominant predator odour could be exploited in these situations.

Olfaction is the main sensory perception in many mammals yet its potential role in wildlife management is not fully realised. Studying olfactory communication provides insights into predator ecology, but it is also of applied importance from both economic and conservation perspectives. Deploying dominant predator pheromones to attract species of lower trophic levels is a novel approach that can contribute to population monitoring and invasive species management. It can also potentially assist in reducing native mesopredator naivety to invasive predators or increasing the success of reintroduction programmes for critically endangered native species, such as the critically endangered black footed ferret (*M. nigripes*) of North America. Future research could test responses of mesopredators to apex predator scent in other biomes to establish whether behaviours are generalised responses or specifically related to species in this study. Combining elements of olfactory communication with technological advancements has the potential to create new tools that will improve the effectiveness of invasive species management.

CHAPTER 5 Niche partitioning in a guild of invasive carnivores



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5.1 Abstract

Conflict is widespread among predators that compete for limited resources. These confrontations establish species hierarchies: top predators control the most productive resources, maximising access to prey; subordinate species attempt to maximise resource acquisition while reducing the risk of a potentially lethal encounter. We investigated whether niche partitioning exists among a guild of invasive predators in New Zealand, as a consequence of interference competition. Camera traps were deployed for 4,405 trap days to record activity patterns by stoats (*Mustela erminea*) in relation to two physically dominant competitors (feral cats *Felis catus* and ferrets *M. furo*) and primary prey species (rodents and lagomorphs). We found compelling evidence of niche partitioning as dominant predators matched prey resources spatially and temporally, while subordinate predators avoided periods of dominant predator activity. Further, we tested for competition by selectively removing cats and ferrets in a pulse perturbation experiment. At the treatment area, stoats were only detected after both larger predators were removed, becoming the most frequently detected predator six months after the perturbation. We suggest that there is spatial partitioning within the predator guild, but that this is incomplete and avoidance is achieved by temporal partitioning within overlapping areas.

5.2 Introduction

Apex predators suppress populations of mesopredators through competitive interactions that limit resource availability, thereby imposing fitness constraints (Creel & Creel, 1996). Interactions may occur indirectly through the exploitation of resources or directly through agonistic encounters, leading to harassment, killing and occasionally the consumption of the subordinate predator (Linnell & Strand, 2000; Polis et al., 1989). Interference competition is frequently the primary form of competition among predators, particularly when food resources are plentiful (Creel, 2001; Schoener, 1982). Mesopredators reduce the risk of an agonistic encounter by altering their behaviour, which requires them to deviate from an optimum resource gathering strategy. Dominant predators are therefore anticipated to be distributed in accordance with prey (resource matching), whereas the distribution of subordinate predators should be based on both prey and safety (safety matching) (Linnell & Strand, 2000; Palomares & Caro, 1999).

Competition among sympatric predators is reduced by subordinate species altering resource utilisation (Durant, 1998; Pianka, 1974). This process, known as niche differentiation, facilitates coexistence rather than the extirpation of the subordinate predator, according to the competitive exclusion principle (Armstrong & McGehee, 1980; Schoener, 1974). Partitioning by coexisting species that forage at the same trophic level can be expressed in several dimensions including temporal, spatial, and/or resources (e.g. diet) (Menge & Sutherland, 1976). Niche theory holds that high resource overlap along any one of these dimension requires resource divergence in another dimension for species to coexist (Fuentes & Jakšić, 1979; Hutchinson, 1978; Molsher, 1999). Differences among competitors in the timing of their activity promotes coexistence within ecological communities through avoidance of direct confrontation and/or by reducing resource overlap (Kronfeld-Schor & Dayan, 1999;

Schoener, 1974). Temporal partitioning reduces both resource competition and interference competition, independent of which form of competition motivated the initial change in activity (Kronfeld-Schor & Dayan, 1999). Similarly, spatial partitioning, by confining activity to different habitats or habitat strata, ameliorates both competitive forms (Tilman, 1994). Low abundance of dominant predators in less productive areas creates an opportunity for subordinate species (Durant, 2000) and plentiful refuges in heterogeneous habitats may also facilitate co-existence (Holt, 1984). For example, weasels (*Mustela nivalis*) exhibit reciprocal distribution with stoats (*M. erminea*) in parts of their native range, being rare or absent in optimal prey habitats, but occurring more frequently in less productive areas (Erlinge & Sandell, 1988). Olfactory communication between competing predators may maintain niche partitioning without the need for direct agonistic encounters (Harrington et al., 2009; Stokes et al., 2011). Weasels are able to distinguish the odour of stoats from conspecific scent and competitor recognition may help weasels maintain spatial segregation (Erlinge & Sandell, 1988). Finally, coexistence may be facilitated by the partitioning of resources based on prey species (Karanth & Sunquist, 2000), prey size (Sinclair et al., 2003) or by evolving morphological differences adapted for prey selection (Krebs, 1978).

Species coexistence and invasion ecology theories are fundamentally connected as niche partitioning may increase invasion success and promote coexistence (Byers & Noonburg, 2003; Chesson et al., 2004). Invasion success partly depends on ‘niche opportunities’ - the potential within a community for an invasive species to have a positive rate of increase from low densities (Shea & Chesson, 2002). Once an invasive species has successfully established, novel trophic interactions develop and perturbing the invaded community can have unforeseen consequences (Gidoin et al., 2015). For example, the removal of feral cats (*Felis catus*) from an oceanic island corresponded to a reduction in seabird breeding success, as Pacific rats (*Rattus exulans*), released from competition and predation by cats, increased their

predation on seabird colonies (Rayner et al., 2007). This type of competitive response is termed mesopredator release, the strength of which is dependent on the productivity and predator diversity within the system (Prugh et al., 2009; Terborgh & Estes, 2010).

New Zealand's unique biodiversity evolved in isolation for over 70 million years, and the almost complete absence of native terrestrial mammals meant that many niches were unoccupied during this period. Introduced carnivorous mammals were presented with a surfeit of niche opportunities: plentiful prey, no native competitors, few mammalian diseases and parasites, and a heterogeneous environment likely to promote coexistence. Feral cats, ferrets (*M. furo*) and stoats are the largest invasive carnivores and are responsible for declines, and in some cases to extinctions, of many native species (Parkes & Murphy, 2003). These carnivores also compete interspecifically, with ferrets and cats dominating the smaller stoats in aggressive encounters (Chapter 2). All three species are subject to human management, initially as agents for biological control, but they are now controlled as pests due to their negative impacts on native biodiversity.

The study of invaded ecosystems provides 'natural experiments' to investigate the fundamental ecological processes underlying interspecific competition and coexistence (Sax et al., 2007). New Zealand is an ideal location to study these relationships, as there are few mammalian predator species and all are subject to control, which allows the influence of individual guild members to be assessed. We recorded the spatiotemporal distribution of stoats, cats and ferrets, and their main prey (lagomorphs, rodents and birds) to test if niche partitioning was driven by prey resources and/or competition.

We made the following predictions:

- The activity of the subordinate predator (stoat) will be timed to avoid periods of high activity by dominant predators as opposed to matching the activity of primary prey (safety matching).
- Dominant predators (cat and ferret) will time their activity to correspond to the activity patterns of preferred prey (resource matching).
- The site occupancy and abundance of the subordinate predator will be negatively correlated with the same measures for dominant predators (safety matching).
- The site occupancy and abundance of dominant predators will correspond to the occupancy and abundance of preferred prey (resource matching).

A pulse perturbation experiment was implemented to reduce the abundance of feral cats and ferrets. Camera traps monitored mesopredator occupancy before and after the treatment to assess whether the removal of ferrets and stoats was successful. Camera traps were also used to determine if stoats responded to changes in the abundance of dominant predators, in accordance with the mesopredator release hypothesis. We predicted that at the removal area:

- The abundance and/or occupancy of subordinate predators will increase post treatment.

5.3 Methods

5.3.1 Study area

We used two study areas – Waitere (treatment area) and Toronui (non-treatment area) – located in the Hawke's Bay region of New Zealand ($\sim 39^\circ$ S, 176° E). Land use is predominantly livestock farming with some cropping. Forest patches, which are scattered across the landscape, are dominated by mānuka (*Leptospermum scoparium*) and kānuka (*Kunzea robusta*) scrub at higher elevations and remnant broadleaf woodland at lower elevation. The two areas were 12.3 km apart, with neither having had any recent history of predator control.

5.3.2 Study species

Stoats are small carnivores, found in a wide range of habitats throughout New Zealand, but are particularly common in forested areas (King, 1983). Feral cats and ferrets are New Zealand's two largest terrestrial carnivores, occupying a range of habitats including forests, tussock, and pastoral farmland (Clapperton & Byrom, 2005; Gillies & Fitzgerald, 2005). Dietary composition is driven by prey availability, so when found in sympatry these carnivores exhibit high dietary overlap both in terms of prey species and size range. Primary prey includes rodents (mice *Mus musculus*, ship rats *R. rattus*, and Norway rats *R. norvegicus*), lagomorphs (rabbits *Oryctolagus cuniculus* and hares *Lepus europaeus*), birds and invertebrates (Jones et al., 2005; King & Moody, 1982; King & Powell, 2007; Langham, 1990; Murphy & Dowding, 1994; Smith et al., 1995; Wodzicki, 1950). In forested areas, the relative importance of birds, insects and rodents increases, while rabbits usually predominate in non-forested areas (King & McMillan, 1982; Murphy et al., 2015). Sexual dimorphism enables male stoats to exploit larger prey, while smaller females can gain access to more rodent prey (King & Powell, 2007; McDonald et al., 2000). With camera-trap data it was not feasible to classify mustelids into age categories based on morphological features, as it is difficult to distinguish visually between juveniles and females. Cats were classified as juvenile based on a conservative size based assessment of photographs; otherwise all cats were classified as adult.

In forested habitat, female stoats may exhibit more nocturnal activity than males due to greater reliance on smaller prey such as mice and weta (Orthoptera: Anostostomatidae) that exhibit nocturnal activity (Alterio et al., 1998). Prey susceptibility to attack depends partly on the predator's hunting behaviour: stoats hunt fossorial, terrestrial, arboreal and aquatic prey (Dowding & Elliott, 2003; King & Powell, 2007; Wilson et al., 1998), ferrets are primarily fossorial, and less frequently terrestrial hunters (Clapperton, 2001; Peach, 2005), while cats

ambush or stalk terrestrial prey (Dickman, 1996). Temporal activity patterns above ground are variable for mustelids: ferrets are almost exclusively nocturnal when active, whereas stoats may be active at any time of the day (Clapperton, 2001; King & Powell, 2007; Sidorovich et al., 2008). Feral cats are adapted for nocturnal or crepuscular activity, but will modify their behaviour to coincide with environmental factors such as prey activity (Fitzgerald & Karl, 1979; Langham, 1992). Both larger predators directly influence stoat demographics through intraguild predation (Wodzicki, 1950) and interference competition (Chapter 2). These mechanisms can severely depress stoat populations and in some areas, apex predators may account for 65% of stoat mortality (Jedrzejewska & Jedrzejewski, 1998). Fear of dominant carnivores also imposes fitness constraints through interference competition that influences stoats' foraging and vigilance behaviour (Chapter 2).

5.3.3 *Experimental design*

Target species were monitored using camera traps on three occasions – autumn (April), winter (May-June) and spring (November) 2014. The duration for each monitoring session was 21 days, an interval considered sufficient for the detection of terrestrial mammals, while also enabling all monitoring stations to be surveyed within a relatively discrete period (Meek et al., 2014). A 6-km² sampling grid with a random starting point was established at each area. At each camera's location, we defined habitat variables (open pasture, forest, or scrub) based on a visual inspection of the dominant vegetation type within a 20-m radius of a monitoring station.

A before-after, control-impact (BACI) design was employed to test the mesopredator release hypothesis. In May 2014, after three weeks of pre-treatment monitoring, pest control targeting feral cats and ferrets was carried out by Hawke's Bay Regional Council. Predator removal took place in winter when food resources are low, which increases the trappability of

the target species. Professional trappers used a combination of leg-hold, cage and kill traps, baited with a variety of lure types, to target predators. Mesopredator release was assessed by comparing changes in occupancy rates of dominant predators (cats and ferrets) and subordinates (stoats), across time and between areas.

Camera trapping was also conducted at the non-treatment area in summer (January–February) 2014 as part of a separate trial. Both studies implemented the same monitoring protocol, although cameras were placed at ecotones in the earlier experiment, as the trial aimed to maximise stoat detections. Data from this earlier summer deployment were used to supplement the BACI data set, so that predictions for niche partitioning could be assessed in all seasons (see below).

5.3.4 *Camera traps and lure*

In total, 80 (40 per study area) Reconyx PC 900 (Reconyx Inc., Holmen, Wisconsin) cameras were deployed at monitoring stations with approximately 500-m spacing. However, a shift of up to 100-m from the predetermined location was used where locations were inaccessible or cameras were at risk of livestock damage. Home ranges of target species were taken into account when deciding on camera spacing as this determines the independence of observations (Bengsen et al., 2012). Five hundred metres is greater than the home range diameter for most of New Zealand's invasive mammalian predators, although some feral cats in pastoral locations have home ranges greater than this camera spacing (Langham, 1992). However, our goal was to describe fine scale reciprocal distribution and habitat use and therefore our spacing was deemed optimal to balance logistical, biological, and statistical requirements. The date and time stamp recorded on each photograph were extracted using R v. 3.1.1 (R Core Team, 2014), with a specially written function (Appendix III: S1).

Each monitoring station was created by fixing a camera to a wooden post, with its base five cm from the ground, the approximate shoulder height of mustelids. Cameras were oriented so that pictures were taken parallel to the gradient of the landscape and all cameras were programmed with identical settings: high sensitivity, three pictures per trigger and no delay between triggers. Vegetation was removed (where necessary) up to 1.5 m from the camera to allow for an unobstructed field of view and to minimise false triggers (Kelly & Holub, 2008). Camera batteries and memory cards were replaced at the completion of each trapping period.

To attract target predators, a lure was placed in a vial 1.5 m in front of the camera and secured with a tent peg. Perforated plastic vials were used to allow odour volatiles to disperse, but to prevent removal of the lure. Each vial (9 cm x 3 cm) was drilled with ~50 holes, five mm in diameter, and sterilised with boiling water before use. A combination of fresh rabbit meat and a pungent lure, derived from predator pheromones, were used as olfactory attractants (Chapter 3). All lures were replenished at the start of each monitoring session.

5.3.5 *Data recording and analysis*

We considered each monitoring station to be an independent sampling unit and analysed data based on observations of both predators and prey. To identify repeated observations of the same individual we plotted histograms of the time elapsed between consecutive photographs for each species (Brook et al., 2012). The median time for consecutive bursts of photographs of the same species was <10 minutes, suggesting that these were repeat detections. We calculated the following variables for analysis: (1) *activity record*, (2) *site use*, and (3) *observation rate*. To avoid autocorrelation, we considered *activity records* of the same species to be photographs obtained more than 30 minutes apart, except when individuals could be reliably distinguished (Linkie & Ridout, 2011). *Site use* is a binary response variable

with 1 indicating a species was detected and 0 indicating non-detection. *Observation rates* were used as an index of abundance for the three predators which accounted for the number of cameras, any camera failures and the number of survey days. We defined *observation rate* as the number of independent observations per 100 trap days (1 trap day = 1 camera trap set for 24 h) (Glen et al., 2014; Rovero & Marshall, 2009). We also recorded any characteristic predator behaviours apparent in the photographs, such as capture of prey or response to the scent lure. All statistical analyses were performed with the software R (R Development Core Team, 2015).

5.3.6 *Activity*

Cameras recorded the time and date of each photograph, providing temporal data on animals' activity. Monitoring occurred in each of the four seasons during 2014, which introduced variation to the relationship between clock time, day/night length and the timing of sunrise/sunset. We therefore rescaled clock time to equal periods of day and night: sunrise at 06:00 h and sunset at 18:00 h. Species activity was classified into four categories: diurnal (occurring between 1 h after sunrise and 1 h before sunset); nocturnal (occurring between 1 h after the sunset and 1 h before the sunrise); cathemeral (activity occurring throughout the 24 h period) and crepuscular (occurring 1 h before and after sunrise and sunset) (Linkie & Ridout, 2011).

Following the methods of Ridout and Linkie (2009), we characterised activity patterns for each predator separately with kernel density estimates. Instead of grouping pictures into discrete time categories, this method treats time of activity as a random sample from an underlying continuous distribution (Linkie & Ridout, 2011). We compared activity patterns to assess the potential for interactions between pairs of species by calculating the coefficient of overlap (Δ), which varies between 0 (no overlap) and 1 (complete overlap). We had

sufficient data across all seasons ($n > 50$ for all species) to use the estimator, Δ_4 , for large sample sizes. For cats, we had sufficient observations ($n > 20$) to compare seasonal overlap with prey, using the estimator Δ_1 for smaller sample sizes. Confidence intervals were obtained by bootstrapping samples 10,000 times. Statistical analyses were implemented using the ‘overlap’ package in the R environment (Ridout & Linkie, 2009).

Before pooling data on stoat temporal activity from the two camera-trap trials we calculated the coefficient of overlap (Δ_1) to ensure that activity patterns did not differ between studies at the non-treatment area. Delta (Δ_1) was .95 indicating that activity data matched substantially and could therefore be combined. We also investigated, using the coefficient of overlap (Δ_1), if there were significant differences in the activity patterns of focal predators among areas and between seasons prior to combining data. Overlap variations were non-significant, with no apparent between-season variation, indicating the data could be analysed collectively (Linkie & Ridout, 2011). Prey species were grouped together where there were no significant differences in activity patterns: rats and mice were grouped into a category ‘rodents’, rabbits and hares were combined into the group ‘lagomorphs’ and all bird species were placed in one group.

5.3.7 *Predator distribution and contributing factors*

Occupancy models that explicitly account for imperfect detection are well suited to camera-trap surveys, and provide an index of abundance for species without identifiable markings (MacKenzie, 2006). We used *site use* as the measure for this analysis and all species were modelled using an independent probability of detection with constant occupancy. Monitoring periods were divided into intervals of 5 days. We ran a single species, single season model for the cats and ferrets at the treatment area in April and for cats in all monitoring periods at the non-treatment area, to estimate *site use*. Due to insufficient detections, naïve *site use* was

calculated for predators in other seasons. Low detection rates for stoats precluded the analysis of co-occurrence patterns with dominant predators using occupancy modelling. All occupancy analyses were undertaken in the software package PRESENCE 9.0 (Hines, 2006)

Using generalized linear mixed models (GLMM), with a Poisson error distribution, from the MASS package in R (Venables & Ripley, 2002), we analysed the effect of a number of predicted detection covariates for the relative abundance of predators. This enabled us to assess the influence of fixed effects while accounting for the variance of any random effects. The response variable for the analysis was the *observation rate* for each predator. The fixed effects included in the model were: *observation rates* for two primary prey groups (rodents and lagomorphs), habitat (open pasture, forest, or scrub), while ‘site’ was entered as a random effect to account for the non-independence of errors associated with repeated measures. Birds were not included as primary prey, as ferrets can only prey on ground nesting species, which were absent from our areas (Clapperton, 2001). Areas were analysed separately and collectively across each season and candidate models were assessed by plotting residuals and testing for overdispersion. Significance levels are reported at $p<0.05$ or as 95% confidence intervals (CI). Behavioural responses, based on stoat approaches to the scent lure, were assessed using Fisher’s exact test.

5.4 Results

A trapping effort of 4,405 trap days generated 769,408 photographs, of which 19,120 were of the targeted mammalian predators and prey. There were an additional 26,212 photographs of 27 bird species (13 native, 14 introduced) (Appendix IV: S1). The number of camera-trap stations, trap days and photographs are summarised in Table 5.1. We recorded 263 independent observations of four carnivores; feral cats 168 (64%), ferrets 72 (27%), stoats 22 (8%) and a weasel 2 (<1%). There were 991 observations of the focal invasive prey,

lagomorphs (421) and rodents (570). Over 90% of identified *Rattus* spp. were ship rats and the remainder were Norway rats. Livestock (cattle, sheep and deer) accounted for the majority of photographs at both areas.

Table 5.1 Summary of camera trapping effort and numbers of independent observations of predators and primary prey (lagomorphs and rodents), at two study areas in New Zealand.

Study area	Survey period	Monitoring stations	Camera trap days	Predators	Prey
<u>Non-treatment</u>	April	38	797	58	83
	May-June	38	797	63	116
	November	38	722	47	284
	Non-treatment total		2,316	168	483
<u>Treatment</u>	April	40	822	78	211
	May-June	37	648	6	154
	November	38	619	11	143
	Treatment total		2,089	95	508

5.4.1 Activity patterns

Activity patterns varied within the predator guild and between their prey (Figure 5.1). Cats were cathemeral, with activity lowest immediately before noon and reaching a peak just after midnight. Increased observation in the afternoon may be partly due to the appearance of juvenile individuals, as at least a third of sightings were classified in this age class. Ferrets were exclusively nocturnal, with all 72 observations occurring between dusk and dawn. Stoats were almost entirely diurnal, with a 0.91 kernel probability of being active during the day, and a third of all activity took place an hour either side of noon. There were nocturnal observations of stoats on five (9%) occasions during the summer months (January – February). Rodents were entirely nocturnal, with the exception of a small number of mice sightings (< 1%) recorded during daylight hours. Birds were diurnal, appearing immediately after first light, with only one observation (morepork *Ninox novaeseelandiae*) at night.

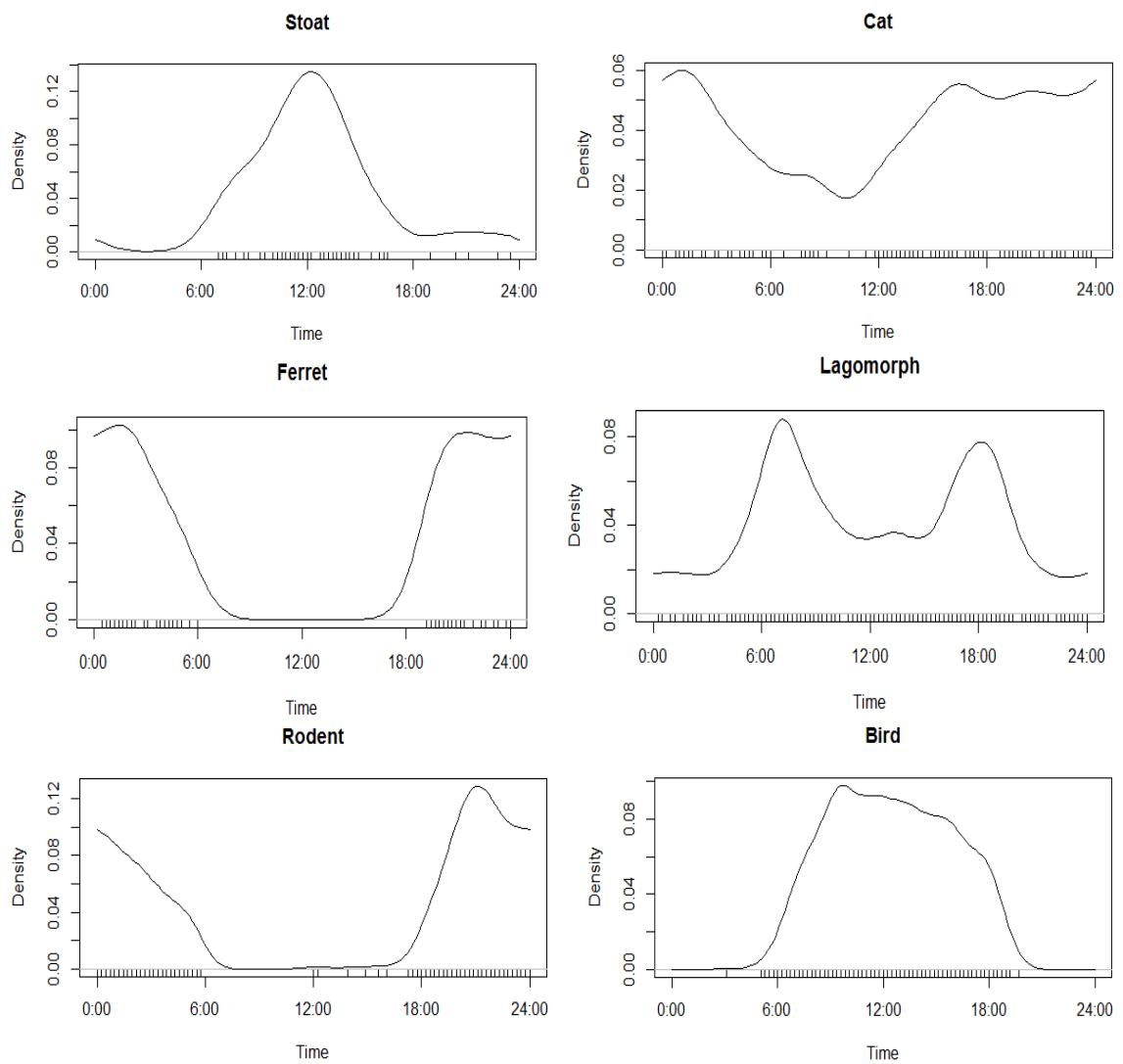


Figure 5.1 Daily activity patterns of birds and invasive mammals recorded during three seasons: autumn (April), winter (May) and spring (November). Stoat activity patterns include additional records for summer (January–February). Species' activity over 24 hours was rescaled to equal periods of daylight (6:00 – 18:00) and night (18:00 – 6:00). The short vertical lines above the x-axis indicate the times of individual photographs.

5.4.2 Stoat overlap with larger predators

Stoats were primarily diurnal, showing minimal overlap with the two dominant predators (Table 5.2, Figure 5.2). Stoats displayed the greatest overlap with cats, but their midday peak

and a slight shift towards mornings corresponded closely with the lowest point of cat activity in the 24 h cycle. Stoats and ferrets had minimal overlap (Table 5.2, Figure 5.2). In contrast, activity for cats and ferrets overlapped considerably (Table 5.2, Figure 5.2), with peaks for both species occurring just after midnight.

Table 5.2 Overlap in temporal activity (Δ_4) among predators and prey at two locations in Hawkes Bay, New Zealand. Bootstrapped 95% confidence intervals are included in parentheses.

	Stoat	Cat	Ferret
Stoat	-	-	-
Cat	$\Delta_4 = 0.43 (0.35-0.55)$	-	-
Ferret	$\Delta_4 = 0.13 (0.05-0.21)$	$\Delta_4 = 0.63 (0.53-0.73)$	-
Lagomorph	$\Delta_4 = 0.55 (0.44-0.65)$	$\Delta_4 = 0.71 (0.65-0.78)$	$\Delta_4 = 0.34 (0.26-0.42)$
Rodent	$\Delta_4 = 0.12 (0.05-0.18)$	$\Delta_4 = 0.63 (0.57-0.70)$	$\Delta_4 = 0.88 (0.82-0.94)$
Bird	$\Delta_4 = 0.80 (0.72-0.88)$	$\Delta_4 = 0.50 (0.44-0.56)$	$\Delta_4 = 0.09 (0.05-0.13)$

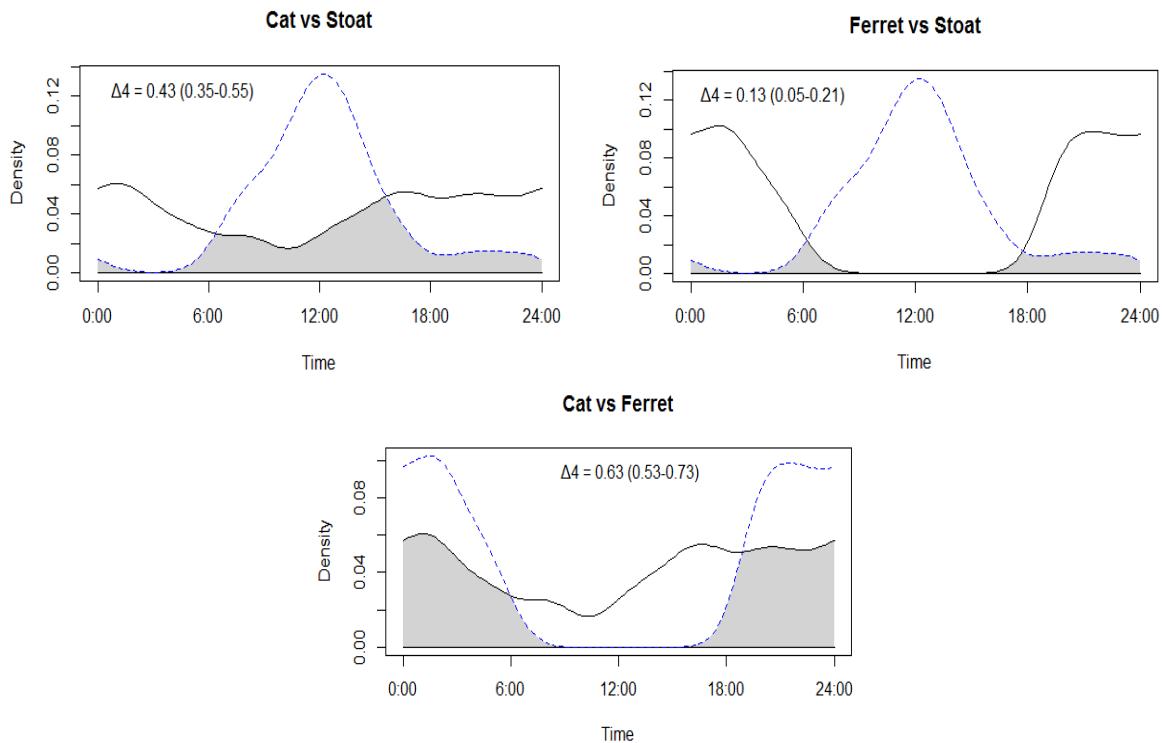


Figure 5.2 Pairwise comparison of daily activity patterns of cats, stoats and ferrets recorded at two farm areas in the Hawke's Bay region of New Zealand. For each pair, the larger predator is shown with a solid line and smaller predator with a dashed line, and overlapping periods of activity are shaded grey. Coefficient of overlap (Δ_4) and bootstrapped 95% confidence intervals are included on the graph.

5.4.3 *Predator overlap with prey*

Stoats' diurnal activity patterns resulted in minimal overlap with rodents (Table 5.2, Figure 5.3). Stoats displayed high overlap with lagomorphs, with evidence of a slight shift in activity towards lagomorph peaks at dawn (Table 5.2, Figure 5.3). Of the common potential prey species stoats had the greatest overlap with birds (Table 5.2, Figure 5.3). Cat cathemeral activity corresponded broadly with primary prey (Table 5.2, Appendix IV: S2) and there was also evidence of increased diurnal activity in spring and summer (Appendix IV: S3). Ferrets

displayed very high overlap with rodents, but comparatively low overlap with birds and lagomorphs despite the latter being primary prey (Table 5.2, Appendix IV: S2).

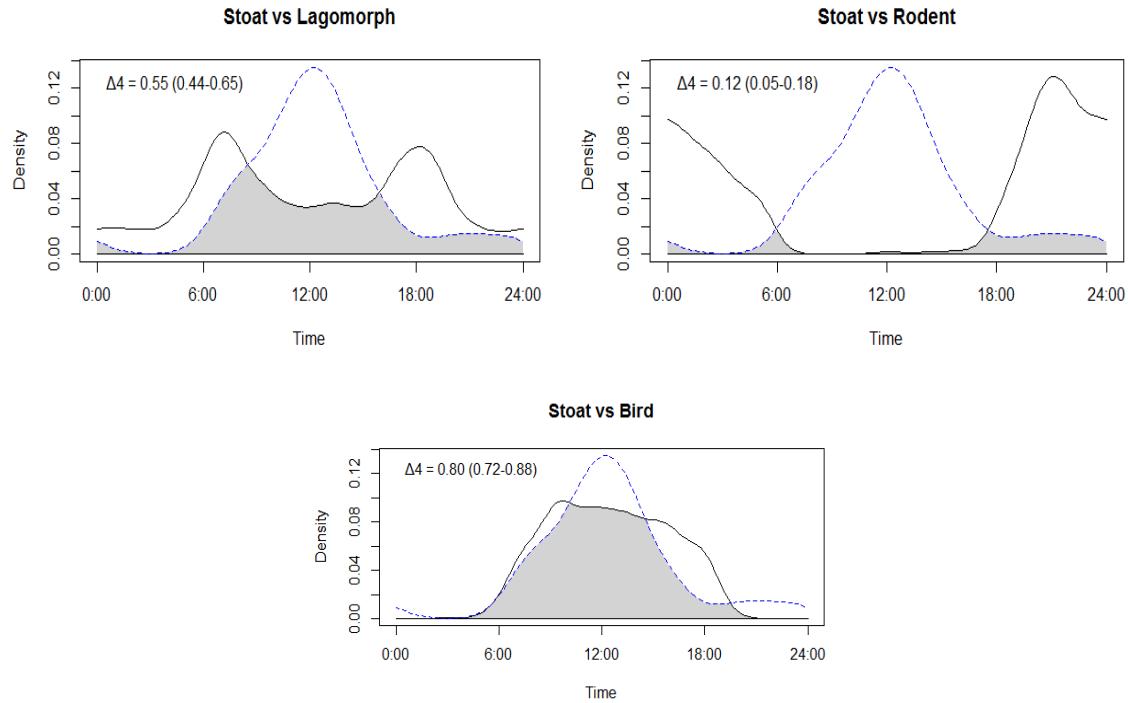


Figure 5.3 Overlap of stoat activity (dashed line) with their main prey (rodents/ lagomorphs/ birds) recorded at two farm areas in the Hawke's Bay region of New Zealand. Coefficient of overlap (Δ_4) and bootstrapped 95% confidence intervals are included on the graph. Overlapping periods of activity are shaded grey.

Prey availability varied considerably between areas, based on pre-control observations in autumn (April). Lagomorphs were the dominant prey at the non-treatment area, with four times more observations than at the treatment area (132 vs. 32), while there was also an approximate four-fold difference in bird sightings, which were highest at the non-treatment area (430 vs. 118). The trend was reversed for rodents with 17 times more rodent prey at the treatment area (265 vs. 16). Cats adjusted their activity patterns to match prey availability, displaying increased diurnal activity at the non-treatment area where lagomorphs and birds

dominated, and were almost entirely nocturnal at the treatment area where rodents were the dominant prey (Appendix IV: S4).

5.4.4 *Predator removal*

Specialist trappers removed 17 cats and 18 ferrets from the treatment area during the 3-week operation. *Site use* models showed a significant decrease in cats ($P=0.0004$) and ferrets ($P=0.0021$) following predator removal, representing a fall of 82% and 76%, respectively (Figure 5.4, Table 5.3). In contrast, *site use* estimates at the non-treatment area increased for both species over the same period (Figure 5.4). Changes in *observation rates* showed comparable results: cats decreased by 78% after predator control, while ferrets decreased by 93% (Table 5.4).

Table 5.3 *Site use* estimates for cats, ferrets, and stoats at two locations in Hawke's Bay. A control operation targeting cats and ferrets was undertaken on the treatment area in May. *Site use* estimates \pm standard error and 95% confidence intervals, naïve estimates highlighted in grey.

Species	Period	Location	Est. occ	SE	95% CI
Cat	April	Non-treat	0.73	0.1325	0.4201 - 0.9099
Cat	May	Non-treat	0.76	0.1122	0.4889 - 0.9164
Cat	November	Non-treat	0.86	0.2161	0.1476 - 0.9957
Cat	April	Treatment	0.57	0.1929	0.2226 - 0.8630
Cat	May	Treatment	0.06	-	-
Cat	November	Treatment	0.08	-	-
Ferret	April	Non-treat	0.05	-	-
Ferret	May	Non-treat	0.08	-	-
Ferret	November	Non-treat	0.03	-	-
Ferret	April	Treatment	0.38	0.0866	0.2253 - 0.5533
Ferret	May	Treatment	0.09	-	-
Ferret	November	Treatment	0.06	-	-
Stoat	April	Non-treat	0.08	-	-
Stoat	May	Non-treat	0.08	-	-
Stoat	November	Non-treat	0.14	-	-
Stoat	April	Treatment	0	-	-
Stoat	May	Treatment	0.03	-	-
Stoat	November	Treatment	0.14	-	-

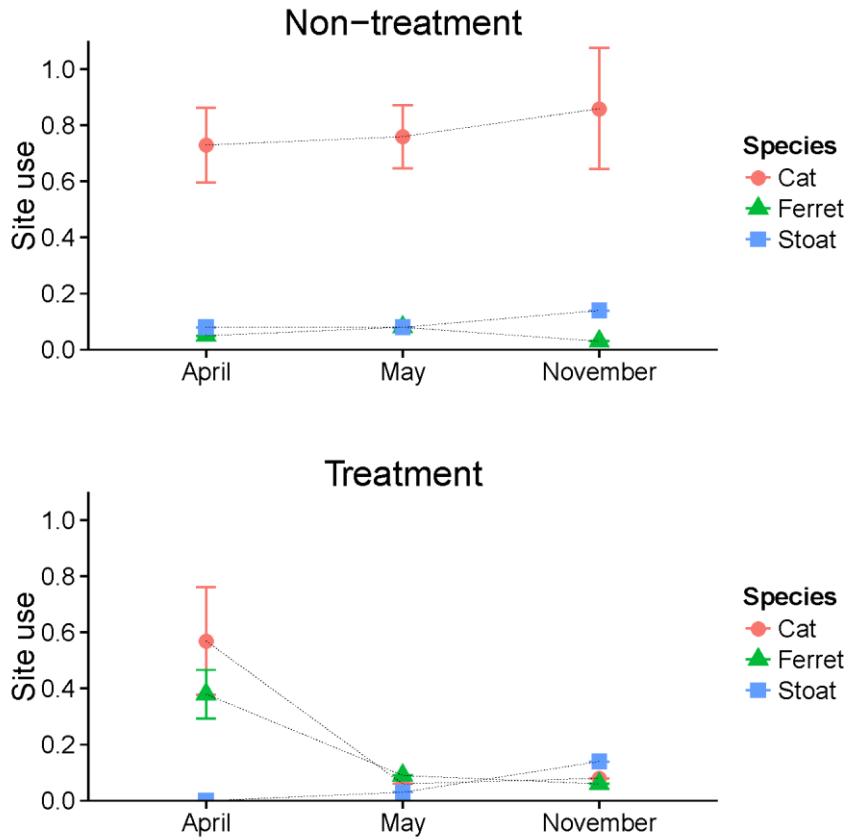


Figure 5.4 *Site use* estimates (\pm 95% CI) and naïve *site use* rates (no error bars) for cats, ferrets, and stoats at treatment (predator removal) and non-treatment areas in the Hawke's Bay region of New Zealand.

Naïve *site use* was used to assess stoat distribution as low numbers of detections precluded detailed analysis (Table 5.3). No stoats were recorded at the treatment area prior to removal of cats and ferrets, and one stoat was recorded during the monitoring period immediately following predator removal (Figure 5.4). Stoats were detected at 14% of monitoring stations in the final monitoring period, six months after the pulse perturbation. Stoat detections were constant between April and May at the non-treatment area, but increased between May and November (Figure 5.4, Table 5.4). We compared stoat activity patterns at the two areas ($\Delta_1 = 0.63$, CI 0.29-0.92) six months after predator removal and found a shift towards later activity

at the removal area (Appendix IV: S5). However, large confidence intervals reflect the low number of observations and make it difficult to draw firm conclusions from these data.

Table 5.4 *Observation rates* (independent observations per 100 trap days) for stoats, cats and ferrets at two study areas within the Hawke's Bay region of New Zealand. A three week predator control operation that targeted ferrets and cats took place at the treatment area between April and May.

Location	April	May	November
<u>Non-treatment</u>			
• Stoat	0.4	0.4	1.1
• Feral cat	7.1	6.4	4.9
• Ferret	0.5	0.7	0.1
<u>Treatment</u>			
• Stoat	0	0.1	0.9
• Feral cat	3.7	0.8	0.7
• Ferret	5.9	0.4	0.3

5.4.5 *Prey and habitat features*

Where there were sufficient observations, we used generalised linear mixed models to test for factors that affected the probability of detecting a predator. The influence of covariates on the *observation rates* of predators could be tested pre-control for cats and ferrets in the treatment area and for cats in the non-treatment area. The *observation rate* of ferrets had a strong positive correlation with that of lagomorphs (GLMM: t -value = 4.03, P = 0.0003).

Observation rates for cats were not significantly correlated with that of primary prey (lagomorphs and rodents) at either area and cats were negatively associated with scrub habitat at the treatment area (GLMM: t -value = -2.25, P = 0.0306). There were insufficient observations to conduct a similar analysis for stoats.

5.4.6 *Spatial distribution*

The two areas differed in predator community assemblage, although cats were the most common predator at both locations (Figure 5.4). Cats were found at 33% of monitoring

stations in the treatment area during the pre-treatment monitoring period, and at 85% of monitoring stations in the non-treatment area, over the three monitoring periods. Ferrets were found at 33% of monitoring stations in the treatment area during pre-treatment, but at just 8% of monitoring stations in the non-treatment area, over all monitoring periods. Where cats and ferrets were both recorded within a monitoring period, they co-occurred at monitoring stations 36% of the time, with sequential sightings less than 5 hours apart on three occasions. Stoats were not detected at the predator removal area during pre-treatment monitoring and were recorded at 23% of the non-treatment areas over the three monitoring periods. At the predator removal site post perturbation, site occupancy of stoats increased to 14% of camera monitoring stations. Stoats co-occurred with cats at 35% of stations within the same monitoring period and both species were photographed just 10 hours apart in one instance. Mustelids never co-occurred at monitoring stations, with one exception where a stoat was recorded six months after ferrets were removed.

The *site use* by primary prey differed between areas. Rats were the most common prey at the treatment area, with *site use* of 45%, while lagomorphs were found at only 15% of stations. This pattern was reversed at the non-removal area; lagomorphs were the most widespread prey species (68%) and rats uncommon (10%).

5.4.7 Additional observations

All instances where a stoat approached and made contact with the pheromone lure were recorded. There was a significant difference between behaviours depending on the time of day (Fishers exact test = 0.0033), as stoats approached and made contact with the lure during daylight but never at night. Predators were recorded with prey on two occasions: a cat was photographed with a mouse at the treatment area in May and a stoat dragged a dead rabbit to the lure at the non-treatment area during November (Appendix IV: S6 & S7).

5.5 Discussion

Observations of niche differentiation in this study support the existence of interference competition between stoats and the two larger predators. Stoats achieve coexistence, as the subordinate members of a predatory guild, by reducing spatial and temporal exposure to dominant predators. However, this avoidance strategy also reduced their overlap with preferred prey. We found strong evidence of temporal partitioning, supporting the niche-complementarity hypothesis, which predicts that high overlap in one dimension will be compensated by low overlap in another (Loreau et al., 2002). Exploitation competition is unlikely to be the limiting factor as rodents and lagomorphs were locally abundant (based on *site use* estimates) and stoat reliance on diurnal prey will reduce resource overlap with dominant predators. Within a monitoring period, stoats co-occurred with cats at less than half of monitoring stations and mustelids were not recorded at the same camera station. Ferrets displayed resource matching, as their distribution was correlated with rabbit abundance. Although sample sizes were small, stoats were only detected at the removal area following the pulse perturbation, supporting the mesopredator release hypothesis.

5.5.1 *Temporal activity*

Stoat activity contrasted with temporal patterns of dominant predators, leading to reduced overlap with primary prey (safety matching). Stoats were almost exclusively diurnal, with camera records peaking at midday, corresponding to the nadir of activity for dominant predators. Cathemeral activity of cats precluded complete avoidance, yet overlap between the species was only 42%. Overlap in activity may have been inflated by the afternoon activity of juvenile cats, which were estimated to be 6-7 months old during the monitoring periods. This is a life stage that probably poses less of a physical threat to stoats compared with adult cats. In a comparable study area, adult cats, particularly males, were more active at night than

subadults (Langham, 1992). Stoats achieved avoidance of ferrets by displaying opposite diel activity cycles, which would considerably reduce the risk of encounters. At the removal area prior to the perturbation, dominant predators displayed almost no diurnal activity and this would appear to create increased foraging opportunities for stoats. However, the main food resource (nocturnal rodents) were monopolised by dominant predators, and diurnal prey were not abundant, so this combination may explain stoats' apparent absence from the area.

When evaluating overlapping activity patterns of mustelids and prey, it is important to consider the difference between prey activity and prey vulnerability, as mustelids' hunting technique allows them to capture sedentary animals. Stoats displayed low temporal overlap with rodents, which is surprising as rats and/or mice are the main dietary component, particularly in forested areas (King & Murphy, 2005). Rats are vulnerable to stoat predation when in burrows, but ship rats, the most frequently recorded rodent at our study areas, usually reside in arboreal nests when inactive (Innes, 2005). Locating inactive ship rats during daylight hours is anticipated to be more difficult than hunting active ship rats that are foraging on the ground at night. A similar mismatch occurred in Hawaii, where the small Indian mongoose (*Herpestes auropunctatus*) failed as an agent of biological control for ship rats, as the mongoose is a diurnal predator and could not access inactive ship rats in arboreal nests (Barun et al., 2011). Mice would be difficult to access when in burrows, particularly for larger male stoats, and stoats' diurnal activity in the study areas reduced the availability of this prey resource. Stoats displayed the greatest overlap with lagomorphs of any mammalian prey. Stoats frequently hunt lagomorphs above ground (Hewson, 1990), requiring concurrent activity patterns, yet stoats' failed to align their activity with the crepuscular peaks displayed by lagomorphs.

Diurnal predators are known to consume more birds and lizards (Macdonald, 1985) and avoidance of dominant predators may therefore increase stoat predation on these diurnal species. Stoats have been directly implicated in the extinction of some indigenous birds (Innes et al., 2010) and cameras recorded native species that are particularly vulnerable to stoat predation, such as rifleman (*Acanthisitta chloris*), North Island robin (*Petroica longipes*) and tom-tit (*P. macrocephala*). An additional fitness cost potentially imposed by temporal constraints is increased intraspecific competition. Female stoats in other areas exploit more nocturnal prey, such as mice and weta (*Hemideina* spp.) (Alterio et al., 1998). The inhibition of nocturnal foraging opportunities effectively reduces the breadth of available prey, which would be of greatest detriment to female stoats.

Dominant predators displayed activity patterns that corresponded to food availability, as both dominant predators and their prey were primarily nocturnal or crepuscular. Ferrets were exclusively nocturnal, which initially seems counterintuitive as this minimises temporal overlap with their primary food resource – lagomorphs (Clapperton, 2001). However, ferrets' spatial distribution was highly correlated with that of lagomorphs, suggesting high reliance on these species. Ferrets are predominantly fossorial hunters and appear to match their temporal activity to rabbit vulnerability below ground. Ferret nocturnal activity overlapped with that of rodents, which can be an important food resource for juveniles and females. As ship rats are primarily arboreal when inactive, this food resource would only be accessible at night, as ferrets are poor climbers. Cats rely on stealth to hunt prey and cannot hunt below ground, so prey vulnerability should correspond closely with prey activity. Temporal activity of cats increased toward the evening peaks of lagomorphs and subsequently tracked the activity of rodents, which maximised their exposure to this primary prey resource. Activity patterns varied seasonally and diurnal activity increased during spring and summer, reflecting the availability of naive avian prey following the breeding season. The suggestion that cats

display seasonal activity patterns to match activity of targeted prey (resource matching) is strongly supported by a dietary study from another Hawke's Bay farm. Langham (1990) reported that rodents were cats' primary prey throughout the year, but that seasonally available birds were the main prey during spring and summer. Cat activity also matched prey availability depending on the area; cats' were primarily nocturnal where rodents were present and increased their diurnal activity when birds and lagomorphs were the primary prey.

5.5.2 Spatial distribution and resource matching

Predators did not display spatial segregation at a landscape scale, but spatial differentiation at monitoring stations, i.e. at the home range scale. This suggests that stoats avoided dominant predators. Stoats never co-occurred with ferrets at the same station within a monitoring period. Stoats co-occurred at monitoring stations with cats on six occasions, but the nocturnal activity patterns displayed by cats at these stations contrasted with the diurnal activity of stoats. Spatial separation and temporal partitioning may be maintained by olfactory communication. On occasions where stoats were nocturnal they did not approach the lure at a monitoring station, which contrasted with behaviours exhibited in daylight hours, when a dominant predator's absence could be confirmed visually.

We provide evidence in support of the prediction that dominant predators would be distributed in accordance with food resources. Ferret distribution corresponded with that of lagomorphs, the largest prey. The energy maximisation premise implies that stoats should also hunt lagomorphs at these locations (Hughes, 1979): stoats' apparent absence is consistent with suppression by dominant predators. Cat distribution was not significantly correlated with prey, although, as these generalist predators were found at the majority of stations, it is difficult to match their distribution to one particular prey species. There was no evidence that the two dominant predators actively avoided each other as they co-occurred at

over a third of monitoring stations and displayed comparable temporal activity. This concurs with another New Zealand study where cats and ferrets were recorded scavenging together (Ragg et al., 2000).

5.5.3 *Mesopredator release*

The pulse perturbation significantly reduced *site use* and *observation rates* for both cats and ferrets, which we predicted would create opportunities for stoats. While records of stoats were few, the increase in the observation rate following dominant predator removal is consistent with the mesopredator release hypothesis. Additionally, it aligns with observations made in other New Zealand studies where stoats appear to increase following the control of cats and ferrets (Gibb et al., 1978; Pierce, 1987). Stoats were detected immediately after dominant predator removal and, six months later, stoats changed from being undetectable to becoming the most common predator at the removal area. Alternatively, it is possible that stoats were responding to increased availability of prey (e.g. fledgling birds), as stoats can seasonally alter their diet (King & Moody, 1982). However, the lack of similar increases at the non-treatment area makes this less likely than mesopredator release.

5.5.4 *Management*

Removal of cats, stoats, and ferrets has been shown to increase the survival of native species in New Zealand (e.g. Alterio et al., 1998; Fitzgerald & Karl, 1979; King, 1983). Although these species are often managed collectively, difference in trappability and reinvasion rates suggests that competition between invasive predators warrants consideration by managers. Dominant predators were extremely slow to recolonise the removal areas, with no discernible increases six months after the pulse perturbation, and this sustained absence created opportunities for stoats. Many studies have demonstrated that the removal of an apex predator can destabilise an ecosystem to the potential benefit of mesopredators (e.g. Courchamp et al.,

1999; Crooks & Soulé, 1999; Rayner et al., 2007). Susceptibility to predation will vary between native species (Parlato et al., 2015) so wildlife managers must consider the consequences of a control operation on invasive predator dynamics.

Predator interactions may create temporal refuges for prey. Dominant invasive predators can benefit native animals by reducing the impacts of an invasive mesopredator (Sergio et al., 2006; Simberloff et al., 2013). For example, Ponui Island has 6% of New Zealand's brown kiwi (*Apteryx mantelli*), despite the presence of feral cats (Colbourne, 2005). Stoats, which are absent from the island, are regarded as a greater threat to kiwi, as they can kill fledglings in underground nests (McLennan et al., 2004). Cats have not been removed from Ponui Island, as they are anticipated to control stoats, which is effectively a management strategy to protect kiwi (Isabel Castro personal communication). Dominant invasive predators may therefore, in certain circumstances, indirectly reduce predation rates on some native species. Understanding the characteristics of a system is critical when deciding on the timing and extent of management intervention.

Our study provides strong evidence of interference competition within a guild of invasive predators, where the subordinate species uses temporal and fine-scale spatial avoidance to coexist with dominant competitors. This illustrates that comprehensive understanding of niche partitioning is important for conservation management. Future research could quantify the influence of invasive predator interactions by investigating the flow-on effect of mesopredator competitive (temporal/spatial) exclusion for native species in New Zealand.

CHAPTER 6 Conclusion



This thesis investigated aspects of interference competition between invasive mammalian predators in New Zealand. The relative simplicity of this predator guild reduces the number of interaction pathways, so that the consequences of competition can be clearly distinguished. My research provides original contributions to the areas of carnivore interactions, niche partitioning and olfactory communication among invasive species.

The initial challenge for my research was to establish whether stoats view larger predators (cats and ferrets) as dominant species in interspecific interactions. In Chapter 2, a pen trial experiment was designed to quantify levels of fear, using a range of behavioural measures (i.e. giving up density (GUDs), vigilance, avoidance, and activity patterns). Stoats perceived larger predators as a threat, altering their foraging behaviours and drastically reducing food intake at ‘high risk’ areas. This pen trial revealed a hierarchy in the predator guild and became the cornerstone of my thesis, as it provided a framework that helped decipher stoat behaviours and occupancy patterns.

The first study led to an investigation of olfactory communication between predators (Chapter 3). An experiment was designed to test stoat behavioural responses to apex predator odour in a foraging macrocosm. Contrary to my predictions, stoats displayed a strong drive to investigate the odour of co-evolved dominant predators and there was no evidence of avoidance, although the odour did provoke increased vigilance. Furthermore, ‘prey’ at a location with the scent of a dangerous adversary was consumed more rapidly than prey at non-scented controls.

The attraction displayed by captive stoats to dominant predator odour was intriguing and this discovery had potential applications for wildlife management. A field experiment (Chapter 4) was devised to test wild mesopredator responses to dominant predator odour. This demonstrated that ferret body odour is a powerful attractant for free-ranging stoats and

provoked eavesdropping behaviour in other mesopredators (hedgehogs and *Rattus* spp.). Kairomones resulted in increased detections (stoat/ hedgehog/ rat) and engagement (stoat/ hedgehog), while monitoring with just a food lure (rabbit meat) would have substantially underestimated the distribution of stoats. Although stoats were attracted to the odour of ferrets, they remained vigilant when approaching the lure and avoided ferret scent at night.

For the final field trial (Chapter 5), I tested for niche partitioning in an ecological community that is dominated by invasive mammalian species. I compared reciprocal activity patterns of predators and prey, at two spatially separated study sites, using mixed models and kernel density estimates. Large dominant predators exhibited ‘resource matching’, both spatially and temporally, while the subordinate mesopredator exhibited ‘safety matching’. Selective removal of larger predators revealed that stoats respond in accordance with the mesopredator release hypothesis, changing from being effectively undetectable to being commonly detected at the treatment site.

6.1 Carnivore interactions - Interspecific competition and foraging

My study supports predictions based on foraging theory (Charnov, 1976; Lima & Dill, 1990; Sih, 1980) and contributes to the literature on fear (Laundré et al., 2001; Mukherjee et al., 2009), by examining responses of a mesopredator when it encounters the visual (Chapter 2) or chemical cues (Chapter 3) of an apex predator. Interference competition between stoats and the two larger predators has previously only been inferred (Keedwell & Brown, 2001; Moller & Alterio, 1999) and my research provides compelling evidence that such a hierarchy exists among these invasive predators. The technique of allocating food, based on a conservative estimate of an animal’s daily energetic requirements, provoked interactions between the predators, yet the extent of any confrontation was always at the discretion of the

mesopredator. Chapter 2 corroborates the predation risk allocation hypothesis, which states that vigilance will increase during periods of high risk (Lima & Bednekoff, 1999). Stoats invariably oriented towards the perceived danger while feeding, which I used as a novel measure of vigilance, and the high correlations with established behavioural measures (Blanchard et al., 1991) demonstrated that it was an appropriate variable for assessing fear.

Findings from the pen experiment have been corroborated in the field, as evidence of niche partitioning confirmed that stoats avoided both large predators. The appearance of stoats following the pulse perturbation (Chapter 5) supports predictions from the mesopredator release hypothesis. My study also contributes to the natural history records for my focal species, which may prove useful to other researchers, as short notes (e.g. Peach, 2005) and unexplained observations (e.g. Dowding & Elliott, 2003) have greatly assisted my own work.

6.2 Interspecific olfactory communication – Mesopredators investigate scent to reduce uncertainty

Olfactory communication between predators is a central component of this thesis, and my research provides new insights into the nature of defensive behaviours, complementing the chemical ecology literature. Olfactory studies (>95%) have almost invariably focused on the behaviours of rodents or herbivores (Apfelbach et al., 2005; Kats & Dill, 1998) and few studies have developed natural macrocosms to investigate foraging behaviour (but see Blanchard et al., 2003b; Blanchard et al., 1998; Dielenberg & McGregor, 2001; Ward et al., 1997). My research is an important addition to the literature as it supplements the relatively few studies that have examined the role of scent in a predator guild (Mukherjee et al., 2009; Vanak et al., 2009). Detection of kairomones routinely results in feeding suppression (e.g. Koivisto & Pusenius, 2003; Weldon et al., 1993) and/or spatial avoidance (e.g. Dickman, 1992; Jedrzejewska & Jedrzejewski, 1990), but mesopredators in my research failed to exhibit

these behaviours, responding with increased feeding at ‘high risk’ areas and attraction to the odour source. However, not all behaviours contrasted with results from other studies, as kairomones also primed anti-predator responses via increased vigilance (Chapters 2 and 3).

This research contributes to our knowledge of carnivore community ecology by supporting research that suggests kairomones can indicate predation risk, but I also discovered that predator odour may confer benefits on an eavesdropping mesopredator. This helps to illuminate observations of reciprocal resource sharing between co-existing mustelids (Dowding & Elliott, 2003), by demonstrating that stoats may use ferret scent to locate resources. My research suggests that stoats, in common with some other species, can distinguish predators by their odour (e.g. Jędrzejewski et al., 1993; Monclús et al., 2005) but mesopredators did not exhibit these behaviours in my research, responding with increased feeding at ‘high risk’ areas and attraction to the odour source. By carefully controlling for the age and amount of predator odour (Chapter 3), I ruled out the possibility that these factors contributed to the lack of avoidance, as has been proposed in other studies (Apfelbach et al., 2005). Temporal variation in scent quality may influence behavioural responses (Bytheway et al., 2013), but ferret odour remained attractive to mesopredators throughout the entire trial (Chapter 4). Odour’s importance as a source of information was demonstrated by increased observations of eavesdropping mesopredators. Rats displayed slight aversion to fresh ferret odour, which decreased over time, and this concurs with another study where rats’ responses diminished as the odour cue aged (Bytheway et al., 2013).

In support of other studies (Brinck et al., 1983; Erlinge & Sandell, 1988; King & Powell, 2007), my results reveal that interactions between mustelids are informed by interspecific chemical cues; weasels avoid stoat odour (Erlinge & Sandell, 1988), mink are attracted to polecat odour (Harrington et al., 2009), and stoats displayed similar attraction to ferret odour

(Chapters 3 and 4). Counter marking by stoats (Chapters 3 and 4), from two different odour sources (anal drag and body rubbing), suggests that interspecific communication occurs between mustelids, and supports the hypothesis from chemical studies that interspecific variations in chemical cues facilitates information exchange between coexisting mustelids (Brinck et al., 1983; Zhang et al., 2002).

6.3 Niche partitioning - Coexistence of invasive predators

The culmination of the thesis was a field trial designed to disentangle the mechanism for coexistence of guild members by searching for evidence of niche partitioning. Intraguild predation theory predicts that dominant predators should match their activity and/or distribution to that of prey (Heithaus, 2001; Linnell & Strand, 2000; Palomares & Caro, 1999) and my research supports this theory as dominant predators overlapped spatially (ferret) and temporally (cat/ ferret) with their primary prey. In contrast, the subordinate species (stoat) was absent from areas and times monopolised by dominant predators, in accordance with the results from pen trials.

The diel cycle gives guild members an opportunity to separate their niches, and my research supports studies that have documented temporal partitioning among carnivores (e.g. Hayward & Slotow, 2009; Schuette et al., 2013). Sympatric predator activity patterns have previously been recorded in New Zealand, using radio-tracking data collected for 16-h per day (Alterio & Moller, 1997a). Developments in camera trapping technologies now allow researchers to compare the activity patterns of mammalian communities across the entire 24-h day. My results support the assertion that dominant predators will match activity to primary prey (Linnell & Strand, 2000); cats varied their temporal activity across seasons and sites, while ferrets' activity also matched that of the most abundant prey. Stoat activity peaked close to midday, when mammalian prey were least active and potentially inaccessible (e.g. mice).

Combining evidence from my research with information on the diet of female stoats (Alterio et al., 1998), suggests that the inhibition of stoats' nocturnal foraging opportunities may be of greatest fitness consequence to females. Restricted activity patterns imposed on stoats could potentially increase predation pressure on threatened diurnal species (e.g. reptiles). The corollary of this is that where the focal predators are sympatric, temporal refuges may reduce predation on particular species (e.g. tree weta *Hemideina*) that are primarily susceptible to stoats at night.

6.4 How do stoats co-exist with dominant carnivores in New Zealand?

Stoats displayed fear when they encountered ferrets (Chapter 2), avoiding them spatially and temporally on pastoral farmlands (Chapter 5), yet were attracted to ferret body odour (Chapters 3 and 4). This suggests that stoats co-exist with ferrets by localised spatiotemporal avoidance and by eavesdropping on ferret kairomones, which helps stoats maintain niche separation without the need for direct physical encounters. Ferret odour may also be used by stoats to locate dens or the remains of prey.

The activity and wide distribution of cats make them difficult to avoid. Stoats co-exist with them by reducing activity when cat activity peaks, reducing spatial overlap (Chapter 5), avoiding close physical encounters (Chapter 2), and using scent cues to prime anti-predator behaviours (Chapter 3).

6.5 Management applications - Behavioural conservation

Understanding chemical communications in ecological communities is of theoretical interest, but it is also of applied importance from a conservation perspective. Integrating the fields of conservation biology and behavioural ecology can reduce invasive species impacts by

providing new tools to solve wildlife management problems (Blumstein & Fernández-Juricic, 2010). My research has a number of practical applications, particularly from a New Zealand perspective, by providing new information and novel solutions to help improve management outcomes.

Gaining greater insights into exotic carnivore interactions and habitat use can improve the predictability of management intervention. Controlling invasive species in isolation can have unintentional and detrimental consequences for native species (Glen & Dickman, 2005; Rayner et al., 2007). Evidence from my research suggests that the removal of cats and ferrets will lead to increased abundance of stoats and/or changes to their behaviour (Chapter 5). Moreover, dominant predators were slow to recolonise the removal site, with no discernible increases six months after the pulse perturbation, and this apex predator vacuum created an opportunity for increased occupancy by mesopredators. Niche partitioning revealed that predator interactions might create temporal refuges and, as native prey may have opposing activity patterns (e.g. diurnal reptiles and nocturnal weta), a predator assemblage that benefits one group may be detrimental for another.

In recent years, the exploitation of sensory mechanisms has become a vital tool to resolve wildlife management issues, yet the potential role of olfaction has not yet been fully explored (Blumstein & Berger-Tal, 2015). Predictable responses to chemical cues could be the ‘Achilles heel’ of invasive mesopredators in New Zealand. Deploying dominant predator pheromones to attract subordinate predators, and in some cases species of lower trophic levels (e.g. hedgehogs in my field experiment), is a novel approach that can contribute to population monitoring and invasive species management.

The discovered pheromone lure has specific attributes that make it a promising tool for wildlife management in New Zealand:

- Long-life – ferret scent maintained its attractiveness to target species over an extended period (1 month); a highly desirable attribute of any lure. This would be of practical and financial benefit where control of invasive species occurs in isolated areas (e.g. Fiordland) or on predator-free islands that are at risk of re-invasion.
- Social lure – attraction to the lure is not based on a response towards food. This is advantageous in many situations, for example: where prey are plentiful, where competitors are few, where predator numbers have been already reduced with a food lure, or where a species invades a new ecosystem.
- Attractiveness –ferret pheromone increased overall detections of focal mesopredators by 63% and revealed more realistic stoat occupancy rates at our study site.
- Engagement – Invasive mesopredators engaged with the lure for significantly longer durations than with a food lure, which could be used to improve identification at camera traps, to increase engagement when collecting biological samples or to increase the likelihood of springing a trap.
- Natural lure – ferret odour is a non-toxic natural lure that is suitable for use in all environments.

The discovery that ferret pheromones attract subordinate predators may have application outside of New Zealand. For example, attraction to ferret cues could improve control efforts of invasive mink (Roy et al., 2006) or generate greater accuracy when surveying native mustelids (Harris & Yalden, 2004). If the attraction to apex predator pheromones holds for species other than those in New Zealand, my findings could assist conservation efforts in other parts of the world.

6.6 Research limitations

This research, as with any academic study, inevitably suffered from some limitations. In the captive odour trial, it would have been informative to test stoat responses to the odour of conspecifics and compare this to the responses to kairomones. While stoats and hedgehogs were clearly attracted to the predator odour, the reasons for this attraction are less well understood. My contention is that interspecific competition explains the behaviours of

mesopredators, but there are some problems with this explanation. At one site, stoats (or a stoat) repeatedly scent marked the ferret odour source, which is difficult to explain if the subordinate predator wanted to remain inconspicuous. Finally, there is always an element of subjectivity when assessing the motivations of animals, which is a limitation of behavioural studies.

The field research was a snapshot in a particular year of two invaded communities, within one geographic area. The stability of this system over the long-term is unknown and the appearance of stoats at the removal site may have been influenced by seasonal variability (e.g. dispersal) as well as mesopredator release. Competitive interactions between mustelids may always be in a state of flux, due to changes in mustelid abundances based on prey resources (Powell & Zielinski, 1983), as opposed to my contention that it is primarily related to interference competition. For the field trial, best practice is that BACI experiments should be replicated, which would have increased my sample size and the reliability of my results. Finally, the data used to assess niche partitioning were collected from one geographic location, within closely related habitat types. Influences of dominant predators may be affected by ecosystem productivity and heterogeneity; information from alternative ecosystems, with different predator communities, would therefore make the conclusions of this thesis even more robust.

6.7 Future research

This thesis has provided some answers, but inevitably it has also raised more questions. The area of most immediate importance for wildlife management is the development of the pheromone lure. Two large-scale control operations have recently been initiated, by Wellington Regional Council and Hawke's Bay Regional Council, to test the lure's effectiveness in control operations. The initial results are promising, as two pilot trials

reported a five-fold increase in capture rates with the addition of the pheromone lure. A second trial will compare encounter rates between ferret odours of different ages to quantify the lure's effectiveness over time. As part of this research, an odour decay function will be derived by quantifying the amount of odour remaining on pheromone saturated material at specific time intervals. A provisional patent (no: 701367) has been received for the lure and the intention is to maximise its uptake to assist management operations in New Zealand.

Future studies could attempt to quantify the timing and pace of species re-invasion after a pulse perturbation. Where resources are limited, predator control operations may be more effective if they match the intensity of control to temporal variations in re-invasion risk. Studying predator interactions in a range of habitat types would help to strengthen my conclusions. Stoats are also vulnerable to predation by diurnal raptors, and often avoid open ground in the presence of these birds (Keedwell & Brown, 2001). Falcons (*Falco novaeseelandiae*) and harriers (*Circus approximans*) were both present at the study sites and the absence of stoats from open pasture could be partly attributed to the presence of diurnal raptors. Further research could investigate the influence of these birds of prey on mustelid site occupancy and temporal activity. Finally, a dietary study could test the prediction that temporal patterns would lead to the partitioning of resources (prey), where the three focal predators are sympatric.

The thesis has raised behavioural questions that could be investigated in the future. Stoats displayed individual differences in behaviours in pen trials (e.g. "shy" vs. "bold" behaviour), which are akin to personalities in humans. Anti-predator behaviours are known to vary between individuals from the same population (Dingemanse et al., 2010), and may be consistent with variation in behavioural traits such as the shy-bold continuum, so this area warrants further investigation in an invasive species context. Furthermore, intraspecific

differences in stoat responses to dominant predators should be investigated, as females seemed to be more risk averse, and the non-significant results when testing between the sexes may relate to a lack of statistical power. Additional research is necessary to understand responses of species from lower trophic levels (e.g. rats and hedgehogs) to ferret odour and to ascertain the motivation for their evident attraction. Finally, counter-marking on top of dominant predator scent by subordinate species is an intriguing area of research that could reveal insights into community ecology.

6.8 Closing thought

At an international conference on the biology and conservation of wild mustelids in 2012, Professor Roger Powell spoke of the importance of truly understanding your study species and how they relate to *their* world. This has proved to be very salient, based on my experiences over the course of my PhD. During pen trials, I interacted with stoats on a daily basis, which revealed their behavioural repertoires that subsequently helped when wild stoat behaviours were recorded on cameras. Over the four years of this research, I have developed a deep appreciation for these charismatic, yet justifiably maligned carnivores and I hope to continue working with these fascinating animals at the juncture of behavioural ecology and conservation.

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Appendices

6.9 Appendix I - Supplementary data for Chapter 2

S1: Stoat facing directly towards the holding cage containing the ferret and cat (*video supplied on a memory stick*).

S2: The cat attempts to pounce on a female stoat (*video supplied on a memory stick*).

S3: The cat attempts to catch a male stoat that climbs onto the holding cage (*video supplied on a memory stick*).

6.10 Appendix II - Supplementary data for Chapter 3

S1: Indicator showing the moment food was seized by a stoat (*video supplied on a memory stick*).

S2: Correlations between behavioural response variables during experimental treatments, where values indicate Pearson's correlation coefficient (r). Responses variables without any observations were excluded from the analysis. Asterisks (*) denote variables that were significantly correlated based on a Pearson correlation above 0.7.

Response variables	Time until first approach	Time when food eaten	Foraging tunnels entered	Time spent at foraging unit	Cautious approach
Time until first approach	-	-	-	-	-
Time when food eaten	0.15	-	-	-	-
Foraging tunnels entered	0.46	0.35	-	-	-
Time spent at foraging unit	0.34	-0.27	0.72*	-	-
Cautious approach	-0.26	-0.17	0.43	0.58	-
Scanning	-0.18	-0.24	0.21	0.3	0.38

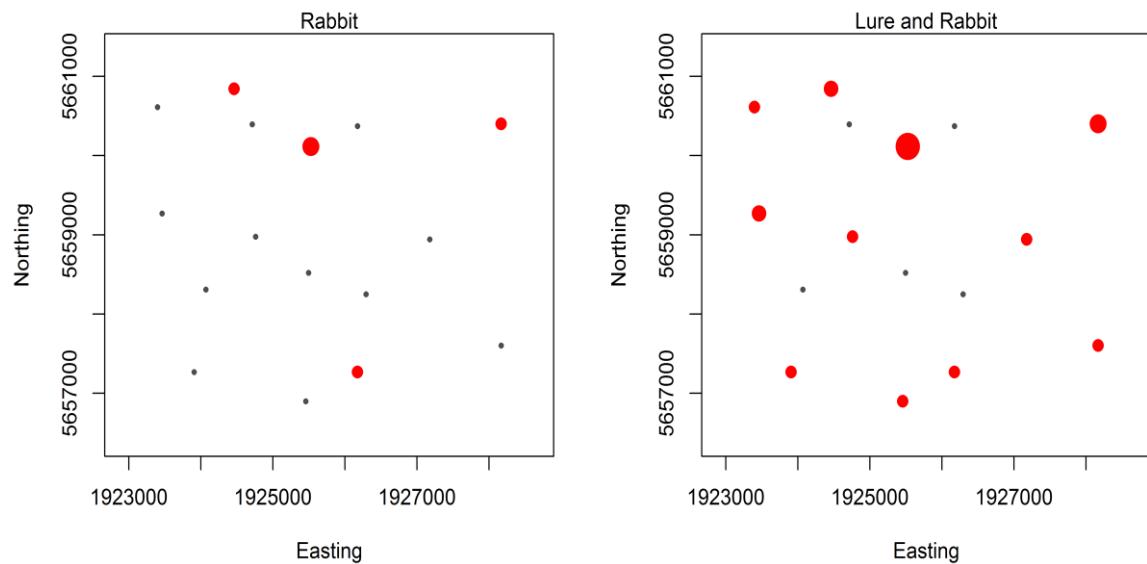
S3: A stoat's initial detection and cautious approach to ferret odour (*video supplied on a memory stick*).

S4: A stoat's initial detection and cautious approach to cat odour (*video supplied on a memory stick*).

6.11 Appendix III - Supplementary data for Chapter 4

S1: Metadata extraction using R (*file and related information supplied on a memory stick*).

S2: Stoat site detections based on rabbit (a) or lure and rabbit (b) treatment.



S3: Stoat scent marks with anal drag beside the ferret pheromone vial.



S4: Hedgehog self-anointing after contact with the pheromone vial.



S5: Ship rat attempting to bite into the pheromone vial.

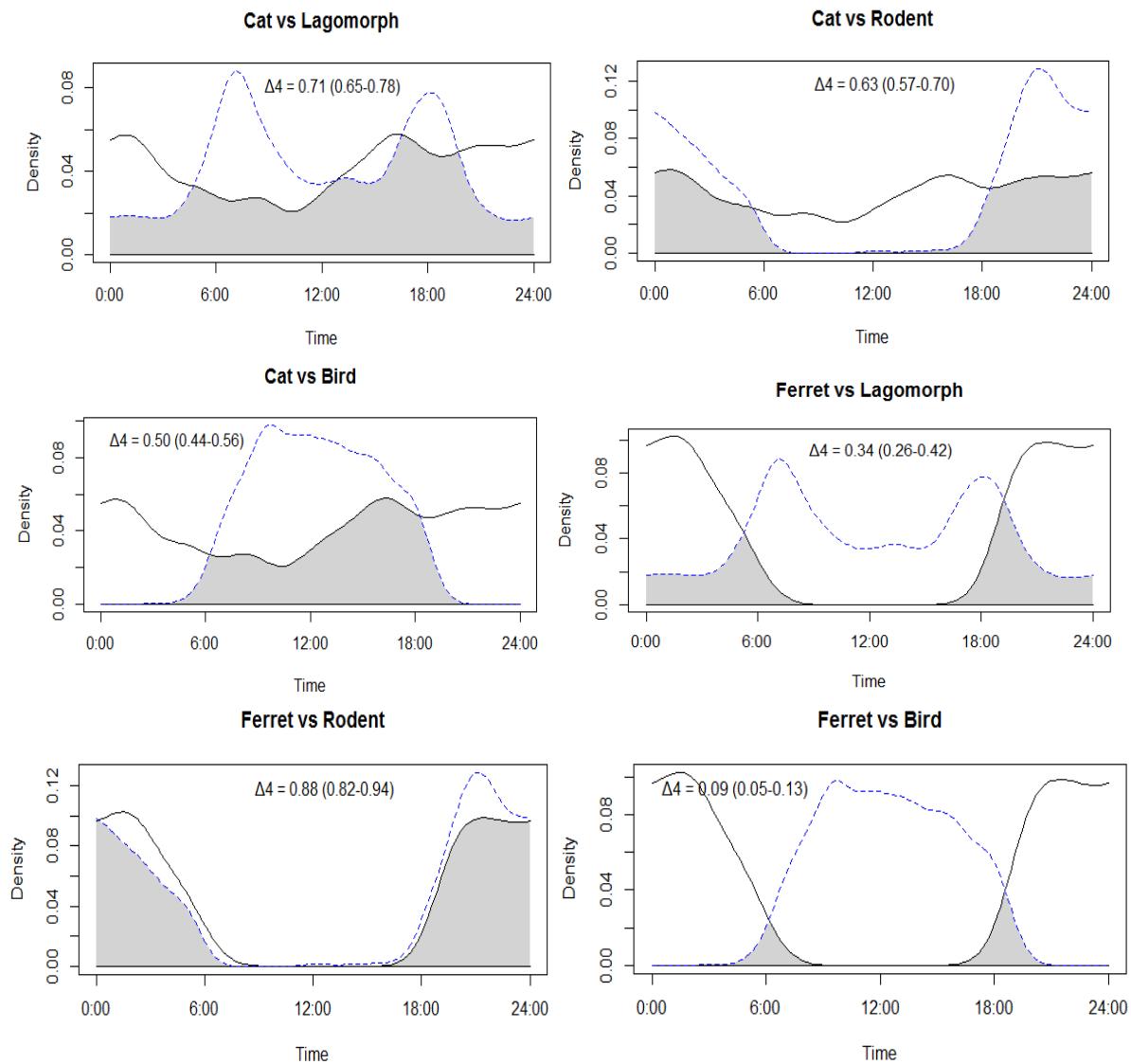


6.12 Appendix IV - Supplementary data for Chapter 5

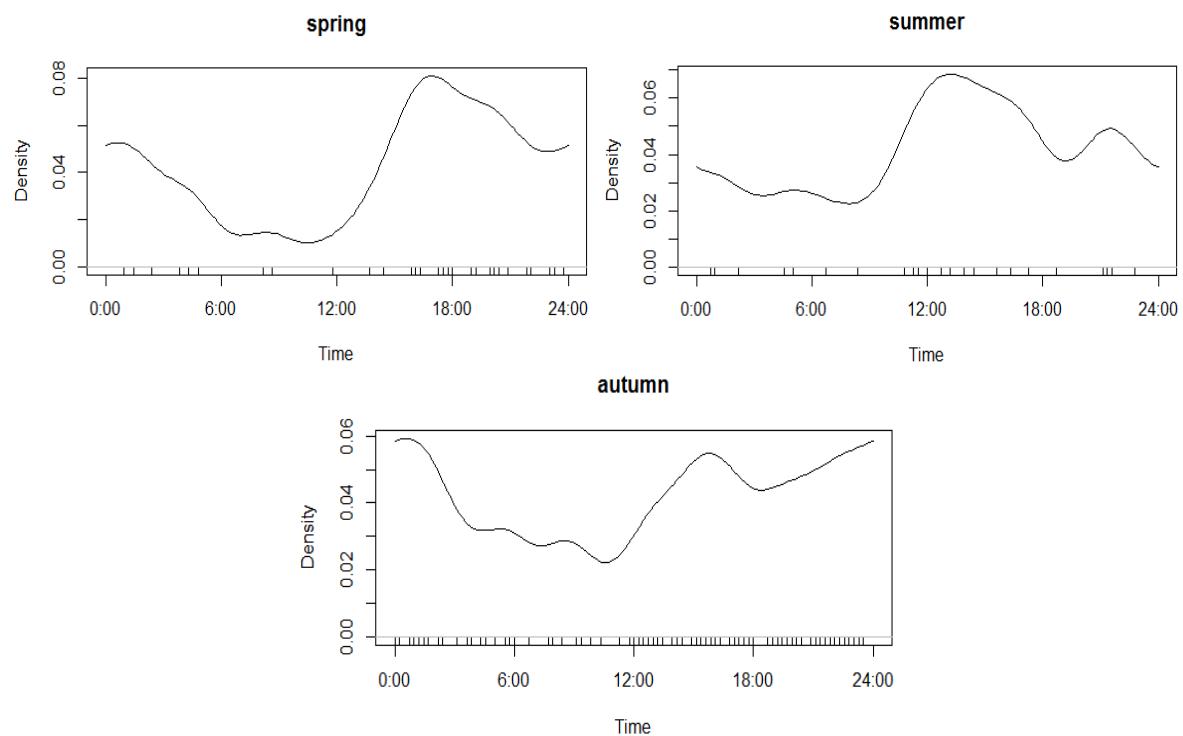
S1: List of bird species recorded during this study.

Common name	Scientific name
<u>New Zealand native species</u>	
Fantail	<i>Rhipidura fuliginosa</i>
Field pipit	<i>Anthus novaeseelandiae</i>
Grey Warbler	<i>Gerygone igata</i>
Kingfisher	<i>Todiramphus sanctus vagans</i>
Morepork	<i>Ninox novaeseelandiae</i>
North Isl. Robin	<i>Petroica longipes</i>
Paradise duck	<i>Tadorna variegata</i>
Rifleman	<i>Acanthisitta chloris</i>
Silveryeye	<i>Zosterops lateralis</i>
Spur-wing plover	<i>Vanellus miles</i>
Swamp Harrier	<i>Circus approximans</i>
Tom-tit	<i>Petroica macrocephala</i>
Tui	<i>Prosthemadera novaeseelandiae</i>
<u>Introduced species</u>	
Australian magpie	<i>Gymnorhina tibicen</i>
Blackbird	<i>Turdus merula</i>
California quail	<i>Callipepla californica</i>
Chaffinch	<i>Fringilla coelebs</i>
Common redpoll	<i>Carduelis flammea</i>
Goldfinch	<i>Carduelis carduelis</i>
Greenfinch	<i>Carduelis chloris</i>
Hedge sparrow	<i>Prunella modularis</i>
Skylark	<i>Alauda arvensis</i>
Song thrush	<i>Turdus philomelos</i>
Sparrow	<i>Passer domesticus</i>
Starling	<i>Sturnus vulgaris</i>
Wild turkey	<i>Meleagris gallopavo</i>
Yellowhammer	<i>Emberiza citrinella</i>

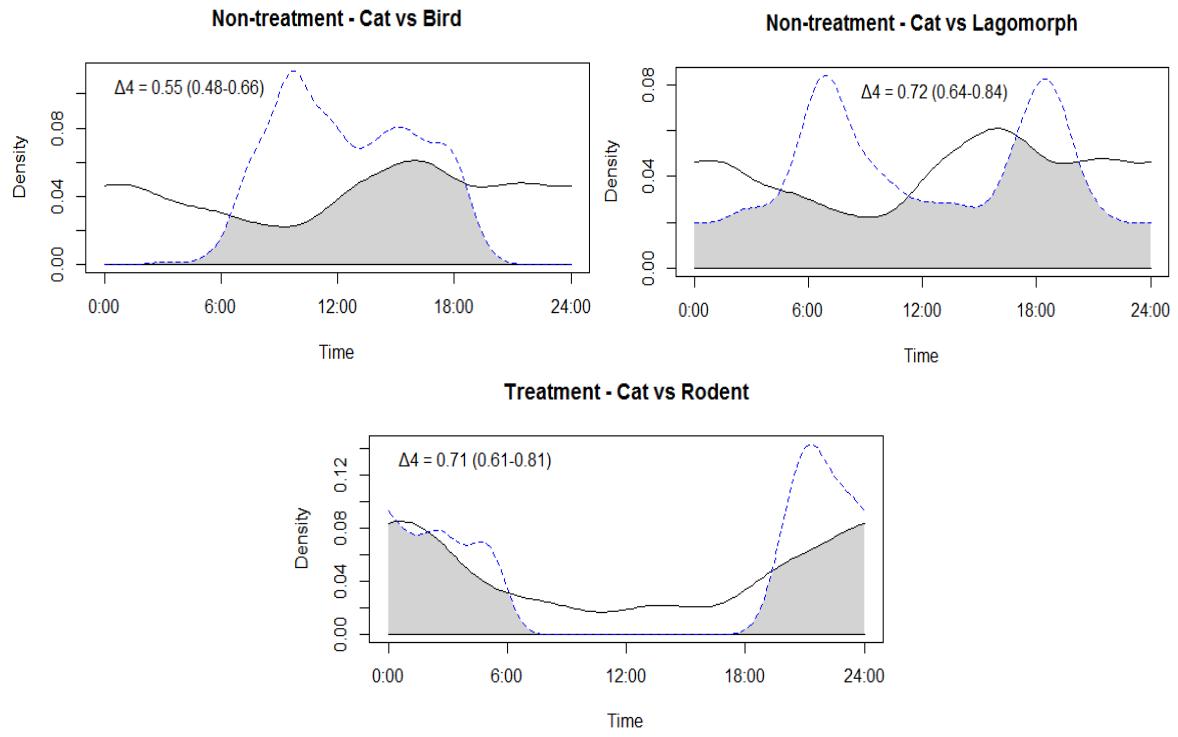
S2: Overlap of dominant predators (cat or ferret; solid lines) activity with their main prey (rodents, lagomorphs or birds; dashed lines) recorded at two farm areas in the Hawkes Bay region of New Zealand. The coefficient of overlap (Δ_4) and bootstrapped 95% confidence intervals are included on the graphs. Overlapping periods of activity are shaded grey.



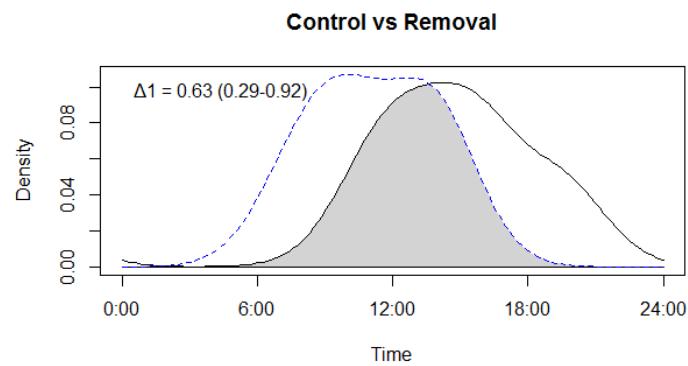
S3: Seasonal (spring/summer/autumn) temporal activity (Δ_1) of cats. There were insufficient observations (< 20) to display winter activity.



S4: Activity of cats (solid line) and coefficient of overlap (Δ_4) compared to the dominant prey species at an area – lagomorphs and birds at the non-treatment/ rodents at the treatment site. Overlapping periods of activity are shaded grey.



S5: Stoat activity patterns at non-treatment (solid line) versus treatment (dotted blue line) areas six months (November) after predator control targeted at cats and ferrets. Overlapping periods of activity are shaded grey.



S6: Cat with mouse at the treatment area (May 2014).



S7: Stoat, with a dead rabbit, investigating the lure vial at the non-treatment area (November 2014).

